UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE ESTUDIOS SUPERIORES IZTACALA

MECANISMOS ECOLÓGICOS E HISTÓRICOS DETERMINANTES EN LA ESTRUCTURACIÓN DE LAS COMUNIDADES DE COLIBRÍES EN MÉXICO

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:

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INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD,
UNIDAD MORELIA, UNAM

MÉXICO, CD. MX., 2020
AGOSTO

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ASUNTO: Oficio de Jurado

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Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **8 de abril de 2019** se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la estudiante **RODRÍGUEZ FLORES CLAUDIA ISABEL** con número de cuenta **507452395** con la tesis titulada **"Mecanismos ecológicos e históricos determinantes en la estructuración de las comunidades de colibríes en México."**, realizada bajo la dirección de la **DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA**, quedando integrado de la siguiente manera:

Presidente:	DRA. EK DEL VAL DE GORTARI
Vocal:	DR. JUAN PABLO JARAMILLO CORREA
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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Cd. Universitaria, Cd. Mx., a 06 de agosto de 2020

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RESUMEN

Los colibríes (Aves: Trochilidae) son las aves nectarívoras más especializadas del continente. En México existen 58 especies pertenecientes a 7 clados filogenéticos, y con gran diversidad morfológica y ecológica. El presente trabajo puso a prueba cómo las interacciones bióticas, los rasgos morfológicos, la biogeografía, las relaciones evolutivas, y las riquezas local y regional determinaron la composición de las comunidades de colibríes en México. Para este fin, se combinó información a escala local, regional y continental. Los resultados indican que las comunidades que habitan localidades con alta estacionalidad, baja precipitación y poca cobertura vegetal están conformadas por pocas especies de hábitos generalistas, cercanamente relacionadas y de reciente evolución; mientras que las comunidades de colibríes en ecosistemas más tropicales, ubicadas en lugares con mayor precipitación y cobertura vegetal, estuvieron compuestas por una mayor riqueza de especies, con distintos orígenes evolutivos y una mayor diversidad morfológica y ecológica. Sin embargo, la mayor cantidad de comunidades de colibríes en el país tienen estructuras filogenéticas aleatorias, donde la combinación de factores históricos y ecológicos, como la historia biogeográfica de la Zona de Transición Mexicana, la diversificación de los clados filogenéticos, las interacciones locales relacionadas con la competencia intra e interespecífica, y la repartición en el uso de los recursos de néctar, se combinan para permitir la coexistencia de comunidades altamente dinámicas espacial y temporalmente. El presente trabajo comprueba como la combinación de información proveniente de distintas escalas temporales y espaciales brinda una perspectiva prometedora para establecer los mecanismos que modelan la composición de las comunidades y la diversidad filogenética en áreas tan bióticamente complejas como México.

ABSTRACT

Hummingbirds (Trochilidae) are the most specialized nectarivorous birds in the Americas. There are 58 hummingbird species in Mexico belonging to 7 phylogenetic clades, showing great morphological and ecological diversity. The purpose of this study was to test how biotic interactions, morphological traits, biogeography, evolutionary relationships, and local and regional species richness influenced the composition of hummingbird community in Mexico. To do so, information at local, regional, and continental scales were combined. The results showed that communities in places with high climatic seasonality, low precipitation and low vegetation cover, were composed of few generalist species, and closely related species that evolved recently; while hummingbird communities located in more tropical ecosystems, with higher precipitation and land cover, were included more species, with more varied evolutionary origins, and higher morphological and ecological diversities. However, most hummingbird communities in Mexico have a random phylogenetic structure, with a combination of different historical and ecological factors, such as the Mexican transition zone, where biogeographical history, clade diversification, local interactions related to intra and inter specific competition, and the division of nectar resources allow the coexistence of highly dynamic communities at various spatial and temporal scales. These results show how a combination of information from different spatial and temporal perspectives provides promising insights to establishing the underlying mechanisms that have shaped community composition and phylogenetic diversity in complex biotic zones, like Mexico.

INTRODUCCIÓN

Establecer los mecanismos que dan origen y mantienen la composición de las comunidades actuales ha sido uno de los objetivos fundamentales en ecología evolutiva (Webb *et al.* 2002, Graham *et al.* 2009, Moen *et al.* 2009). Es ampliamente reconocido que una gran variedad de procesos ecológicos y evolutivos actúan a diferentes escalas temporales y espaciales sobre las especies que componen las comunidades (Levin 1992, Moen *et al.* 2009). Sin embargo, hasta hace poco, la aproximación a esta pregunta había sido principalmente estudiada desde la perspectiva ecológica, evaluando cómo los procesos denso-dependientes, las interacciones bióticas, las características ecológicas y fisiológicas de las especies, y las restricciones ambientales determinan su presencia o ausencia en una comunidad. Con el desarrollo de técnicas moleculares y la obtención de filogenias, ha sido posible integrar el aspecto histórico a la discusión, ya que esta información permite establecer la estructura filogenética de las comunidades, reconstruir la historia evolutiva de caracteres ecológicos a lo largo de la filogenia, dilucidar procesos de especiación y extinción, y correlacionar información ambiental y biogeográfica con procesos de diversificación genética (Webb *et al.* 2002, Valiente-Banuet & Verdú 2007).

Entre los procesos más frecuentemente estudiados a la hora de establecer cómo se ensamblan las comunidades, se encuentran el filtro ambiental y la exclusión competitiva, y más recientemente la facilitación ecológica (Valiente-Banuet & Verdú 2007). Elegir un grupo que permita probar el efecto de dichos procesos no es sencillo, ya que este debe cumplir con varias características (Graham *et al.* 2009), como ser un grupo diverso en el que sea posible encontrar varias especies coexistiendo en una misma comunidad, y tener características de tipo morfológico, ecológico y/o fisiológico (entre otras) susceptibles a gradientes ambientales y que presenten cierto grado de conservadurismo evolutivo. Uno de los grupos que cumple con estos requerimientos es el de los colibríes (Aves: Trochilidae).

Los colibríes son un grupo de aves americano, cuyo centro de origen se encuentra en las tierras bajas de los Andes (Stiles 1981). Se han descrito alrededor de 331 especies de 104 géneros de los cuales 46 son monotípicos (McGuire *et al.* 2009). McGuire *et al.* (2009) propusieron 9 clados para clasificar los colibríes (Topacios, Ermitaños, Mangos, Coquetas, Brillantes, Patagona, Gemas de Montañas, Abejas y Esmeraldas), siendo los Topacios el grupo basal de la filogenia. Cada grupo tiene una historia evolutiva particular, la cual se refleja en sus patrones morfológicos, biogeográficos y de diversidad (McGuire *et al.* 2014). Los colibríes de Centroamérica y de Norteamérica son más recientes y pertenecen en su mayoría a los grupos de las Gemas de las Montañas, las Abejas y las Esmeraldas. En general, los colibríes son más diversos y abundantes en las zonas montañosas a lo largo de su distribución, que en las zonas bajas. Son un grupo representativo de los distintos ecosistemas del continente, y se pueden encontrar más de 20 especies coexistiendo en la misma comunidad (Cotton 1998, Arizmendi 2001, Gutiérrez-Zamora & Rojas 2001). Los colibríes son aves pequeñas (2.2-20.2 g), con características morfológicas bastante homogéneas y dietas compuestas exclusivamente por néctar y pequeños artrópodos (Schuchmann 1999). Sin embargo, pequeñas variaciones en la morfología del pico (largo y curvatura principalmente) y en las alas (cargas de disco alar y la amplitud del aleteo) tienen efectos significativos en el uso de los recursos (Rodríguez-Flores & Stiles 2005) y en la aerodinámica del vuelo, especialmente a gran altitud donde las bajas temperaturas, la baja densidad del aire y la tensión de oxígeno representan condiciones estresantes para animales tan pequeños (Stiles *et al.* 2005, Stiles 2008).

El conjunto de factores bióticos y abióticos determinantes para que una especie sobreviva se conoce como nicho ecológico (Hutchinson 1957). Asimismo, el conjunto de estas variables y sus valores límite crean un espacio multidimensional que posee las características bajo las cuales un individuo, población o especie tiene la capacidad de persistir. Dicho espacio se define como el "nicho fundamental" (Vázquez 2005). Debido a que las especies no viven en aislamiento, sino por el contrario, están en continua relación con otras especies que pueden compartir o no los mismos valores del nicho fundamental. Vázquez (2005) redefinió el concepto de "nicho realizado" de Hutchinson (1957) como "un subconjunto del espacio ambiental en el cual el individuo, población o especie focal existe por restricciones impuestas por la estocasticidad demográfica y la dispersión".

En el proceso de estructuración de las comunidades bióticas, distintas fuerzas (tanto positivas como negativas) pueden actuar de manera conjunta o independiente (Webb *et al.* 2002). El caso de las comunidades de colibríes, donde coexisten numerosas especies con requerimientos de nicho similares, se espera que haya atracción fenotípica y que las especies tiendan a ser incluidas en el mismo nicho. Sin embargo, y simultáneamente, se espera que se presenten interacciones negativas entre individuos que ocupen en mismo nicho o hábitat, incrementándose la intensidad de la repulsión fenotípica a medida que se incrementa la similitud ecológica. La intensidad y direccionalidad de estas interacciones afectan directamente la composición de las comunidades, al favorecer cambios en el nicho realizado de las especies, la intensidad de la exclusión competitiva (a una escala de vecindario o a la escala de comunidad) y la posterior distribución de los taxa en subnichos (o localidades) (Webb *et al.* 2002).

En las comunidades de colibríes es frecuente que las especies exploten los mismos recursos de néctar (Stiles 1985, Arizmendi & Ornelas 1990, Arizmendi 1994, Gutiérrez-Zamora & Rojas 2001, Rosero 2003, Rodríguez-Flores 2004, Lara 2006), por lo que el traslape en el nicho alimenticio, favorecido por la similitud en la estructura corporal básica de los colibríes, crea condiciones propicias para que la competencia actúe como fuerza modeladora sobre estas comunidades (Des Granges 1979). Estudios en diferentes comunidades de colibríes han descrito mecanismos ecológicos que estarían favoreciendo la coexistencia de las especies dentro de las comunidades al disminuir la competencia entre los individuos. Algunos de estos mecanismos están relacionados con diferencias en las preferencias de los recursos de néctar por parte de los colibríes (Rodríguez-Flores 2004), con variaciones en el comportamiento de forrajeo (Feinsinger & Colwell 1978, Des Granges 1979, Stiles 1985, Lara *et al.* 2009, Rodríguez-Flores 2009), y con movimientos poblacionales entre comunidades vegetales a nivel de paisaje siguiendo la floración de las plantas (Des Granges 1979, Gutiérrez-Zamora & Rojas 2001, Rosero 2003). Otras estrategias están relacionadas con diferencias en la preferencia de microhábitats dentro de un ecosistema (Gutiérrez-Zamora & Rojas 2001, Ritchie 2002), con variaciones morfológicas interespecíficas en caracteres como el peso, el largo y la curvatura del pico (Rodríguez-Flores 2004, Rodríguez-Flores & Stiles 2005), y con segregación espacial y temporal en el uso de las especies vegetales (Des Granges 1979, Ornelas *et al.* 2002, Lara 2006, Lara *et al.* 2009). Varios de estos mecanismos se sustentan en las características morfológicas y fisiológicas de los colibríes, que les permiten establecer la heterogeneidad en la distribución de los recursos presentes en un momento dado, y así forrajear de manera óptima (Ritchie 2002).

Como se mencionó anteriormente, además de estos mecanismos ecológicos actuales existen otros procesos históricos y biogeográficos que influyen sobre la diversidad y ensamble de especies en las comunidades. En el caso de las aves, existe un patrón claro de riqueza respecto a la latitud, con un mayor número de especies en las zonas ecuatoriales que en las zonas templadas, siendo notable la diversidad de aves en las áreas montañosas tropicales (Stevens 1992, Thomas *et al.* 2008). Este patrón es también evidente en los colibríes, con la mayor riqueza de especies encontrándose en Colombia, Ecuador y el norte de Perú, donde habitan más de 150 especies (Tilford 2008); mientras que en áreas más septentrionales la diversidad disminuye drásticamente (por ejemplo en Estados Unidos de América con solo 17 especies) (AOU 1998, Arizmendi & Berlanga 2014).

Hasta el momento existen pocos trabajos que integren una perspectiva filogenética, ecológica y biogeográfica en el estudio de las reglas de ensamble de las comunidades de colibríes. Los trabajos pioneros en este sentido son los de Graham *et al.* (2009) y Parra *et al.* (2010), quienes establecieron el papel del filtro ambiental *vs.* la competencia en la estructura filogenética de las comunidades de colibríes en Ecuador. Ellos encontraron que el papel que juega cada uno de estos procesos varió con la altitud y con las barreras biogeográficas. En el caso de las comunidades de tierras bajas, estas estuvieron compuestas por especies lejanas filogenéticamente, mientras que las especies de mayor altitud estaban altamente emparentadas; asimismo mostraron el efecto de los Andes como una barrera importante, que impidió la dispersión del grupo, y cómo los gradientes ambientales de precipitación y temperatura promovieron el cambio en la composición de las comunidades de colibríes.

Aunque no con colibríes, el trabajo de Moen *et al.* (2009) brindó un aporte importante en el estudio de estructura de comunidades, ya que a diferencia de los caracteres ambientales usados por Graham *et al.* (2009) y Parra *et al.* (2010), ellos incluyeron caracteres ecológicos de las especies en el estudio de la estructura filogenética de las comunidades. Por medio de cálculos simples, Moen *et al.* (2009) pudieron establecer si dos caracteres ecológicos importantes para las ranas arborícolas (hábitat en el estado larval y tamaño corporal) en diferentes comunidades, se originaron *in situ* (dentro de la comunidad en la que habitan actualmente) o se originaron en otra parte y luego se añadieron a la comunidad por dispersión. Sus resultados permitieron poner a prueba varias hipótesis sobre la composición de comunidades, más específicamente el papel de la elevación para crear patrones de estructura de comunidades en una región, la capacidad de las especies para invadir comunidades con características similares, la frecuencia de eventos de dispersión entre áreas con condiciones climáticas similares, y las diferencias en las tasas de diversificación ecológica entre linajes que invaden una región más recientemente, respecto a otros que invadieron la misma área en un tiempo anterior.

Los estudios de interacciones mutualistas entre animales y plantas han encontrado una tendencia general en la naturaleza hacia las interacciones difusas y anidadas donde un grupo de especies generalistas interactúa con subconjuntos de especies generalistas y especialistas, favoreciendo la coexistencia de las especies y brindando tolerancia a la pérdida de especies (Bascompte & Jordano 2014). Así mismo, otras características de las interacciones mutualistas entre diferentes especies (que no necesariamente comparten un origen evolutivo) es que son facultativas y de baja especificidad (donde una especie no necesita de la otra para sobrevivir), y varían en el tiempo y el espacio, (Bascompte & Jordano 2014). En el caso particular de los colibríes y sus recursos de néctar, la estrecha relación entre unos y otros (Gutiérrez-Z. *et al.* 2004), reflejada en claras adaptaciones morfológicas y fisiológicas tanto de colibríes como de plantas (Schuchmann 1999), evidencia la posibilidad de que las especies participantes en este mutualismo impongan una selección permanente unas a otras, permitiendo que las historias de vida y los rasgos ecológicos se estén remodelando continuamente entre sí (Thompson 2010). El análisis de las redes ecológicas es una vía formal para visualizar, explorar, y abordar los patrones que están detrás de las múltiples interacciones involucradas en ensambles de especies (Jordano 2010). En el caso particular de los colibríes y sus recursos de néctar, el estudio desde la perspectiva de las redes de interacción permite analizar el grado de asimetría en las dependencias entre las especies, la complejidad y la estructura de las interacciones (Bascompte & Jordano 2007). Más recientemente también se ha podido (a partir de la aparición de las hipótesis filogenéticas) establecer el papel de la historia evolutiva y la complementariedad fenotípica en los patrones de interacción (Rezende *et al.* 2007).

Trabajos que integra la información biogeográfica, filogenética, ecológica e histórica, abren la puerta para evaluar distintas hipótesis sobre los factores que modelaron las distribuciones de los rasgos ecológicos de las especies en las comunidades actuales (Webb *et al.* 2002). Dada la conocida relación que existe entre morfología y ecología en los colibríes, esta aproximación filogenética permitiría establecer qué caracteres han evolucionado con el grupo y reconstruir el origen, dispersión y mantenimiento de estos caracteres en las comunidades.

En México, se han reportado 58 especies de colibríes (Arizmendi & Berlanga 2014) pertenecientes a seis de los nueve grupos taxonómicos propuestos por McGuire *et al.* (2009). Estas especies poseen una importante diversidad de morfologías y tamaños corporales, y habitan en una gran diversidad de ecosistemas y altitudes (Des Granges 1979, Arizmendi 1994, Schondube *et al.* 2004, Lara 2006, Arizmendi *et al.* 2008, Lara *et al.* 2009). Las comunidades de zonas montañosas están compuestas por un promedio de ocho especies de colibríes que visitan entre ocho y 15 especies de plantas (Lara 2006, Arizmendi *et al.* 2008), aunque existen algunas excepciones, como las comunidades de colibríes de la Reserva de la Biosfera Sierra de Manantlán y del Nevado de Colima, donde habitan más de 15 especies a lo largo del año (Des Granges 1979, Santana 2000, Arizmendi 2001). Los estudios de comunidades de colibríes en México han brindado evidencia del efecto de la competencia en la estructuración de estas comunidades, y cómo varios de los mecanismos mencionados anteriormente pueden estar actuando como estrategias de coexistencia (Des Granges 1979, Arizmendi 2001, Ornelas *et al.* 2002, Lara 2006, Lara *et al.* 2009, Rodríguez-Flores 2009). Toda esta gama de morfologías, historias evolutivas y mecanismos ecológicos presentes en las comunidades de colibríes en México, sumada a la compleja historia biogeográfica del país, abre la puerta para integrar los patrones de diversidad local y regional a través de diferentes gradientes ambientales y características ecológicas, buscando encontrar información que nos permita entender los mecanismos que han modelado la composición y estructura filogenética de las comunidades de colibríes en México.

Este trabajo puso a prueba tres hipótesis principales:

1) Si la estrategia de forrajeo por néctar y la dominancia entre las especies de colibríes se modifica en función de la composición (Feinsinger & Chaplin 1975, Feinsinger &

Colwell 1978, Des Granges & Grant 1980, Lara 2006), el estatus migratorio (Des Granges 1979, Arizmendi & Ornelas 1990), el tamaño corporal (Des Granges 1979, Arizmendi & Ornelas 1990), el sexo y la edad de los individuos (Feinsinger & Chaplin 1975, Des Granges 1979, Calder & Calder 1994, Russell 1996, Baltosser & Russell 2000, Stiles *et al.* 2005), así como por la abundancia de recursos florales, se espera que las especies residentes con tamaño corporal mediano e intermedio sean dominantes (Lyon 1976); que los machos sean dominantes sobre las hembras (Wolf 1969, Kodric-Brown & Brown 1978, Snow & Snow 1980); que los adultos sean dominantes sobre los juveniles (Feinsinger & Chaplin 1975); y que haya una relación directa entre la disponibilidad de néctar con la territorialidad y los comportamientos agresivos.

2) Si los procesos biogeográficos sumados a los procesos de diversificación de los distintos clados (Dalsgaard *et al.* 2013, McGuire *et al.* 2014) han influenciado la selección de rasgos e historias de vida tanto de colibríes como de plantas (Thompson & Medel 2010, Abrahamczyk & Renner 2015), se espera un gradiente que lleve a la generalización. Es así como los linajes de colibríes de colonización y diversificación más reciente poseerán morfologías menos especializadas (tamaño corporal pequeño a mediano, picos rectos de tamaño intermedio) que les permitan usar una mayor diversidad de recursos florales (Jordano 2010, McGuire *et al.* 2014, Abrahamczyk & Renner 2015), que aquellos con un origen más antiguo.

3) Si la importancia de la competencia y del filtro ambiental como procesos estructuradores históricos de las comunidades de colibríes dependen de las características de las barreras biogeográficas como la altitud, la ubicación geográfica y

las características de la vegetación (Graham *et al.* 2009, Parra *et al.* 2010), se espera que las comunidades de colibríes que habitan las zonas bajas de México estén compuestas por especies filogenéticamente lejanas (sobredispersión filogenética), evidenciando el efecto de la exclusión competitiva en la ausencia de otros factores ecológicos estresantes; mientras que las especies que componen comunidades a mayores altitudes estén emparentadas filogenéticamente (agrupamiento filogenético) debido al filtro ambiental impuesto por la elevación. En cuanto a las barreras biogeográficas, se espera que las comunidades de colibríes que habitan en vertientes opuestas de cadenas montañosas como las Sierras Madre Oriental y Occidental, sean diferentes en su composición, pero que presenten estructuras filogenéticas similares.

OBJETIVO GENERAL

Dilucidar el papel de algunos mecanismos ecológicos e históricos como fuerzas determinantes en la estructuración de las comunidades actuales de colibríes en México.

OBJETIVOS ESPECÍFICOS:

1) Explorar el papel de la dominancia y territorialidad como mecanismos ecológicos estructuradores de una comunidad de colibríes al oeste de México.
2) Explorar el papel de la morfología, la evolución filogenética, y la biogeográfica como mecanismos estructuradores a escala continental, mediante el análisis de la arquitectura de la red de interacción mutualista entre colibríes y sus plantas.
3) Dilucidar el papel de la competencia y de los filtros ambientales como procesos estructuradores de las comunidades de colibríes en México.

CAPÍTULO 1

THE DYNAMICS OF HUMMINGBIRD DOMINANCE AND FORAGING STRATEGIES DURING THE WINTER SEASON IN A HIGHLAND COMMUNITY IN WESTERN MEXICO

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The dynamics of hummingbird dominance and foraging strategies during the winter season in a highland community in Western Mexico

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Keywords
agonistic interactions; dominance; foraging strategy; hummingbird; territoriality; *Trochilidae*; resource competition.

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Abstract

Coexistence between ecologically similar species can promote competition for resources. Hummingbirds (Aves: *Trochilidae*) are nectarivorous birds that usually coexist in sympatry, and visit flowers using different foraging behaviors and levels of aggressiveness as a strategy to diminish resource competition. Here, we describe the dynamics in territorial and dominance behaviors in a hummingbird community inhabiting a highland during winter in Western Mexico. We explored in natural conditions how foraging strategies and dominance status of the hummingbirds was influenced by community species composition, sex, age and size of the individuals, floral abundance, and nectar resource availability. The community studied was composed of 11 species (four residents, three altitudinal migrants, three latitudinal migrants), and all possible combinations of dominance and territoriality were found. Differences in the dominance status and foraging behavior were related to the species, sex, age and body size of the individuals, as well as the number of flowers in the patches, and the abundance of the migratory species over time. The aggressive and territorial species preferred the places with more flowers, and started the majority of the interactions attacking even birds that did not visited the flowers. The subordinate non-territorial hummingbirds visited floral patches of different sizes, did not start aggressive interactions and when they were involved in one, this occurred during their visits to the territorial hummingbird's flowers. Hummingbird dominance changed during the winter and at the end of the season, when the latitudinal migrant species left our study site, the resident species were more abundant, dominant and territorial. Dominance status and foraging behavior, together with floral preferences and the spatial distribution of nectar resources, acted as mechanisms organizing this hummingbird community.

Introduction

Resource dynamics is a key process that can model animal distributions (Bennett *et al.*, 2014), and some models, as the 'ideal free distribution', predicts that consumer densities will match with resource availability (Fretwell & Lucas, 1969). One example of this occurs in nectarivorous birds where the variation in resource abundance regulates the abundance of birds (Bennett *et al.*, 2014; Schmid *et al.*, 2015). However, this distribution in nature may be affected by other factors that can change resource use. One of these factors is biotic interactions, and in scenarios where the species have competitive differences, the dominant species (usually larger) will modify the habitat choices of subordinate species (Fretwell, 1972).

Hummingbirds (Aves: *Trochilidae*) are physiologically specialized nectarivorous birds (Schuchmann, 1999; Lotz & Martínez del Rio, 2004), considered generalists from an ecological perspective because they visit many different plant species to cover their energetic demands (Calder, 2004). In hummingbird communities, it is frequent to find several species living in sympatry, and a temporal and spatial overlap of the nectar resources that they use (Stiles, 1985; Collins, Grey & McNee, 1990; Arizmendi, 2001; Gutiérrez-Zamora & Rojas, 2001; Lara, 2006). The overlap in feeding niches of ecologically similar species increases the potential for competition for resources (Morin, 1999). The partition of resources among hummingbird species has been explained by different mechanisms related to: differences in nectar resource use (Lyon, 1976; Justino, Maruyama & Oliveira, 2012), variations in foraging behavior (Feinsinger & Colwell, 1978; Stiles, 1985; Sandlin, 2000a; Lara, Lumbreras & González, 2009), population movements at the landscape scale following plant blooming (Des Granges, 1979; Gutiérrez-Zamora & Rojas, 2001), microhabitat differences (Gutiérrez-Zamora & Rojas, 2001; Ritchie, 2002), interspecific morphological variations in traits such as weight, beak length and curvature (Stiles, 1975; Lyon, 1976; Snow & Snow, 1980; Rodríguez-Flores & Stiles, 2005; Maglianesi, Böhning-Gaese & Schleuning, 2015), spatial and temporal segregation in floral use patterns (Ornelas *et al.*, 2002; Lara, 2006; Lara *et al.*, 2009) and phylogenetic relationships among species (Martin & Ghalambor, 2014). Several of these mechanisms are based on the hummingbird's abilities and movement capabilities, all of which allow them to use a heterogeneous distribution of nectar resources at a given time, and take appropriate decisions on the basis of their morphological and physiological characteristics (Ritchie, 2002; Bacon, Hurly & Healy, 2011).

Hummingbirds visit flowers using two main behavior types: (1) territorial and (2) non-territorial or trapliners (Feinsinger & Chaplin, 1975). Territorial hummingbirds select a group of flowers and establish their feeding territory there (Wolf, 1969; Des Granges & Grant, 1980). Non-territorial hummingbirds use different groups of blooming plants that can be isolated and/or undefended by a territorial hummingbird, and usually visit these flowers by following circuits or foraging routes in specific sequences (Feinsinger & Colwell, 1978; Temeles *et al.*, 2006; Ohashi & Thomson, 2009). In addition to foraging strategies, the dominance among individuals affects the way they interact and visit their nectar resources, and can be related to sex, age and morphology (Wolf, 1969; Feinsinger & Chaplin, 1975; Carpenter *et al.*, 1993). However, although these classifications describe properly the types of behaviors observed, these are too simplistic because the foraging and dominance patterns within individuals of a species are not static, but rather constitute a gradient where individuals can use all behaviors throughout their life (Feinsinger, 1976; Des Granges, 1979; Collins *et al.*, 1990; Cotton, 1998).

The purpose of this study was to investigate the relationship between dominance and territoriality in a dynamic hummingbird community located at Western Mexico and composed by latitudinal migrants (same species studied at many sites in USA and Canada), residents (as other communities studied in Central America) and altitudinal migrants sharing a complex array of nectar sources (Arizmendi, 2001). In this community, we studied a gradient from small to large species, resident to altitudinal to latitudinal migrant to see behavioral responses used to coexist. To this end, we tested three hypotheses: (1) If sex, age and size of the individuals affect hummingbird dominance and foraging strategies (Feinsinger & Colwell, 1978; Des Granges, 1979; Snow & Snow, 1980; Calder & Calder, 1994; Russell, 1996; Stiles *et al.*, 2005; Justino *et al.*, 2012), we hypothesized that the large- and medium-sized resident species (>5 g following Stiles & Wolf, 1979; Schuchmann, 1999) would be territorial and dominant over the other hummingbird species (Lyon, 1976). In the case of age and sex, we expected that males would be dominant over females in the species with plumage sexual dimorphism (Wolf, 1969; Kodric-Brown & Brown, 1978; Snow & Snow, 1980), and adults would be dominant over the juveniles in the monomorphic species (Feinsinger & Chaplin, 1975). (2) If hummingbird foraging and dominance strategies change as a function of community composition (Feinsinger & Chaplin, 1975; Feinsinger & Colwell, 1978; Des Granges & Grant, 1980; Lara, 2006), then we expected that when hummingbird species composition changed in our study site, the hierarchy between the species would change as well. (3) If floral abundance and nectar resource availability modify the level of territoriality (Lyon, 1976; Ewald & Carpenter, 1978; Kodric-Brown & Brown, 1978; Snow & Snow, 1980; Dearborn, 1998; Baltosser & Russell, 2000; Lara *et al.*, 2009; Justino *et al.*, 2012) and the foraging strategy of hummingbirds (Feinsinger & Colwell, 1978; Carpenter, 1987a; Ohashi & Thomson, 2009), then we expected a positive relationship between nectar availability and aggressiveness and territoriality.

Materials and methods

Study area

The Sierra de Manantlán Biosphere Reserve is located in the Sierra Madre Occidental, between Jalisco and Colima States. In the central-western part of the Reserve is Las Joyas Scientific Station (LJSS), which encompasses an area of 1245 hectares (19°35′–19°37′N, 103°15′–104°37′W) (Lara & Ornelas, 2001). The LJSS has altitudinal gradient changes ranging from 1500 to 2242 m.a.s.l., a mean annual temperature of 15.5°C, mean annual precipitation of 1826 mm and a vegetation mosaic of different types of forest and perturbation levels including secondary vegetation, pine and cloud forest (Jardel *et al.*, 1990). This area is submitted to controlled and uncontrolled fires, a mechanism to maintain forest biodiversity and vegetation mosaic. The data used in our research were collected from 14th January to 22nd March 2008. We focused on the winter season because this is the time of the year with the highest hummingbird diversity and flower abundance. Latitudinal migrants arrive to this area on November and leave on March, while the altitudinal migrants stay in LJSS from November to June (Arizmendi, 2001).

Hummingbird species composition

To establish whether the composition of the hummingbird community changed during the winter season, we performed six capture sessions using 5 mist nets (6 × 3 m, 25 mm) for 8 hours beginning at sunrise (See Appendix S1 for capture session dates). Each individual captured was identified, aged, weighted, banded and classified as resident, latitudinal migrant and altitudinal migrant following Arizmendi (2001). We used the mass of each hummingbird as a direct indicative of size (Snow & Snow, 1972; Stiles, 1995), and we supplemented our weight data with observations from Contreras-Martínez (2014) (Appendix S2).

Dominance and foraging strategies

To characterize the dominance and foraging strategies used by the hummingbirds, we conducted 118 focal observation sessions, 68 in secondary vegetation, 27 in cloud forest and 23 in pine forest. During each monitoring session (minimum 2 hours, maximum 4 hours, in the morning and in the afternoon, 2 days per week, with two to three observers), we recorded the number of aggressive interactions, the identity (species, sex and age) and migratory status of the interacting hummingbirds, which individual initiated each aggressive interaction and the result of this (winner vs. loser). As well, we recorded the number of flowers visited for each hummingbird during the foraging bout, and counted the number of open flowers of each plant species in the patch at the end of the observation period.

Selasphorus rufus and *S. sasin* are nearly indistinguishable species that have been reported at our study site (Arizmendi, 2001). Because *S. sasin* is a scarce species at Central-western Mexico and was rarely caught during the Manantlán Bird Monitoring and Banding Program (Contreras-Martínez, 2014), we called all the individuals of these species recorded during the focal observations '*S. rufus*'.

Dominance categories

In order to understand the hierarchy of the hummingbirds in this community, we evaluated the proportion of interactions won by each hummingbird species discriminating these records at the intraspecific level. Based on the species, sex and/or age, we grouped the hummingbirds (see Statistical methodology section) and assigned to each group a specific dominance category, from highly aggressive (dominant), through intermediate dominance (subdominant), to lower dominance (subordinate) (Des Granges, 1979).

Foraging strategies

Based on the foraging behavior recorded during the focal observations, we explored differences between hummingbirds at the interspecific and intraspecific levels. Each hummingbird was sorted into one of two foraging behaviors. We classified as territorial hummingbirds those birds that permanently visited the same group of flowers, staying at the same place at least 60 minutes without long-distance movements. Those hummingbirds that did not stay in the same floral patch and showed evasive or inconspicuous behavior were considered non-territorial hummingbirds.

Floral abundance and nectar resource availability

We classified all the floral patches observed according to the abundance and number of species found blooming together. The three classifications were as follows: **large monospecific** patches, **small monospecific** patches and **mixed** patches. In addition, we recorded the type of vegetation (cloud forest, pine forest or secondary vegetation) and the number of open flowers in the patch during the observation sessions.

To establish the relationship between energy availability (calories) and hummingbird foraging behavior, we characterized the nectar production for six plant species (*Lobelia laxiflora*, *Ipomoea orizabensis*, *Moussonia deppeana*, *Salvia iodantha*, *S. mexicana*, and *Fuchsia encliandra*). These plants species were the most abundant and most intensively used by hummingbirds in the area during the fieldwork. Specifically, between nine and 40 floral buds were bagged at night. To avoid nectar consumption by mites, we applied wax at floral pedicels and peduncles (Lara & Ornelas, 2001). At sunset of the next day, we used microcapillary tubes and a hand refractometer (ERMA, 0–32% Brix) to establish nectar volume (accumulated) and sugar concentration. Also, we used the recompilation of Ornelas *et al.* (2007) to obtain information about the nectar volume and concentration of other plant species visited by hummingbirds in our community. We calculated the number of calories per flower using the formula proposed by Stiles (1975), and established the calories produced in all floral patches studied. When possible, we characterized floral territories, identifying the territory holder, the size of the territory and the number of open flowers of each plant species.

Statistical methodology

Previous to model selection process, we followed the protocol for data exploration proposed by Zuur, Ieno & Elphick (2010). During the model selection process, we ran the saturated model with different random slopes and intercepts, corrected for heteroscedasticity and correlation, and used Akaike information criterion and X^2 distributed likelihood ratio test for model comparisons and estimating model parameters (Johnson & Omland, 2004; Zuur *et al.*, 2009).

Effect of hummingbird size, age and sex on dominance and territoriality

To analyze whether the proportion of aggressive encounters won by the hummingbirds was related to species, age, sex and migratory status, we fitted a generalized linear mixed model (GLMM) with binomial distribution and logit link (Zuur *et al.*, 2009). To control pseudoreplication between pairs of interactions, we used the variable 'number of interaction' (identity for the winner and loser of the same interaction) as a random effect. To avoid problems with model estimation, in these analyses, we concatenated the aggressive interactions of *Amazilia violiceps*, *Tilmatura dupontii* (altitudinal migrants) and *Selasphorus calliope* (latitudinal migrant) under a single group. Each one of these species had less than 11 interactions during all the fieldwork and lost between 91 and 100% of all the aggressive encounters where they participated. The statistically significant differences between hummingbird species, sex, age and/or migratory status were used to classify hummingbird species into different dominance groups.

For each dominance group, we applied Spearman correlation test (r_s) to assess the strength of the relationship between the proportion of interaction won, the proportion of interactions that it initiated and the proportion of interactions that occurred when the hummingbirds were visiting flowers. Also, we used post hoc multiple comparison test to evaluate the relationship between aggressiveness (dominance categories), territoriality (foraging categories) and body size (Appendix S2).

In order to establish whether the aggressiveness of the hummingbirds changed over time and type of vegetation, we fitted a Zero-altered negative binomial (ZANB) model to solve the problem of overdispersion and the excessive number of zeros in our data. In this model, the response variable was the number of aggressive interactions, and we tested the effect of sampling day (Julian day), type of vegetation, flower number in the patch (log 10 transformed) and time of observation (minutes since the beginning of the session) as explanatory variables in the binomial and negative binomial part of the ZANB model.

In order to establish whether hummingbird dominance and territoriality changed through time, we fitted GLMM's with binomial distribution and logit link. The response variable was the proportion of interactions won. Time was the explanatory variable and we included this as a factor dividing the sample period in 2-week intervals. Because the aggressive interactions recorded during the same monitoring session are correlated with each other, we included session as a random intercept. We ran individual analyses for each dominance group (16 levels), dominance categories (three levels), foraging strategy (two levels) and migratory status (three levels).

Hummingbird community composition

We analyzed differences in hummingbird abundance between mist-net sessions using generalized linear models (GLM). We fitted a GLM with Poisson distribution and log link (Zuur *et al.*, 2009), where the number of hummingbird captured each season was the response variable, and session identity (included as a factor) and the hummingbird species were the explanatory variables. Because previous results at the same area found that changes in abundance of nectarivorous birds through the year was explained by the arrival of latitudinal and altitudinal migrants (Arizmendi, 2001), we also fitted a similar model but using migratory status as the independent factor.

Floral abundance and nectar resource availability

In order to establish whether the number of flowers available for the hummingbirds was different depending on vegetation and patch type, we fitted a generalized least squares model with an exponential variance function structure. In this model, the response variable was the number of flowers, and type of vegetation and type of patch were the explanatory variables.

To analyze the effect of the abundance of nectar resources on the aggressive interactions between hummingbirds, we constructed a two-by-two contingency analysis for hummingbird's dominance groups (defined previously with the GLMM models) and the type of floral patch (large monospecific patches, small monospecific patches and mixed patches). We conducted this analysis to compare the number of aggressive interactions observed against the number of interactions expected from the number of floral patches of each type sampled.

We used the Spearman correlation test (r_s) to assess the association between number of calories produced at floral patch and number of visits and aggressive encounters. We used a Mann–Whitney U test to test differences in the number of calories produced in floral territories defended by dominant and subdominant territorial hummingbirds.

All analyses were done using R software version 3.1.2 (R Development Core Team, 2014). Model selection process were performed using packages 'base' (R Development Core Team, 2014), 'pscl' (Wickham, 2009), 'blme' (Dorie, 2014), 'MCMCglmm' (Hadfield, 2010) and 'lme4' (Bates *et al.*, 2014). Post hoc multiple comparison tests were carried out with the general linear hypothesis function (glht) in the package 'multcomp' to the different fitted models (Hothorn, Bretz & Westfall, 2008). We used the Bonferroni correction for multiple testing, and an alpha of 0.05 or less to determine significance. All figures were done with the package 'ggplot2' (Wickham, 2009).

Results

Effect of hummingbird size, age and sex on dominance and territoriality

Dominance and foraging strategies

The focal observation sessions totaled 312 hours and 27 minutes, during which we recorded 1196 aggressive interactions that involved 11 hummingbird species (Table 1). During the focal observations, we identified 90 territories defended by five hummingbird species (Table 1).

We found variability in dominance between hummingbirds as a function of species ($X^2 = 460.490$, d.f. = 8, $P < 0.001$), sex ($X^2 = 90.125$, d.f. = 1, $P < 0.001$), age ($X^2 = 6.621$, d.f. = 1, $P = 0.010$) and migratory status of the birds ($X^2 = 62.000$; d.f. = 2; $P < 0.001$).

Large- and medium-sized resident species (*Lampornis amethystinus* and *Eugenes fulgens*) were dominant over the other hummingbird species (Table 1). In dimorphic species, males were generally dominant over females independently of age (i.e. *Lampornis amethystinus* and *Hylocharis leucotis*, Fig. S1, Tables 1 and 2). In the monomorphic *Amazilia beryllina* and *Colibri thalassinus*, adults won a higher percentage of aggressive interactions compared with the juveniles, but these differences were not statistically significant (Fig. S1, Table 2). This pattern did not hold in species such as *E. fulgens*, *Atthis heloisa*, *Selasphorus calliope* and *S. platycercus*, were dominance did not change with sex and/or age (Tables 1 and 2). Respect to migratory status, altitudinal migrant species won the majority of the aggressive encounters where they participated, whereas latitudinal migrant species lost most of these interactions, and resident species had an intermediate level of dominance (Table 1).

The analyses including the proportion of interactions won by the whole species, or parts of these regarding sexes or ages, defined 16 dominance groups (Table 1). Each one was assigned to one of the three dominance categories (dominant, subdominant and subordinate) and one of the two foraging behavior (territorial and non-territorial). Dominant and subdominant species were territorial, and non-territorial hummingbirds were subordinated (Table 1). The exceptions were males of *H. leucotis* and individuals of *E. fulgens*. Males of *H. leucotis* were classified as subordinate following our dominance criteria, but we observed three individuals holding feeding territories at

Table 1 Dominance categories and foraging strategies used for the 11 hummingbird species recorded at Las Joyas Scientific Station during winter

Species	Age	Sex	Total	WON %	BEG %	FLO %	COD	STR	Terr	Migratory status
Amazilia beryllina[a]			**546**	**61.36**	**60.81**	**54.58**	**SubD**	**Territorial**		Altitudinal migrant
	Juvenile		77	55.84	55.84	64.94	SubD	Territorial	2	
	Adult		369	61.79	60.98	52.12	SubD	Territorial	31	
Amazilia violiceps[a]			**2**	**0.00**	**0.00**	**100.00**	**SubO**	**Non-territorial**	0	Altitudinal migrant
Atthis heloisa[b]			**35**	**28.57**	**31.43**	**65.71**	**SubO**	**Non-territorial**		Resident
	Adult	Female	17	17.68	17.65	82.35	SubO	Non-territorial	0	
	Adult	Male	13	38.46	46.15	61.54	SubO	Non-territorial	0	
Colibri thalassinus[a]			**56**	**83.93**	**89.29**	**51.79**	**Dom**	**Territorial**		Altitudinal migrant
	Juvenile		1	0.00	0.00	0.00	Dom	Territorial	1	
	Adult		43	90.70	93.02	48.84	Dom	Territorial	5	
Eugenes fulgens[b]			**29**	**34.48**	**17.24**	**62.07**	**SubD**	**Non-territorial**		Resident
		Female	11	45.46	18.18	63.64	SubD	Non-territorial	0	
		Male	9	44.44	33.33	66.67	SubD	Non-territorial	0	
Hylocharis leucotis[b]			**400**	**17.00**	**15.25**	**67.25**	**SubO**			Resident
	Juvenile	Female	7	0.00	0.00	71.43	SubO	Non-territorial	0	
	Juvenile	Male	32	18.75	9.38	71.88	SubO	Territorial	1	
	Adult	Female	86	6.98	5.81	67.44	SubO	Non-territorial	0	
	Adult	Male	216	22.22	17.59	67.59	SubO	Territorial	2	
Lampornis amethystinus[b]			**399**	**75.44**	**76.44**	**62.16**		**Territorial**		Resident
		Female	27	44.44	44.44	62.96	SubD	Territorial	2	
		Male	341	82.70	83.87	63.93	Dom	Territorial	33	
Selasphorus calliope[b]			**16**	**0.00**	**0.00**	**75.00**	**SubO**	**Non-territorial**		Latitudinal migrant
		Female	4	0.00	0.00	100.00	SubO	Non-territorial	0	
		Male	5	0.00	0.00	100.00	SubO	Non-territorial	0	
Selasphorus platycercus[b]			**47**	**4.25**	**6.38**	**74.47**	**SubO**	**Non-territorial**		Latitudinal migrant
	Juvenile	Male	11	0.00	0.00	72.73	SubO	Non-territorial	0	
	Adult	Female	14	7.14	7.14	64.29	SubO	Non-territorial	0	
	Adult	Male	1	0.00	0.00	100.00	SubO	Non-territorial	0	
Selasphorus rufus[b]			**187**	**43.85**	**42.78**	**57.75**				Latitudinal migrant
	Juvenile	Female	12	25.00	25.00	83.33	SubO	Non-territorial	0	
	Juvenile	Male	45	51.11	46.67	82.22	SubD	Territorial	5	
	Adult	Female	94	45.75	45.75	52.13	SubD	Territorial	8	
	Adult	Male	1	0.00	0.00	0.00	SubO	Non-territorial	0	
Tilmatura dupontii[b]			**33**	**9.09**	**0.00**	**78.79**	**SubO**	**Non-territorial**		Altitudinal migrant
		Female	33	9.09	0.00	78.79	SubO	Non-territorial	0	

Bold values correspond to the dominance and foraging behavior at species level.

Records are classified at intraspecific level by age and/or sex.

Total, number or aggressive interactions recorded; WON, percentage of won encounters; BEG, percentage of encounters began by this hummingbird species; FLO, percentage of encounters that involved flower visitation; COD, categories of dominance; Dom, dominant; SubD, subdominant; SubO, subordinate; STR, foraging strategy; Terr, number of territories recorded.

[a] Monomorphic hummingbird species.

[b] Hummingbird species with sexual dimorphism.

the end of winter (Fig S2). *E. fulgens* was non-territorial during the winter, but had an intermediate dominance with respect to other hummingbird categories (Table 1).

The test between size and the proportion of won interactions ($r_s = 0.345$; $n = 16$; $P = 0.095$) showed that dominant and subdominant hummingbirds were similar in size (Kruskal–Wallis test, $P = 1.000$). Although Fig. 1a shows that these two categories were larger than the subordinated hummingbirds, the size showed no significant effects (Kruskal–Wallis test, $P = 0.144$ and $P = 0.251$ respectively). Similarly, although no statistically significant, larger hummingbirds were generally territorial compared with the smaller ones (Kruskal–Wallis test, $P = 0.288$, Fig. 1b), with exception of *E. fulgens*, a non-territorial large hummingbird (7.233 ± 0.764 g, Table 1).

Hummingbird community hierarchy and dynamic

As hummingbird community composition and abundance changed through winter (see below), the number of aggressive interactions changed too ($\chi^2 = 5.580$, d.f. = 1, $P = 0.018$) depending upon hummingbird dominance and foraging behavior

Table 2 Likelihood ratio test for the generalized linear mixed models fitted to test the differences in the proportion of interactions won by the different hummingbird species at the intraspecific level (sex and/or age)

Species	Level	X^2	P
Amazilia beryllina	Age	2.698	0.100
Amazilia violiceps	Age	[a]	
Atthis heloisa	Age	[a]	
	Sex	2.132	0.144
Colibri thalassinus	Age	[a]	
Eugenes fulgens	Age	[a]	
	Sex	0.257	0.612
Hylocharis leucotis	Age	0.062	0.804
	Sex	**11.005**	**<0.001**
	Age × Sex	0.911	0.340
Lampornis amethystinus	Age	0.050	0.823
	Sex	**14.551**	**<0.001**
	Age × Sex	1.330	0.249
Selasphorus calliope	Age	[a]	
	Sex	[a]	
Selasphorus platycercus	Age	[a]	
	Sex	[a]	
Selasphorus rufus	Age	0.493	0.483
	Sex	0.002	0.963
	Age × Sex	**4.598**	**0.032**
Tilmatura dupontii	Age	[a]	
	Sex	[a]	

Female and adult were the levels set as reference to the models. The statistically significant differences ($\alpha = 0.005$) are indicated with bold values.

[a] Models not fitted because the response variable (win vs. lose) for these categories had constant or practically constant values (Table 1), causing problems with deviance estimations.

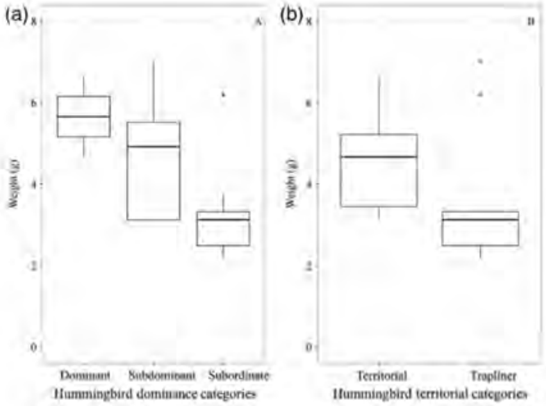

Figure 1 Relationship between hummingbird size (weight in grams), aggressiveness (a) and foraging behavior (b). Hummingbird records were analyzed at inter- and intraspecific level to classify hummingbirds into one dominance and territorial category (see text for details). Box encloses the 50% of the data and it is divided by the median (horizontal line); the upper and lower adjacent indicate 0.95 and 0.05 quantiles respectively. Points are considered to be outliers.

(Fig. 2). Also vegetation ($X^2 = 48.822$, d.f. = 1, $P < 0.001$), number of flowers ($X^2 = 9.819$, d.f. = 1, $P = 0.002$) and the time of observation ($X^2 = 15.938$, d.f. = 1, $P < 0.001$) had a significant effect in the model.

The proportion of interactions won by territorial and non-territorial hummingbirds did not change when comparing the beginning and the end of winter season ($X^2 = 2.902$, d.f. = 4, $P = 0.574$, and $X^2 = 5.294$, d.f. = 4, $P = 0.258$ respectively). However, during the last 2 weeks of March, non-territorial hummingbirds won more aggressive encounters (Fig. 2b).

In the same way, the proportion of aggressive interactions won by dominant hummingbirds did not change over time ($X^2 = 5.059$, d.f. = 4, $P = 0.281$), in contrast to subdominant and subordinate hummingbirds ($X^2 = 10.925$, d.f. = 4, $P = 0.027$, $X^2 = 16.796$, d.f. = 4, $P = 0.002$ respectively) (Fig. 2a). At the end of the winter season, the proportion of interactions won by the subordinate hummingbirds increased notably ($X^2 = 8.094$, d.f. = 1, $P = 0.004$), whereas the number won by the subdominant hummingbirds decreased ($X^2 = 4.996$, d.f. = 1, $P = 0.025$) (Fig. 2a). Specifically, the proportion of interactions won by *H. leucotis* males changed with time ($X^2 = 16.474$, d.f. = 4, $P = 0.002$), and these birds won significantly more aggressive encounters at the end of the winter season ($X^2 = 4.145$, d.f. = 1, $P = 0.041$) (Fig. S2c). The same pattern was observed in individuals of *A. heloisa* (Fig. S2c). In contrast, adult females of *S. rufus* were highly dominant at the beginning of the season, afterward the proportion of interactions won by them decreased significantly ($X^2 = 229\,920.2$, d.f. = 1, $P < 0.001$) (Fig. S2b). For the subordinated latitudinal and altitudinal migrant categories, the number of won interactions did not change notably over time, moreover during the last 2 weeks of March, the adult males and juvenile females of *S. rufus* and the individuals of *S. platycercus* and *S. calliope* lost practically all the interactions where they were involved (Fig. S2c).

Hummingbird community composition

For a total of 90 net hours, we caught 117 individuals belonging to 10 hummingbird species (Appendix S1). Hummingbird community composition and abundance change over time ($X^2 = 19.967$; d.f. = 5; $P = 0.001$). We caught fewer hummingbirds toward the end of the winter ($X^2 = 11.772$, d.f. =1, $P < 0.001$) and not all the species were caught in the same proportion ($X^2 = 131.992$; d.f. = 9; $P < 0.001$). Species such as *A. beryllina* and *S. rufus* were caught more frequently than the other species. Although the migratory status did not have an effect on the number of hummingbirds caught ($X^2 = 0.1552$; d.f. = 15; $P = 0.155$), as the sampling period advanced, the number of hummingbirds belonging to latitudinal migrant species diminished (Appendix S1).

Floral abundance and nectar resource availability

Fourteen plant species were used by hummingbirds as nectar resources (Appendix S3). The number of flowers available for the hummingbirds was different depending on vegetation

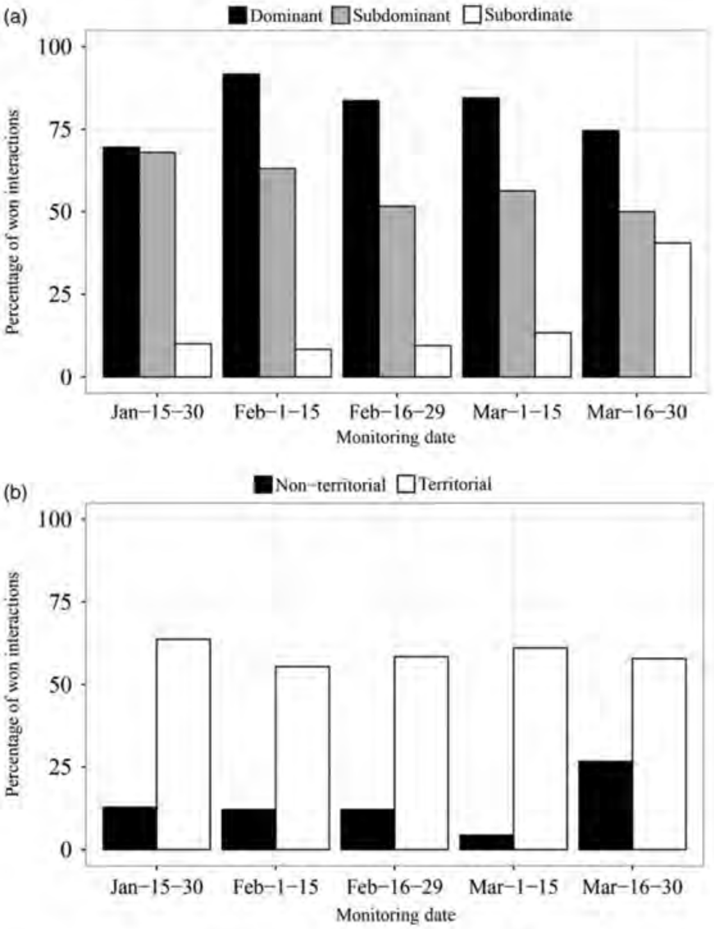

Figure 2 Proportion of aggressive interactions won by hummingbirds at Las Joyas Scientific Station during winter (2-week periods). Hummingbird species are discriminated by dominance categories (a) and foraging strategy (b).

and patch type ($L = 18.597$; d.f. $= 15$; $P < 0.001$), with more flowers in secondary vegetation (mixed patches) and cloud forest (large monospecific and mixed patches) (Fig. 3). Most species used by hummingbirds grew in disturbed areas, and only *M. deppeana*, *Ipomoea hederifolia* and *Salvia albocaerulea* grew exclusively inside the forest (Appendix S3).

Resource availability and aggressive hummingbird interactions

The number of aggressive interactions changed significantly between the different types of floral patches ($\chi^2_{(0.05,26)} = 323.91$; $P < 0.001$), and almost all the interactions occurred at patches with abundant flowers (37.611% at large monospecific patches and 56.294% at mixed patches).

Hummingbirds responded differently to floral availability as a function of their dominance status and foraging strategy. Generally, a hummingbird that started an interaction would win it ($r_s = 0.957$; $n = 16$; $P = 0.001$), and the majority of the interactions that involved subordinate hummingbirds happened when these birds were visiting flowers ($r_s = 0.587$; $n = 16$; $P = 0.008$) (Table 1).

Hummingbird aggressiveness and patch preferences were related with the number of flowers and the type of floral patch. In the small monospecific patches, we observed lower activity, with only a few hummingbirds showing aggressive behavior in these patches (males of *L. amethystinus* and individuals of *A. beryllina*) ($U_{\text{type of patch}} = 0.13$; $P < 0.001$, Table 3). Some species (*H. leucotis*, *E. fulgens* and *S. platycercus*) did not prefer a particular patch type between large monospecific and mixed, but we did find cases where the different dominance groups interacted more aggressively in one particular floral patch type than in others (Table 3). For example, in *L. amethystinus*, the males were more aggressive and visited the flowers of the large monospecific patches, while the females interacted in all type of patches indiscriminately. In the case of *S. rufus*, the subdominant individuals of

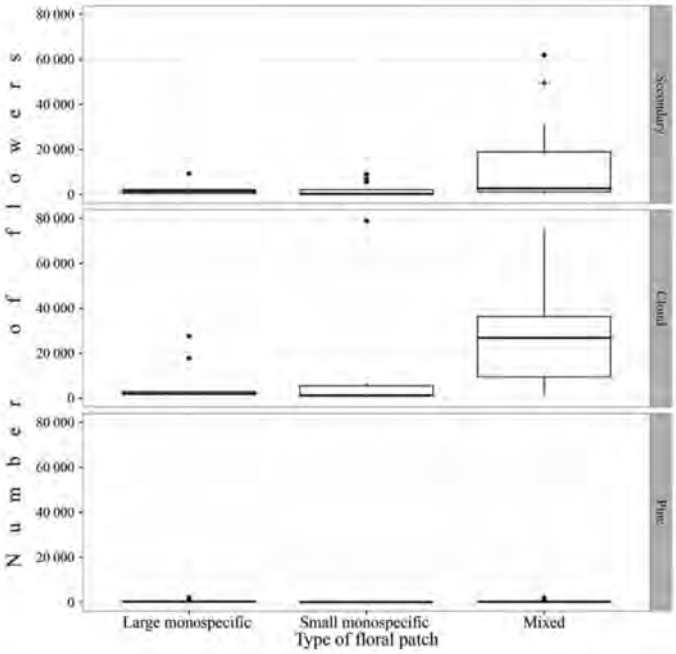

Figure 3 Number of flowers in the patches visited by hummingbirds during winter. Patches are classified by type of vegetation (secondary, cloud and pine forest), and according to the abundance and number of species found blooming together (large monospecific, small monospecific and mixed). Box encloses the 50% of the data and it is divided by the median (horizontal line); the upper and lower adjacent indicate 0.95 and 0.05 quantiles respectively. Points are considered to be outliers.

this species (juvenile males and adult females) interacted more frequently in mixed patches, compared to the subordinated individuals, which interacted principally in large monospecific patches (Table 3).

The number of flowers visited and the number of aggressive interactions were positively and significantly correlated with the number of calories produced by the flowers in the different patches studied ($r_s = 0.831$; $n = 91$; $P < 0.001$ for visits; $r_s = 0.724$; $n = 91$; $P < 0.001$ for aggressive interactions). However, the number of calories produced in floral territories defended by dominant and subdominant territorial hummingbirds were not statistically different ($n = 23$, $P = 0.4876$, $W = 64$, Mann–Whitney U test).

Discussion

Dominance and territoriality were not fixed attributes of the species in this hummingbird community, and changed as a function of hummingbird species, sex, age and size. Similarly, hummingbird foraging and dominance strategies change as a function of community composition, floral abundance and nectar resource availability. As expected, a close relationship between dominance and territoriality was found (Cotton, 1998): a dominant individual was generally a territorial one, while a subordinate hummingbird always acted as a non-territorial. In this community, size was not always the best predictor of dominance and territoriality, and can be explored as a trait associated with phylogenetic clustering.

Effect of hummingbird size, age and sex on dominance and territoriality

Different authors have proposed that the pattern of dominance and foraging behavior between hummingbirds into a community may be defined by hummingbird body size and predisposition for territorial behavior (Feinsinger & Colwell, 1978; Des Granges, 1979; Justino *et al.*, 2012). In this community, large hummingbirds (because of their high energetic requirements) were dominant and moved between different habitats looking for resources with abundant nectar to establish feeding territories. Furthermore, latitudinal migrants (generally smaller) tended to be subordinate to the resident species and were forced to follow a non-territorial strategy (as observed by Wolf, Stiles & Hainsworth, 1976; Des Granges & Grant, 1980) (Fig. 1, Table 1).

The pattern where larger competitors exclude and influence the habitat use of the smaller and less dominant species support the 'ideal despotic distribution'. Body size effect has been documented in other systems as nectarivorous birds in Australia, where bigger birds are limiting the access to nectar to the smaller birds (Bennett *et al.*, 2014). Specifically for the community studied here, the cases where this pattern was not supported exemplify as other factors are acting together with

Table 3 Number of aggressive encounters recorded at the different type of floral patches

Hummingbird dominance groups	Large monospecific	Small monospecific	Mixed
Amazilia beryllina	329	8	333
Amazilia violiceps	0	1	1
Atthis heloisa	6	0	32
Colibri thalassinus	11	0	71
Eugenes fulgens	7	1	21
Hylocharis leucotis female	49	0	57
H. leucotis male	130	4	137
Lampornis amethystinus female	18	1	9
Lampornis amethystinus male	264	27	100
Selasphorus calliope	6	0	10
Selasphorus platycercus	16	1	27
Selasphorus rufus subdominant	42	1	110
Selasphorus rufus subordinate	9	0	6
Tilmatura dupontii	32	0	2

The interactions are discriminated by hummingbird dominance group. *Selasphorus rufus* subdominant included adult females and juvenile males; *S. rufus* subordinate include juvenile females and adult males.

body size to modify dominance and foraging behavior. Territoriality can be a very expensive strategy when resources are limited (Carpenter, 1987a), and in our community, a large territorial and dominant species as *E. fulgens* (Lyon, 1976; Des Granges, 1979) used a non-territorial behavior visiting the flowers defended by smaller territorial hummingbirds with impunity ('territory-parasite' *sensu stricto* Feinsinger & Colwell, 1978). This indicates that probably the amount of nectar offered by the flowers in our study site at this time was not enough to support a high population density and cover the energetic requirements related with a territorial strategy.

Other explanation to the lack of support for our predictions with respect to the dominance of larger competitor, is the hypothesis that suggests that smaller species can win aggressive contest against larger ones if these interact with distantly related species or with species poorly known (Martin & Ghalambor, 2014). This hypothesis could explain the fact that *Colibri thalassinus* (Mangoes clade *sensu stricto* McGuire *et al.*, 2009) and *A. beryllina* (Emeralds clade *sensu stricto* McGuire *et al.*, 2009), the two altitudinal migrants, won the majority of their interactions against *E. fulgens*, a resident and larger species that belongs to a different phylogenetic clade (Mountain gems clade *sensu* McGuire *et al.*, 2009).

As expected, territoriality and dominance changed at intraspecific level depending on age and sex of the individuals (Carpenter *et al.*, 1993). The lack of sexual dimorphism in the plumage of some hummingbird species as *Panterpe insignis*, suggested that the females are dominant because both sexes converge in the color of the areas that are important for territoriality and aggressive displays (Wolf, 1969). In the community we studied, it was true for monomorphic species as *C. thalassinus* and *A. beryllina* (Tables 1 and 2). Also, in dominant hummingbird species with plumage sexual dimorphism (e.g. *L. amethystinus* here), males and females usually have different foraging behaviors: adult and juvenile males are territorial and dominant over the adult and juvenile females that are subordinate and/or secondary territorial (Feinsinger & Colwell, 1978) (Tables 1 and 2). As observed with body size, our results showed that although the dominance and territoriality responded as expected in some cases, it was evident that other factors are modifying the dominance and territoriality at intraspecific level. In the particular case of *S. rufus*, our results suggested that hummingbird density modified the pattern expected for dominance. The adult males are dominant and highly territorial in the reproductive (Healy & Calder, 2006) and migratory (Kodric-Brown & Brown, 1978) areas of United States of America and Canada. However, in the LJSS (a wintering area), the adult males of *S. rufus* were subordinated to the adult females and juvenile males of the same species (Table 1, C. Rodríguez-Flores and M. C. Arizmendi pers. obs.). Stiles *et al.* (2005) stated that females of the majority of hummingbird species rarely defended territories during the winter, being generally subordinate to the males. But in the absence or low number of males, the females can show territorial behavior (Stiles *et al.*, 2005). We recorded adult males very occasionally during the observation periods, and only one was caught during the mist-net sessions. These results and the observations made during subsequent visits to different areas of the Reserve (C. Rodríguez-Flores, pers. obs.), supported the hypothesis of altitudinal segregation between sexes (Schondube *et al.*, 2004) with males establishing territories in the eastern side of the Sierra and at lower elevations, compared with females and juveniles. Additionally, Kodric-Brown & Brown (1978) suggested that at high elevation (>2500 m a.s.l.), the aggressive ability of male *S. rufus* decreased because of their high wing disk loading.

In the community studied by us, the majority of the aggressive interactions occurred between species of different migratory and dominance status. Des Granges (1979) found a similar pattern, and he interpreted it as a consequence of ecological segregation and co-adjustment of the niches of species that are coexisting. In our community, *L. amethystinus* (males) and *E. fulgens* interacted strongly with individuals of **other** dominance category but of the **same** migratory status. In the specific case of the males of *L. amethystinus*, their territorial and dominant behavior increased the number of aggressive interactions with individuals of *E. fulgens* and *A. heloisa*; two non-dominant species that as *L. amethystinus* were resident too.

Hummingbird community composition

We found that hummingbird foraging strategies and dominance were dynamic over time. This change occurred as a function of community composition (related with migration pattern) and the resulting change in hummingbird density of a particular species (or age/sex category) (Appendix S1, Fig. S2, Stiles, 1973; Lyon, 1976; Bennett *et al.*, 2014). The change in the composition and abundance of the hummingbird community occurred as expected, with few hummingbirds caught in the last 2 weeks of March because of the departure of the long-distance migrant species (Appendix S1, Arizmendi, 2001). This pattern was supported by the number of altitudinal and latitudinal migrant hummingbirds caught with mist nets, and although these data are not conclusive with respect to the resident species (Appendix S1), our behavioral observations showed an increase in the number of aggressive interactions and visits to the flowers by resident species at the end of March, specially *H. leucotis*. Departure dates for the northwood latitudinal migration of *S. rufus* based on records at Nevado de Colima (69.5 km east of the study site) in previous years were between January 22nd to February 12th (Des Granges, 1979) and February 20th to March 21st (Schondube *et al.*, 2004). Our results showed that, even on March 21st, some individuals of *S. rufus*, *S. platycercus* and *S. calliope* were still at our study site.

Our data showed that *H. leucotis* and *A. heloisa* were subordinate species during winter, but at the end of March, the individuals of these species won a higher proportion of aggressive encounters against more dominant species such as *S. rufus*, *A. beryllina* and *L. amethystinus* (Fig. S2, Appendix S4), and additionally, its abundance increased over the following months with the highest density on summer (Arizmendi, 2001). In the particular case of *H. leucotis*, Lyon (1976) proposed that the flexible feeding behavior repertoire of this species was the factor that explained the success of this species in montane Mexico. These observations suggested that, over time, the foraging strategy and the dominance should change as a function of community composition (Sandlin, 2000b), with the resident species becoming more abundant with respect to the migrant species, and in consequence more territorial and dominant (Des Granges, 1979; Des Granges & Grant, 1980; Arizmendi & Ornelas, 1990).

Floral abundance and nectar resource availability

Different studies have suggested that hummingbird territoriality is determined by nectar availability (Feinsinger, 1976; Feinsinger & Colwell, 1978; Kodric-Brown & Brown, 1978; Cotton, 1998; Justino *et al.*, 2012). In our study site, the foraging strategy used by the different hummingbird dominance categories did not change as a function of habitat or the plant species they used as nectar resources during winter season. The only exception was the males of *L. amethystinus*. These birds visited the flowers of *M. deppeana* and *I. hederifolia* at the cloud and pine forest (respectively) using a traplining strategy, but in secondary forest, these individuals were territorial and defended floral patches of *Salvia mexicana*, *S. albocaerulea* and *L. laxiflora* (Appendix S5). Change in foraging behavior is an alternative to get resources when the optimal feeding territories are occupied (Schondube *et al.*, 2004) or to exploit the difference in nectar availability between habitats (Lara, 2006). At regional scale, hummingbird nectar resources are not uniformly distributed, and these resources were located principally in the secondary vegetation and along stream banks in the cloud forest. Further, flower abundance was variable over time and decreased substantially in spring (Arizmendi, 2001). Restriction in nectar availability (at spatial and temporal scale) determines the competitive pressure between hummingbirds (Carpenter, 1987b), which foraging strategies are profitable, and nectar exploitation patterns (Feinsinger, 1976). As expected, the nectar-rich areas at local scale (like large monospecific and mixed patches), attracted more competitors increasing territoriality and aggressive behavior between hummingbirds. The presence of small floral patches, generally undefended, acted as feeding areas where different hummingbird species, independently of the species, can feed with minimum conflict (Lyon, 1976).

Competition exerts a strong force on hummingbird behaviors (Sandlin, 2000a), and in this community, differences in the utilization of floral resources and habitat acted as mechanisms that favored hummingbird coexistence as suggested by Feinsinger (1976). In the case of floral use, these differences have been proposed as a mechanism that decrease the competition between species that use similar resources, favoring resource partitioning, and consequently decreasing the probability of injury during aggressive encounters with other individuals (Des Granges & Grant, 1980; Ritchie, 2002; Lara *et al.*, 2009). In our study site, *L. amethystinus* used principally the large monospecific patches, but the altitudinal migrant species, especially *C. thalassinus*, used the mixed patches more frequently (Table 3). Because these species are the more dominant species in our community, the more plausible explanation is the tendency to diverge functionally through segregation of nectar resources. Respect to habitat use, spatial segregation is one of the mechanisms that affect directly hummingbird community organization (Des Granges, 1979; Rodríguez-Flores, 2004), and in LJSS, species like *A. beryllina* and *S. rufus* used more the secondary vegetation areas in comparison with pine forest specialist species like *S. platycercus* (Contreras-Martínez, 2014). The preference of this species in pine forest corresponded to a behavioral strategy, where a low hierarchy species prefers habitats with low floral abundance and aggressiveness (Fig. 3) to avoid the more competitive habitats, while use poorer and dispersed resource patches (Carstensen *et al.*, 2011).

Conclusion

Hummingbird capability to evaluate and respond to changes in their environment is crucial to allow their coexistence and prevalence. Our study showed how hummingbird aggressiveness and territoriality are plastic traits that responded to spatio-temporal variations in community composition, hummingbird density and floral availability. Compared to other studies where nectar availability is the main factor controlling hummingbird distribution and territoriality (Lyon, 1976; Wolf, 1978; Des Granges, 1979; Gutiérrez-Zamora & Rojas, 2001), our results showed that local abundance and hummingbird migration pattern together with nectar availability are crucial components to explain the dynamic nature of dominance and territoriality in this community as found for other nectarivorous birds, the Noisy Miners (Bennett *et al.*, 2014). This complex and highly dynamic arrangement in which hummingbirds show high plasticity in resource use both in time and space and among species can be the key evolutive trait that has made hummingbirds one of the less threatened bird families in the Neotropics (Schuchmann, 1999).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Proportion of interactions won (number of interactions won/(number of interactions won + number of interactions lost)) by hummingbirds at Las Joyas Scientific Station during winter. Hummingbird species are discriminated by sex (a) and age (b).

Figure S2. Proportion of aggressive interactions won by hummingbirds at Las Joyas Scientific Station during winter (2-week periods).

Appendix S1. Number of hummingbird caught during the mist-net sessions at Las Joyas Scientific Station.

Appendix S2. Mean body weight for the different sex and age of the hummingbirds at Las Joyas Scientific Station, Mexico.

Appendix S3. Plants visited by hummingbirds in Las Joyas Scientific Station, Mexico.

Appendix S4. Aggressive interaction matrix between hummingbird dominance groups habiting Las Joyas Scientific Station (Mexico). In parenthesis is indicated the total number of aggressive interactions recorded between these two species.

Appendix S5. Interaction matrix between hummingbirds and plants at Las Joyas Scientific Station during winter.

Supporting Information

Figure 1 Supporting Information.

Proportion of interactions won (number of interactions won / (number of interactions won + number of interactions lost)) by hummingbirds at Las Joyas Scientific Station during winter. Hummingbird species are discriminated by sex (A) and age (B). AMBE: *Amazilia beryllina,* AMVI: *Amazilia violiceps,* ATHE: *Atthis heloisa*, COTH: *Colibri thalassinus*, EUFU: *Eugenes fulgens*, HYLE: *Hylocharis leucotis,* LAAM: *Lampornis amethystinus*, SECA: *Selasphorus calliope*, SEPL: *Selasphorus platycercus*, SERU: *Selasphorus rufus,* TIDU: *Tilmatura dupontii.* The fifth letter on hummingbird species names at figure A represents sex (F: female, M: male) and age at figure B (A: adult, J: juvenile). *Asterisks* indicate significant differences between sexes of the same hummingbird species (post-hoc tests, $P > 0.05$).

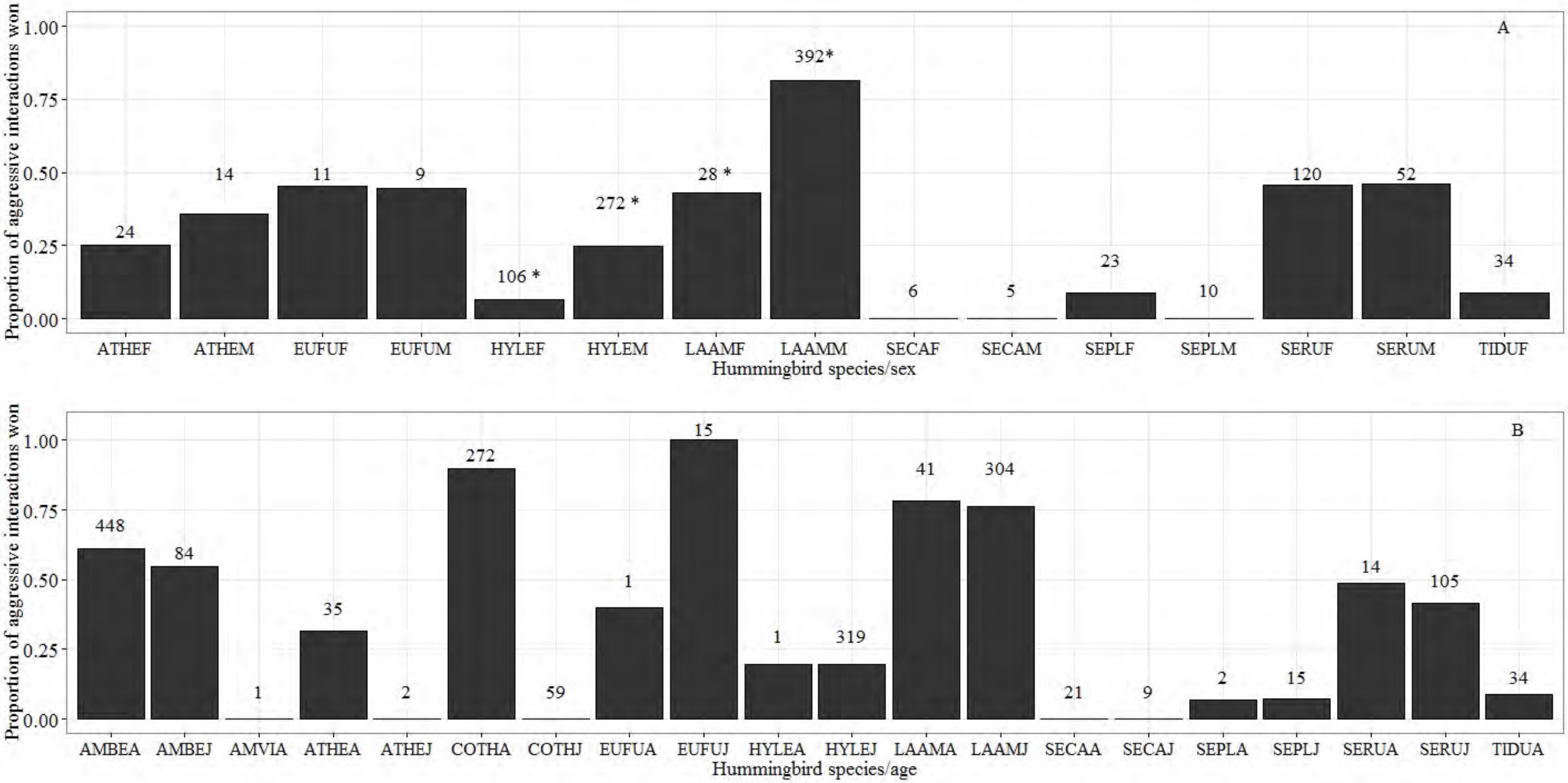
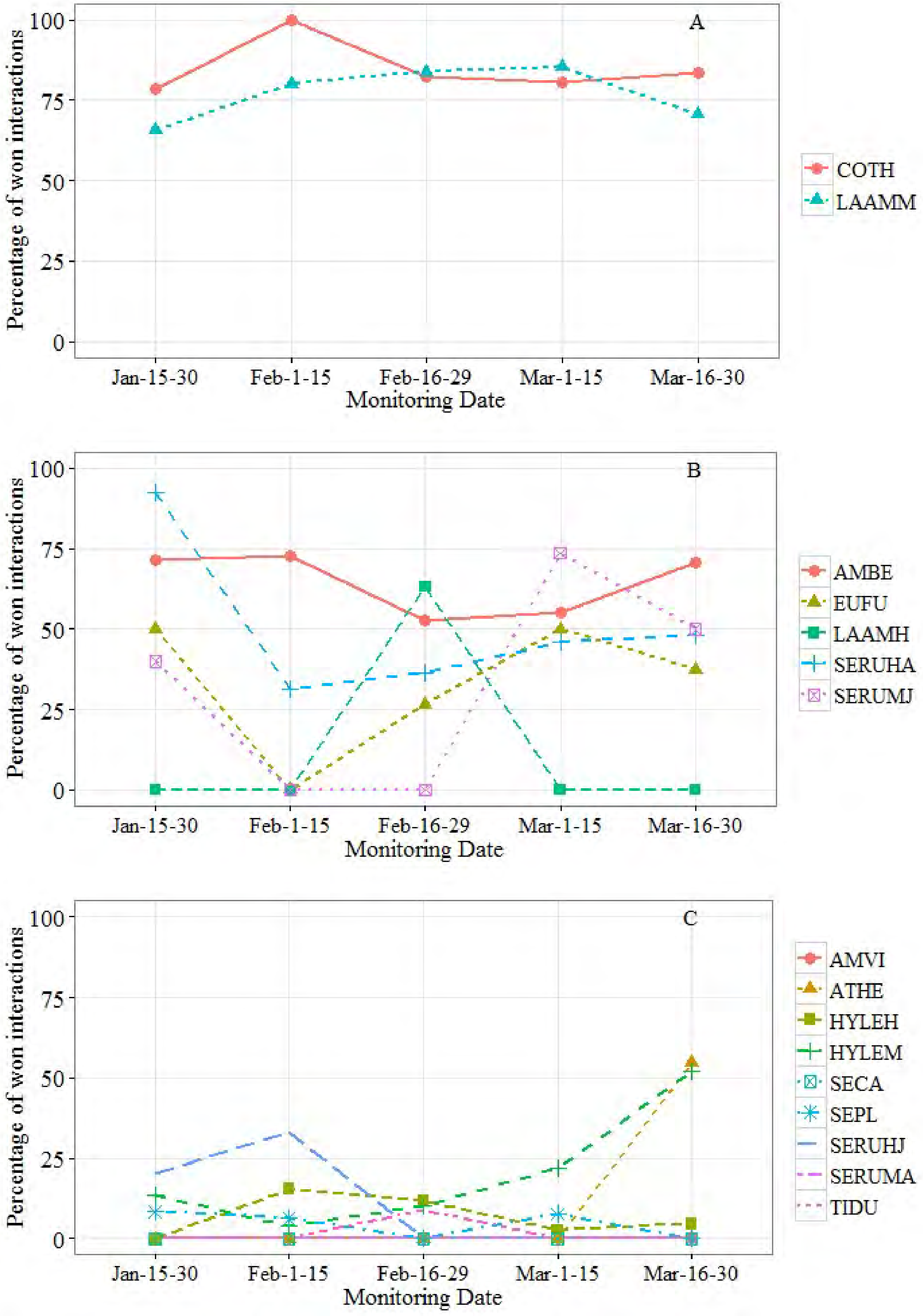

A
Proportion of aggressive interactions won
1.00
0.75
0.50
0.25
0.00
24
14
11
9
106 *
272 *
28 *
392*
6
5
23
10
120
52
34
ATHEF
ATHEM
EUFUF
EUFUM
HYLEF
HYLEM
LAAMF
LAAMM
SECAF
SECAM
SEPLF
SEPLM
SERUF
SERUM
TIDUF
Hummingbird species/sex
B
Proportion of aggressive interactions won
1.00
0.75
0.50
0.25
0.00
448
84
1
35
2
272
59
1
15
1
319
41
304
21
9
2
15
14
105
34
AMBEA
AMBEJ
AMVIA
ATHEA
ATHEJ
COTHA
COTHJ
EUFUA
EUFUJ
HYLEA
HYLEJ
LAAMA
LAAMJ
SECAA
SECAJ
SEPLA
SEPLJ
SERUA
SERUJ
TIDUA
Hummingbird species/age

Figure 2 Supporting Information.

Proportion of aggressive interactions won by hummingbirds at Las Joyas Scientific Station during winter (two weeks periods). Hummingbird species are discriminated by dominance groups. A) Dominant, B) Subdominant and C) Subordinate categories. For each hummingbird group, the first four letters correspond to the species name, and the subsequent (s) to sex and age. A: adult, J: juvenile, H: female, M: male. AMBE: *Amazilia beryllina,* AMVI: *Amazilia violiceps,* ATHE: *Atthis heloisa*, COTH: *Colibri thalassinus*, EUFU: *Eugenes fulgens*, HYLE: *Hylocharis leucotis,* LAAM: *Lampornis amethystinus*, SECA: *Selasphorus calliope*, SEPL: *Selasphorus platycercus*, SERU: *Selasphorus rufus,* TIDU: *Tilmatura dupontii.*


A
Percentage of won interactions
0
25
50
75
100
Jan-15-30
Feb-1-15
Feb-16-29
Mar-1-15
Mar-16-30
Monitoring Date
COTH
LAAMM
B
Percentage of won interactions
Monitoring Date
AMBE
EUFU
LAAMH
SERUHA
SERUMJ
C
Percentage of won interactions
Monitoring Date
AMVI
ATHE
HYLEH
HYLEM
SECA
SEPL
SERUHJ
SERUMA
TIDU

Appendix S1: Number of hummingbirds caught during the mist nets sessions at Las Joyas Scientific Station. Hummingbird species are grouped by their migratory status (bold). Number of individuals and hummingbird species caught in each session are showed. Dates are in day/month format.

	Date						
Species/Date	01/22	01/27	02/14	02/27	03/11	03/19	Total across sessions
Residents	8	7	7	4	9	3	38
Atthis heloisa	3	4	3	2	1	2	15
Eugenes fulgens	0	0	0	0	1	0	1
Hylocharis leucotis	5	2	4	2	7	1	21
Lampornis amethystinus	0	1	0	0	0	0	1
Altitudinal migrants	6	9	10	3	1	2	31
Amazilia beryllina	5	8	10	2	1	2	28
Amazilia violiceps	0	1	0	0	0	0	1
Colibri thalassinus	1	0	0	1	0	0	2
Latitudinal migrant	14	9	8	10	6	1	48
Selasphorus calliope	0	0	0	4	0	0	4
Selasphorus platycercus	1	3	1	0	1	0	6
Selasphorus rufus	13	6	7	6	5	1	38
Total across species	28	25	25	17	16	6	117
Total species caught	6	7	4	6	6	5	

Appendix S2: Mean body weight for the different sex and age of the hummingbirds at Las Joyas Scientific Station, Mexico.*: information taken from Contreras Martínez (2014)

Species	Age	Sex	Sample Size	Mean Body Weight (g)	Standard Deviation
Amazilia beryllina			30	4.600	0.513
	Juvenile		25	4.440	0.323
	Adult		5	5.400	0.57
Amazilia violiceps			1	6.200	
Atthis heloisa			14	2.293	0.24
	Adult	Female	4	2.325	0.287
	Adult	Male	3	2.033	0.058
Colibri thalassinus			4	4.850	0.751
	Juvenile		1	4.300	
	Adult		3	5.033	0.802
Eugenes fulgens			3	7.233	0.764
		Female	1	6.400	
		Male	2	7.650	0.354
Hylocharis leucotis			40	3.595	0.303
	Juvenile	Female	8	3.386	0.204
	Juvenile	Male	21	3.657	0.26
	Adult	Female	4	3.275	0.126
	Adult	Male	8	3.850	0.233
Lampornis amethystinus			27	6.170	0.675
		Female	11	5.520	0.530
		Males	17	6.649	0.415
Selasphorus calliope			136*	2.482*	0.197*
		Female	70*	2.457*	0.151*
		Male	61*	2.523*	0.223*
Selasphorus platycercus			7	3.029	0.355
	Juvenile	Male	5	3.020	0.356
	Adult	Female	1	3.400	
	Adult	Male	380*	3.150*	0.220*
Selasphorus rufus			29	3.128	0.171
	Juvenile	Female	17	3.135	0.193
	Juvenile	Male	9	3.111	0.154
	Adult	Female	3	3.133	0.115
	Adult	Male	1035*	3.131*	0.363*
Tilmatura dupontii			5*	2.250*	0.089*
		Female	4*	2.100*	0.010*

Appendix S3: Plants visited by hummingbirds in Las Joyas Scientific Station, Mexico. SV: Secondary vegetation; CF: Cloud forest; PF: Pine Forest. H: hummingbirds, B: non-hummingbird birds, I: Insects.

Family	Species	Vegetation type	Floral Visitors
Asteraceae	*Cirsium jaliscoense* G.L.Nesom	SV	H-B-I
	Vernonia sp. Schreb.	SV	H-I
Campanulaceae	*Lobelia laxiflora* Kunth	SV	H-B-I
Convolvulaceae	*Ipomoea hederifolia* L.	PF	H-I
	Ipomoea orizabensis (G. Pelletan) Ledeb. ex Steud.	SV	H-B-I
Gesneriaceae	*Moussonia deppeana* (Schltdl. & Cham.) Hanst.	CF	H-I
Lamiaceae	*Salvia albo-caerulea* Linden	CF	H-B-I
	Salvia iodantha Fernald	PF-SV	H-B-I
	Salvia mexicana L.	CF-SV	H-B-I
Onagraceae	*Fuchsia encliandra* Steud.	PF-SV	H-I
Orobanchaceae	*Castilleja arvensis* Schltdl. & Cham.	SV	H-I
	Lamourouxia multifida Kunth	PF-SV	H-I
Rosaceae	*Rubus adenotrichos* Schltdl.	SV	H-I
Scrophulariaceae	*Buddleja sessiliflora* Kunth.	SV	H-I

Appendix S4: Aggressive interaction matrix between hummingbird dominance groups habiting Las Joyas Scientific Station (Mexico). In parenthesis is indicated the total number of aggressive interactions recorded between these two species. *: Indicates that these species were not observed interacting. MS: Migratory status, RE: resident, LM: latitudinal migrant, AM: Altitudinal migrant. adu: adult, juv: juvenal. ♀: female, ♂: male. WIN: Number of total interactions won by this category.

		Loser																*WIN*
MS	Winner	*A. beryllina*	*A. violiceps*	*A. heloisa*	*C. thalassinus*	*E. fulgens*	*H. leucotis* ♀	*H. leucotis* ♂	*L. amethystinus* ♀	*L. amethystinus* ♂	*S. calliope*	*S. platycercus*	*S. rufus* ♀ adu	*S. rufus* ♀ juv	*S. rufus* ♂ adu	*S. rufus* ♂ juv	*T. dupontii*	
AM	*Amazilia beryllina*	140 (281)	1 (1)	6 (6)	4 (24)	5 (7)	35 (38)	66 (75)	2 (11)	22 (91)	2 (2)	22 (22)	20 (22)	5 (5)	1 (1)	13 (18)	21 (23)	365
AM	*Amazilia violiceps*	0 (1)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0
RE	*Atthis heloisa*	0 (6)	*	4 (8)	0 (1)	*	1 (2)	0 (1)	*	0 (5)	*	*	4 (9)	*	*	1 (3)	*	10
AM	*Colibri thalassinus*	20 (24)	*	1 (1)	4 (8)	6 (6)	3 (3)	5 (9)	2 (2)	2 (3)	1 (1)	3 (3)	7 (7)	*	*	4 (4)	*	58
RE	*Euegnes fulgens*	2 (7)	*	*	0 (6)	1 (2)	1 (1)	1(1)	1 (1)	3 (8)	*	1 (1)	*	*	*	*	*	10
RE	*Hylocharis leucotis* ♀	3 (38)	*	1 (2)	0 (3)	1 (1)	*	2 (11)	*	0 (49)	1 (1)	*	0 (1)	*	*	*	*	8
RE	*Hylocharis leucotis* ♂	9 (75)	*	1 (1)	4 (9)	1(1)	2 (11)	13 (26)	0 (2)	3 (100)	1 (1)	3 (3)	14 (27)	*	*	0 (2)	1 (1)	52
RE	*Lampornis amethystinus* ♀	9 (11)	*	*	0 (2)	1 (1)	*	2 (2)	*	*	*	*	*	*	*	*	*	12
RE	*Lampornis amethystinus*♂	69 (91)	*	5 (5)	1 (3)	3 (8)	0 (49)	97 (100)	*	41 (82)	*	3 (3)	*	*	*	*	9 (10)	228
LM	*Selasphorus calliope*	0 (2)	*	*	0 (1)	*	1 (1)	0 (1)	*	*	*	0 (1)	0 (4)	*	*	0 (5)	*	1
LM	*Sekasphorus platycercus*	0 (22)	*	*	0 (3)	1 (1)	*	0 (3)	*	0 (3)	1 (1)	2 (2)	0 (1)	*	*	0 (5)	*	4
LM	*Selasphorus rufus* ♀ adu	2 (22)	*	5 (9)	0 (7)	*	0 (1)	13 (27)	*	*	4 (4)	0 (1)	4 (8)	1 (1)	1 (1)	5 (6)	*	35
LM	*Selasphorus rufus* ♀ juv	0 (5)	*	*	*	*	*	*	*	*	*	*	0 (1)	*	*	1 (2)	*	1
LM	*Selasphorus rufus* ♂ adu	0 (1)	*	*	*	*	*	*	*	*	*	*	0 (1)	*	*	*	*	0
LM	*Selasphorus rufus* ♂ juv	5 (18)	*	2 (3)	0 (4)	*	*	2 (2)	*	*	5 (5)	0 (5)	1 (6)	1 (2)	*	*	*	16
AM	*T. dupontii*	2 (23)	*	*	*	*	*	0 (1)	*	1 (10)	*	*	*	*	*	*	*	3

Appendix S5: Interaction matrix between hummingbirds and plants at Las Joyas Scientific Station during winter. *: illegitimate visits. Number: number of floral patches sampled that included the species.

Family	Number	Species	*Amazilia beryllina*	*Amazilia violiceps*	*Atthis heloisa*	*Colibri thalassinus*	*Eugenes fulgens*	*Hylocharis leucotis* male	*Hylocharis leucotis* female	*Lampornis amethystinus* male	*Lampornis amethystinus* female	*Selasphorus calliope*	*Selasphorus platycercus*	*Selasphorus rufus* subdominant	*Selasphorus rufus* subordinate	*Tilmatura dupontii*
Asteraceae	24	*Cirsium jaliscoense*	49	1	0	3	45	0	7	8	0	2	7	12	0	0
	2	*Vernonia sp.*	2	0	11	0	0	1	1	0	0	0	0	4	1	0
Campanulaceae	37	*Lobelia laxiflora*	116	0	3	196	25	13	4	44	17	1	10	39	4*	0
Convolvulaceae	10	*Ipomoea hederifolia*	1	0	0	0	0	1	0	52	1	0	1	0	0	0
	11	*Ipomoea orizabensis*	2*	0	0	0	20	0	0	1	2	0	2*	0	0	0
Gesneriaceae	12	*Moussonia deppeana*	0	0	0	0	0	0	10	41	8	0	0	0	0	0
Lamiaceae	1	*Salvia albo-caerulea*	0	0	0	0	0	0	0	24	4	0	0	0	0	0
	47	*Salvia iodantha*	248	7	11	23	0	67	12	3	0	12	24	189	21	1
	55	*Salvia mexicana*	502	0	12	35	3	283	106	618	46	7	37	50	0	29
Onagraceae	19	*Fuchsia encliandra*	25	0	4	1	1	23	1	0	1	1	33	19	0	0
Orobanchaceae	6	*Castilleja arvensis*	0	0	0	0	0	1	0	0	0	2	1	10	0	0
	2	*Lamourouxia multifida*	0	0	0	0	0	6	0	0	0	0	0	0	0	0
Rosaceae	3	*Rubus adenotrichos*	6	0	1	0	0	4	0	0	0	0	0	0	0	0
Scrophulariaceae	1	*Buddleja sessiliflora*	0	0	2	0	0	0	0	0	0	0	0	0	0	0

CAPÍTULO 2

ARE HUMMINGBIRDS GENERALISTS OR SPECIALISTS? USING NETWORK ANALYSIS TO EXPLORE THE MECHANISMS INFLUENCING THEIR INTERACTION WITH NECTAR RESOURCES

Citation:

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RESEARCH ARTICLE

Are hummingbirds generalists or specialists? Using network analysis to explore the mechanisms influencing their interaction with nectar resources

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Abstract

Mutualistic interactions are powerful drivers of biodiversity on Earth that can be represented as complex interaction networks that vary in connection pattern and intensity. One of the most fascinating mutualisms is the interaction between hummingbirds and the plants they visit. We conducted an exhaustive search for articles, theses, reports, and personal communications with researchers (unpublished data) documenting hummingbird visits to flowers of nectar-rewarding plants. Based on information gathered from 4532 interactions between 292 hummingbird species and 1287 plant species, we built an interaction network between nine hummingbird clades and 100 plant families used by hummingbirds as nectar resources at a continental scale. We explored the network architecture, including phylogenetic, morphological, biogeographical, and distributional information. As expected, the network between hummingbirds and their nectar plants was heterogeneous and nested, but not modular. When we incorporated ecological and historical information in the network nodes, we found a generalization gradient in hummingbird morphology and interaction patterns. The hummingbird clades that most recently diversified in North America acted as generalist nodes and visited flowers with ornithophilous, intermediate and non-ornithophilous morphologies, connecting a high diversity of plant families. This pattern was favored by intermediate morphologies (bill, wing, and body size) and by the low niche conservatism in these clades compared to the oldest clades that diversified in South America. Our work is the first effort exploring the hummingbird-plant mutualistic network at a continental scale using hummingbird clades and plant families as nodes, offering an alternative approach to exploring the ecological and evolutionary factors that explain plant-animal interactions at a large scale.

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Introduction

Mutualisms, such as seed dispersal and pollination, are key factors explaining the distribution and persistence of biodiversity on Earth [1]. Notably, mutualisms create complex networks of interacting species whose relationships vary in type, strength, and duration [2, 3]. Interacting species impose reciprocal selective pressures on each other as they interact over ecological and evolutionary time. The properties of the resulting interaction networks can help to describe and explain current biodiversity patterns [3].

Hummingbirds (Aves: Trochilidae) are specialized nectarivorous birds that act as pollinators, transporting gametes among flowers [4]. The hummingbird diversity pattern shows a strong latitudinal gradient throughout the Americas [5, 6]. Hummingbirds colonized South America approximately 22 million years ago, yet their center of diversification, as revealed by molecular phylogenetics, is in the Neotropics [7, 8]. In particular, hummingbirds diversified into nine clades, some of which had a rapid rate of species diversification as a result of adaptation to new ecological niches and dispersion to new geographical areas [9]. Hummingbirds morphology and ecology (including relationships with flowers) reflect phylogeny, and hummingbird clades have characteristic morphologies that influence resource use, flight capabilities, competitive skills and environmental filtering, important mechanisms structuring hummingbird communities (Fig 1) [10, 11].

Theoretical predictions about the factors influencing the interaction between hummingbirds and the plants they use as nectar resources can be tested based on the biogeography of hummingbirds and plants as well as the ecology of hummingbird and plant interactions. The pollination system resulting from the co-evolution of hummingbirds and plants in the Western Hemisphere can be further described using network properties.

Examining 31 plant-hummingbird networks, Dalsgaard *et al.* [12] found that biotic specialization decreases with decreasing latitude and that hummingbird species richness, contemporary precipitation, and Quaternary climate-change velocity were key predictors of biotic specialization. Similarly, Martín-González *et al.* [13] investigated hummingbird-plant diversity patterns and found a significant association between network structure (complementary specialization and modularity) and species' phylogenetic signals at a macroecological scale, suggesting a close co-evolutionary association between hummingbirds and their nectar plants. Also, Vitória *et al.* [14] studied how species' evolutionary histories shaped the interaction network between hummingbirds and plants in the Atlantic Forest in Brazil and concluded that morphology and phenological matching among species were more important than evolutionary history in structuring the studied plant-hummingbird network.

The hemispheric scale of interactions between hummingbirds and their nectar plants also allow comparisons between niche conservatism versus niche evolution theories. The range of environmental conditions that are inhabitable by species, enabling them to maintain viable populations, comprises the fundamental niche [15]. Niche conservatism occurs when the colonization and dispersion of species are limited as a result of environmental changes affecting their ancestral niche. Conversely, niche evolution occurs when species disperse and colonize new habitats with environmental conditions differing from those of their ancestral fundamental niche [15]. Based on environmental conditions and species diversity patterns in 188 New World vertebrate families that originated in North and South America (including hummingbirds), Smith *et al.* [16] found that many families with a southern origin exhibited niche conservatism and had lineages restricted to Neotropical areas, whereas many families with a northern origin were distributed across Nearctic and Neotropical areas. These results suggest that northern lineages have contributed more to high tropical biodiversity than southern lineages have contributed to northern temperate biodiversity [16].

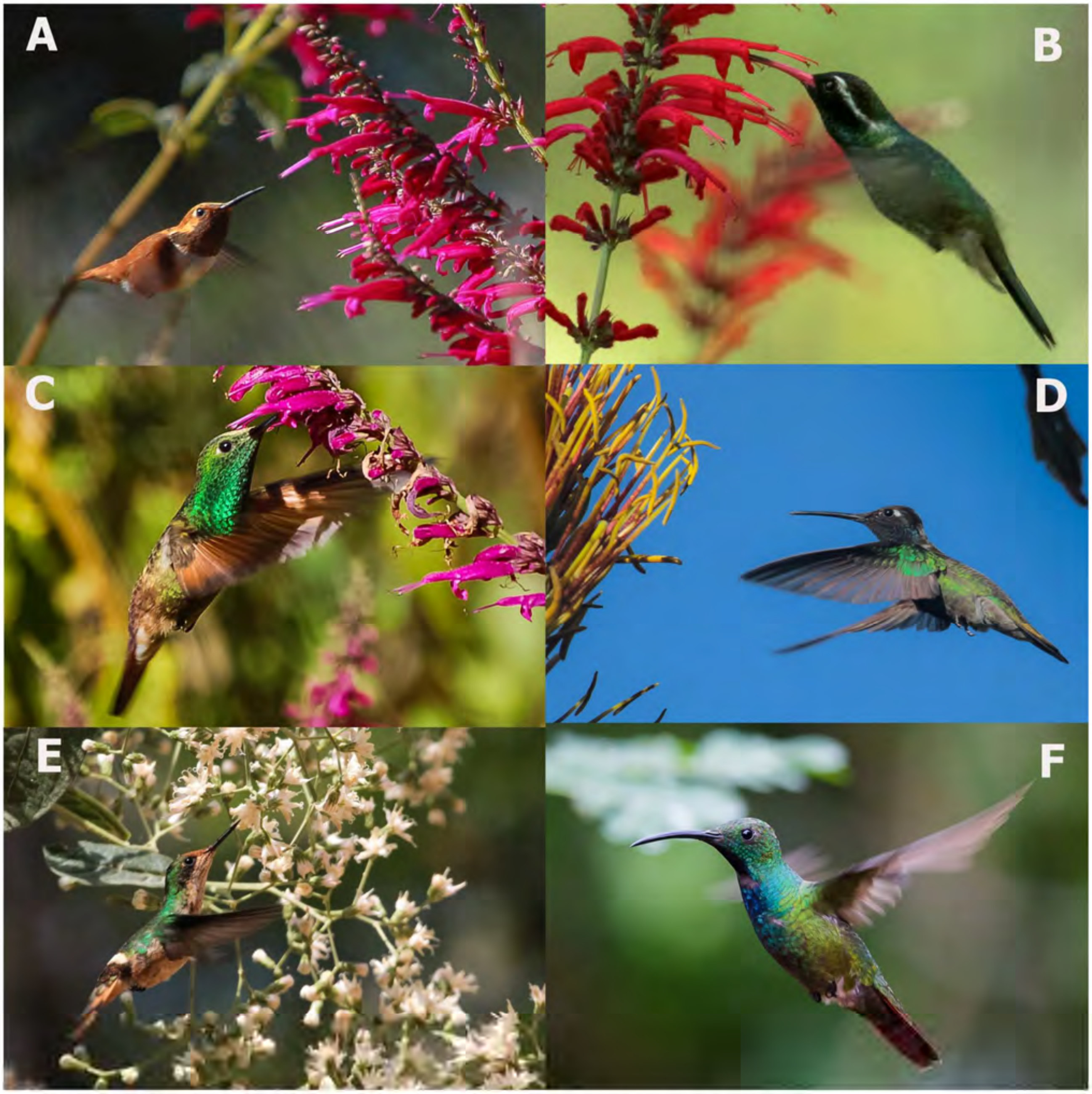

Fig 1. Photographs of hummingbirds and their nectar resources. *Salvia iodantha* (Lamiaceae) flowers are visited by long-distance seasonal migrant species including *Selasphorus rufus* (Bee clade, A), and resident hummingbirds *Hylocharis leucotis* (B) and *Amazilia beryllina* (C) of the Emerald clade at the temperate forests of the Sierra de Manantlán, Jalisco, Mexico. D. *Eugenes fulgens* (Mountain Gems clade), a large altitudinal migrant, visits flowers with different morphologies including those of Agave species (Asparagaceae). E. *Lophornis brachylophus* (Coquette clade) visits the flowers of many non-ornithophilous plant species as *Vernonatura cordata* (Asteraceae). This coquette is an endemic, range-restricted species and endangered by habitat destruction. F. *Anthracothorax prevostii* (Mangoes clade) is a widely distributed species in the lowlands with a curved bill that can be easily identified by its brilliant colors. Photographs by Carlos Soberanes-González.

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Accordingly, hummingbird diversity reflects both niche evolution and niche conservatism patterns. For example, hummingbird diversity in the Neotropics is the highest in moist cloud forests at middle elevations [7, 17], where many species and clades (i.e., Brilliants) have limited ranges [17], reflecting niche conservatism. Conversely, the evolutionary history of Bee Hummingbirds, the most northern, most recent hummingbird clade with the highest rate of net diversification [9, 18], suggests a release of niche conservatism constraints, resulting in niche evolution. Licona-Vera and Ornelas [18] explored the phylogenetic and biogeographical relationship among Bee Hummingbirds (Mellisugini) and their nectar plants to assess the evolution of long distance seasonal migration in this clade. Their results suggest that the historical range expansion of this clade is connected with the biogeography of their host plants and the colonization of new ecological niches. Along these same lines, Abrahamczyk & Renner [19] found that diversification within hummingbird-pollinated clades in temperate North America and South America regions was a gradual and continuous process due to habitat specialization and allopatric speciation in which independent plant species switched from insect to hummingbird pollination.

However, integrating the historical biogeography and ecology of hummingbird clades and their nectar resources remains largely unexplored at the hemispheric scale. [20]. Previous studies have examined mutualistic networks based on community and site records. We aimed to construct a mutualistic network between the nine hummingbird clades and their nectar plant families based on records of hummingbird visits to plants. Moreover, we aimed to combine phylogenetic, morphological, latitudinal, elevational, and biogeographical information in order to identify the ecological and evolutionary mechanisms driving the interaction and specialization between hummingbirds and plants used by hummingbirds as nectar resources. Some researchers have highlighted the need to understand the ecological, evolutionary, and historical mechanisms explaining the architecture of mutualistic networks and to compare these interactions at different scales [21, 22]. We opted to use hummingbird clades because the limits between these clades are clear in terms of phylogeny, ecology, and evolution, although the placement of genus *Patagonia* is still controversial. Overall, each hummingbird clade has a unique evolutionary history that is reflected in their current distribution, morphology, and ecology [7, 9].

As the plant-hummingbird network is based on mutualistic interactions (i.e. interactions involving mutual benefits among partners [23] (Fig 1), we predicted that the presently analyzed network would behave like previously described mutualistic networks. In particular, (1) we expected the connectivity distribution to be highly heterogeneous because most hummingbird species visit few plant species, and few hummingbird species are more connected than expected by chance. Also, (2) we expected the network to be nested because hummingbird and plant specialist nodes typically interact with subsets of species that are mainly connected with generalist nodes. Finally, (3) we expected the network to be modular because some species subgroups tend to interact more strongly among themselves than with other species [1, 23–25].

To explore the connection pattern between hummingbirds and their nectar resources from an evolutionary and geographical perspective, we tested the following two hypotheses using phylogenetic, biogeographical, morphological, and distributional information. First, we posited that biogeographical evolution acting along with hummingbird clade diversification [9, 26] has affected species co-occurrences and, consequently, has influenced life-history traits of birds and plants [3, 19]. On the basis that a monophyletic ancestor of hummingbirds from tropical South America later colonized Andean South America (Brilliant and Coquette clades), the Caribbean, and North America (Mango, Bee, and Mountain Gem clades) [9], we hypothesized that there is a morphological trend toward generalization among recent colonizing lineages wherein morphologies tend to facilitate access to nectar from a higher diversity of flower resources [9, 19, 27]. Specifically, we expected that hummingbird species in generalist nodes would have small- to medium-sized (intermediate length) straight bills. With respect to plants, we expected that flowers visited by generalist hummingbirds would have more varied morphologies, from typically ornithophilous flowers to more entomophilous ones (*sensu* Faegri & Van der Pijl [28]). Secondly, taking into account that biogeographical patterns are the result of ecological and environmental processes that influence colonization and dispersion at different ecological and spatial scales [15], we expected that hummingbird clades with a center of diversification in North America (i.e., those with lower niche conservatism) would have wider elevational and latitudinal ranges than those that mainly diversified in South America [29, 30], thus favoring the colonization of South America by northern hummingbird lineages. Finally, we expected that northern lineages (Bee and Mountain Gem clades) would interact with more plant families.

In the present paper, we first describe the mutualistic network of the hummingbird clades and plant families used as nectar sources at a continental scale, and then explore the factors explaining the connection pattern from an ecological and evolutionary perspective. We found that the evolution of clades, hummingbird and plant morphology, biogeographical region, and the center of diversification were the factors that best explained the patterns in this network.

Materials and methods

Ethics statement

An ethics statement is not required for the present study. No specific permits were required for the described methodology. Researchers who shared unpublished data from local studies had the full knowledge that these data would be used to analyze the geographical patterns of mutualistic networks. Our field studies did not involve endangered or protected species, and hummingbird morphological measurements were mainly obtained by JFO from museum specimens (see Acknowledgments). No live animals were manipulated.

Hummingbird-plant interactions

Data collection. We compiled data for hummingbirds and their nectar plants conducting exhaustive searches in academic databases, search engines, and online university libraries using the following key words: "hummingbird," "Trochilidae," "flower," "visit," and "pollination." Additionally, we obtained information from the bird and specialized hummingbird literature, including unpublished theses, records, and personal communications from experts.

For hummingbirds, we followed the nomenclature of the South American Classification Committee (SACC) [31] and the American Ornithologists' Union (AOU) [32] and, for plants, we followed the nomenclature of TROPICOS [33] and the World Checklist of Selected Plant Families [34]. For plants, we determined the category of native vs. non-native using the distribution maps in TROPICOS [33] and JSTOR Plant Science [35].

Network matrix. Using the compiled information, we constructed a qualitative matrix with hummingbird species in the columns and plant species in the rows. In this binary matrix, 1 indicates an interaction between a hummingbird and a plant species, and 0 otherwise. We discarded the option of using a quantitative matrix because of the high variability in the methods used by the different sources (in terms of sampling effort, time lag, and area sampled, for example), which could affect the observed pattern and subsequent interpretations [36]. Also, in most cases, the authors did not provide an estimate of the number of interaction events. We constructed a second matrix using the same principles described above but excluding the plant species that were non-native to the New World. We conducted all network analyses with and without non-native plant species to minimize the potential confounding effects of non-native plant species on the evolutionary patterns detected in the network.

Because we were interested in mutualistic relationships at the global level, we grouped hummingbird species by clade or lineage according to McGuire *et al.* [7] and plant species by family. Mutualistic networks were graphed using the "plotweb" and "visweb" functions in the bipartite package [37] in R version 3.1.2 [38] in conjunction with pajek [39].

Hummingbird and plant phylogeny. To explore whether the architecture of the mutualistic network corresponded with the evolutionary history of the nodes, we built the phylogenies for the nodes included in the network and coupled these with the mutualistic network. This comparison allowed us to detect correspondences in an ecological and evolutionary context. Plant phylogeny was built at the family level using Phylomatic [40] and following Davies *et al.* [41], and hummingbird phylogeny was drawn using the ape package [42] in R version 3.1.2 [38] following the codes used by McGuire *et al.* [7] for hummingbird clade classification.

Network analysis

Connectivity distribution. Connectivity distribution is a measurement of network robustness or resiliency that describes how interactions are distributed across nodes [4]. Species phenology and morphological co-adaptations can operate as constraints that prevent or favor the occurrence of network interactions [4, 28, 29]. In mutualistic networks, the frequency distribution of the number of interactions per node is heterogeneous; in other words, the number of interactions across nodes varies more than expected by chance [23]. In these networks, a few nodes have a large number of connections (generalist nodes) in comparison to the bulk of the nodes, which have few connections (specialist nodes) [23]. Using matrices with and without non-native plant species, we calculated the cumulative frequency of the interactions between all species in the network. We tested whether the observed probability fit one of three different distributions: (1) exponential, (2) power-law, or (3) truncated power-law [30, 43–45]. Adjustment to a particular distribution provides information about the scale of a network and its resistance to node loss [23, 30]. Mutualistic networks adjusted to the power-law distribution have a scale-free degree distribution. These networks are robust in face of random node extinction but are fragile to extinctions at the most connected nodes [23]. We obtained the Akaike Information Criterion (AIC) for each fit and chose the fit with the lowest value as the best fit [44]. Statistical tests for the AIC and the distribution comparisons were performed using the "brainwaver" package [46] in R version 3.1.2 [38].

Nestedness. Nestedness is a property concerning the pattern of connections in a network given the identity of the nodes [23]. In a nested network, specialist nodes interact with certain species that form perfect subsets of species with which generalist nodes interact, offering robustness and tolerance to node loss [30, 47]. Node abundance, phenotypic complementarity, and phylogenetic history have been proposed as factors underlying a nested pattern and have important consequences for how co-evolution acts on mutualistic interactions [48–50]. We estimated matrix nestedness using a Nestedness metric based on Overlap and Decreasing Fill (NODF) [51]. Perfectly nested networks have high values of NODF, wherein 0 indicates a compartmentalized matrix and 100 a perfectly nested matrix [51]. The ANINHADO software [52], and the vegan [53] and Metacom [54] packages in R version 3.1.2 [38] were used to estimate the NODF values and to test whether the degree of nestedness departed statistically from the random expectation. The choice of the correct null models is crucial, and because all null models have pros and cons, the best strategy is to select a suite of null models that allows identifying the ecological factors that structure the network [23, 55]. We selected three null models that differ in the way they are constrained: Erdos-Renyi (ER), CE and fixed-fixed (FF) [1, 52, 55]. The ER model is the least constrained binary null model where the "1s" in the original matrix were randomly assigned; in other words, each cell in the interaction matrix had the same probability of being occupied. This null model is prone to Type I error detecting nestedness when a matrix is random [55]. In the CE model, the probability of having an interaction in the simulated matrix was estimated as the arithmetic mean of the connection probabilities of the focal plant and animal species [52]; in biological terms, this probability was proportional to the level of generalization of plants and animals in the original matrix [1, 52]. CE model offers and unbiased estimates of overall connectivity and had a low rate of Type I and II errors [23]. Finally, the FF model is the most constrained null model, and it constrains matrix size, marginal totals, and frequency. These constraints favor a more conservative model where the more elements of the original matrix are incorporated, decreases the occurrence of Type I error, but is prone to Type II error [56]. We generated 3000 random nets, or 1000 for each null model. Because we used a phylogenetic approach for network construction and data interpretation, we also calculated the NODF and generated 3000 random nets (1000 for the ER model, 1000 for the CE model, and 1000 for the FF model) using the non-ordered option in the ANINHADO software [52], and "bipartite" [57] and "metacom" [54] packages. We requested that the program uses the phylogenetic order provided by us to calculate nestedness (see Hummingbird and plant phylogeny section above). For each null model we estimated the arithmetic mean of the 1000 random networks and the standardized effect size (SES). SES was calculated as the difference between the observed values and the mean of the simulated values, divided by the standard deviation of the simulated values.

Modularity. Modularity describes the degree to which a network is organized in compartments or subsets of nodes that are highly connected and interact more frequently with each other, influencing network stability and persistence [24,58]. Phenological and morphological complementary are two mechanisms acting in a modular network that define the role of each node and that connect nodes within and/or between modules [58]. To explore whether the hummingbird-plant network was modular, we used an algorithm based on simulated annealing (SA) implemented in the NETCARTO program [59,60]. This algorithm was designed for unipartite networks, enabling us (1) to measure the degree to which the network was organized into clearly defined modules by calculating an index of modularity (M) for each network, (2) to identify the number of modules within the network and the number of nodes belonging to each module, and (3) to assign a role to each node according to its topological properties [58, 61–63].

For the hummingbird-plant network, we examined whether the obtained modularity index was significantly more modular than the modularity index calculated for 200 random networks (100 for ER model and 100 for FF model; [63]). Additionally, for ER and FF null models we estimated the arithmetic mean and SES as described above. Because the results of the SA algorithm may vary in different runs, we ran the modularity analysis 50 times and calculated the mean and standard deviation. Species were included in a particular module if they were assigned to the module in > 90% of the runs [64].

We characterized each node in the network based on its topological properties. Specifically, each node was characterized by comparing its position with that of other nodes in its own module, z (standardized within-module degree) and how well it connects to nodes in other modules using c (among-module connectivity), and its placement in the zc-parameter space [58]. Following Olesen *et al.* [58], we sorted all species into four roles using $z = 2.5$ and $c = 0.62$ as cutoff values. A *peripheral* node has few links inside its own module but rarely with other modules ($z \leq 2.5$ and $c \leq 0.62$). A *connector* node links different modules ($z \leq 2.5$ and $c \geq 0.62$). A *module hub* maintains the coherence of its own module ($z \geq 2.5$ and $c \leq 0.62$). And, a *network hub* is a "supergeneralist" node that maintains the coherence of both the network and its own module ($z \geq 2.5$ and $c \geq 0.62$). Furthermore, we tested the suitability of these cutoffs exploring if the location of each node in the zc-space agreed with the theoretical role in the network, and analyzing the behavior of z and c values when the number of internal and external links in the modules changed [58]. We are aware about the limitations of modularity estimates in qualitative networks, and the recent advances in the establishment of efficient algorithms to identify modules in quantitative bipartite networks using null models [37]. However, the algorithm used here performed adequately identifying modularity as those with similar algorithms for binary qualitative matrices [63].

Morphological information

To explore the relationship between morphology and network architecture (in terms of connectivity, nestedness, and modularity), we examined morphological information for the flowers and hummingbirds included in our network. For plants, we used the classical pollination syndromes with modifications [65]. We detected three main morphological groups in the flowers visited by hummingbirds and combined some of the traits used by Faegri & van der Pijl [65], Proctor & Yeo [28], Rocca & Sazima [66], Thomson *et al.* [67], and Wilson *et al.* [68] to describe these groups. More specifically, we classified each species, genus, and family as ornithophilous, intermediate, or non-ornithophilous and then established the most common characteristics of these morphologies (see Table 1 for flower characteristics). This classification was exclusively made for the plant records included in this study. Ollerton *et al.* [69] expressed caution over the use of pollination syndromes because they may inadequately describe the diversity of floral phenotypes or predict the most common pollinators. We are aware of these limitations, but for the hummingbird-plant matrices, we are not interested in making inferences about the pollinators but rather in having a conceptual framework for characterizing the morphological traits of the flowers that hummingbirds visit.

For hummingbirds, we used information previously collected by Núñez-Rosas *et al.* [70], J. Hernández (pers. comm.), JFO, and Schuchmann [4] to calculate the mean and standard deviation of the body weight, wing chord, and bill length (exposed culmen) of 292 hummingbird species (around 89% of all extant species). We further classified these species by bill curvature: recurved, straight, curved, or strongly curved. We used these trait categories because they provide information about the size of hummingbirds and traits are associated with their access to and use of nectar resources [71, 72].

Table 1. Floral morphology classification.

Ornithophilous flower*	Intermediate flower**	Non-ornithophilous flower***
Diurnal anthesis.	Diurnal and/or nocturnal anthesis.	Diurnal and/or nocturnal anthesis.
Corolla with vivid colors, often scarlet, red, or orange (very rarely purple). If corolla has non-vivid colors (yellow or white), it strongly contrasts with the calyx and/or floral bracts.	Corolla yellow, white, blue-violet, or purple (very rarely red or orange), but with contrasting patterns.	Generally non-vivid colors (principally yellow and white), rarely purple or orange corollas, but without strong contrast.
Lip or margin absent (if present, curved backwards), flower hanging with inclined orientation, zygomorphy frequent, less pronounced landing platform.	Margin generally very expanded, pronounced landing platform. Actinomorphy and zygomorphy may be present. Flowers have different orientations.	Actinomorphic flowers, principally oriented upwards. If margin or lip present, it forms a landing platform.
Pedicel may be elongated, and pedicel and inflorescence axis may be delicate.	Pedicel and inflorescence axis robust or delicate.	Pedicel short. Pedicel and inflorescence axis robust.
Exerted anthers and stigma. Pollen load deposited with precision on the pollinator.	Pollen load deposited with precision on pollinators but more dispersed compared with ornithophilous morphologies.	Exposed reproductive organs. Pollen load deposited more dispersedly on pollinators.
Mainly tubular and bilabiate flowers. Deep tube or spur, wider than intermediate flowers (wide enough to allow the hummingbirds' beak to effectively enter the corolla tube).	Urceolate, funnelform, and salverform flowers.	Principally rotate- and brush-shaped flowers. If campanulate, generally shallow.

*Flowers pollinated by hummingbirds described by Faegri & van der Pijl [65], Proctor & Yeo [28], Thomson *et al.* [67], and Wilson *et al.* [68] with modifications.

** Flowers pollinated by moths, butterflies, and bats described by Faegri & van der Pijl [65] and Proctor & Yeo [28] with modifications.

*** Flowers pollinated by perching birds and/or bees described by Rocca & Sazima [66] and Faegri & van der Pijl [65] with modifications.

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Biogeographical distribution and center of diversification

To assess the biogeographical distribution of hummingbird species, we calculated the latitudinal and elevational gradient for the hummingbird species included in the matrix and counted the number of biogeographical regions in each species' range.

To define whether each species was distributed in the Nearctic, Neotropical, and/or Austral region, we used the range maps from ebird [73] and del Hoyo *et al.* [74]. We estimated the total number of species in each clade and genus occurring in each of these regions. We defined the Nearctic, Neotropical, and Austral biogeographical regions according to the Sclater-Wallace system [16, 75] considering the modifications for bird genera proposed by Rueda *et al.* [75]. The Nearctic region extends from Alaska to the Trans-Mexican Volcanic Belt (around 19° to 20° N). The Neotropical region includes the tropical lowlands adjacent to the Mexican highlands and extends southwards, including the northern and central portions of South America. Finally, the Austral region comprises the southern Andes from Peru to the Patagonia (Fig 1C in Rueda *et al.* [75]).

For the latitudinal range, we used unpublished data from Ornelas [76]. We established the northernmost and southernmost range limits for each hummingbird species and calculated the mean latitudinal range for each genus and clade. To obtain distributional information for plants, we consulted distribution maps from TROPICOS [33], The Plant List [77], and the International Union for Conservation of Nature's Red List of Threatened Species [78].

For the elevational distribution, we defined the elevational range of each species as the difference between the minimum and maximum elevation where each species has been recorded, excluding all records referred as "possible" or "rarely". Then, we estimated the mean elevational range for each clade. We calculated these ranges for hummingbird species using information from Arizmendi *et al.* [79], Bleiweiss [80], Ornelas [76], and Schuchmann [4].

We assigned the center of diversification to each hummingbird species based on published studies on molecular phylogenetics, species diversification, and ancestral biogeographical inferences for hummingbirds [7, 9, 81]. The two geographical areas were North America (from Alaska to the Isthmus of Panama) and South America following Smith *et al.* [16].

We only considered mainland species, excluding hummingbird species from the Caribbean and other oceanic islands, because hummingbirds are principally a mainland avian group with less than 5% of species inhabiting islands. Besides, phylogenetic relationships between hummingbird insular species, specially the relationships between migrant and resident species, are still controversial making the inference about the center of diversification difficult [9, 18]. Finally, the complexity and uniqueness of the Caribbean region in terms of geological history, climate, and biogeography [82], makes this region difficult to classify in terms of biogeographical regions, being included interchangeably in the Neotropical or Nearctic region depending on the classification and focal study group [75].

Hummingbird niche conservatism analysis

To test whether niche conservatism in hummingbirds was related with the center of diversification and/or clade identity, we fitted Generalized Linear Models (GLM) with binomial distribution to logit link and probit link functions, respectively [83]. We defined species distributed in two or three of the biogeographical regions (see above) as a success (corresponding with a value of 1 for the binomial response variable) and species distributed in only one of these as a failure (corresponding with a value of 0 for the binomial response variable). The independent variables were center of diversification (categorical variable with two levels) and clade (categorical variable with 8 levels). In these models, we excluded the Patagona clade because it has only one species (*Patagona gigas*).

We tested for overdispersion using the protocol proposed by Zuur, Ieno, and Elphick [84]. All analyses were performed in R software version 3.3.0 [85]. The model selection process was performed using the "base" (R Development Core Team, 2014) and "car" packages [86]. Post-hoc multiple comparison tests of the different fitted models were carried out using the general linear hypothesis function (glht) in the "multcomp" package [87]. We used the Bonferroni correction for multiple testing and an alpha of 0.05 or less to determine significance. Plots were made using the "ggplot2" package [88].

Results

Hummingbird-plant interactions

We compiled records on hummingbird-plant interactions from 124 reports (see S1 Table) and four personal communications, analyzing up to 4532 interactions between 292 hummingbird species and 1287 plant species.

The binary network included species records from all the nine hummingbird clades (*sensu* McGuire *et al.* [9, 29]) and from 105 native and non-native plant families (S2 Table). The hummingbird clades and plant families were connected by 409 links. The hummingbird genera with the most species in the matrix were *Amazilia* (27 species), *Phaethornis* (17), *Chlorostilbon* (14), *Coeligena* (9), *Lophornis* (9), *Campylopterus* (8), *Eriocnemis* (7), *Hylocharis* (7), *Anthracothorax* (7), and *Metallura* (7) (Table 2). The plant families with most species used by hummingbirds were Fabaceae (121 species), Bromeliaceae (81), Rubiaceae (70), Lamiaceae (69), Gesneriaceae (54), Ericaceae (51), Acanthaceae (51), Asteraceae (45), Malvaceae (37), and Bignoniaceae (35) (S1 Table).

The binary matrix with only native plant species also included all the nine hummingbird clades, which interacted with 100 plant families through 385 links (Fig 2, S1 Fig). Plant families such as Myrtaceae, Rutaceae, and Strelitziaceae had fewer connections in this matrix, and families such as Musaceae, Oleaceae, Pittosporaceae, Vitaceae, and Xanthorrhoeaceae were excluded. All species in these families were classified in the network as "exotic."

We identified a core composed of generalist nodes including the Bee and Emerald hummingbird clades and the Asteraceae, Bromeliaceae, Gesneriaceae, Campanulaceae, Rubiaceae, Lamiaceae, Ericaceae, Marcgraviaceae, Solanaceae, Malvaceae, Fabaceae, Loranthaceae, and Heliconiaceae plant families (Fig 2, S1 Fig). When the network nodes were ordered phylogenetically (Fig 3), the nodes of the more recent hummingbird lineages (Emeralds and Bees; [9]) were generalist and linked with a greater diversity of plant families from across the plant phylogeny. The nodes of the Hermit, Topaz, and Patagona clades were strongly connected to both basal (Heliconiaceae, Bromeliaceae, Costaceae, Musaceae) and more recent plant families (Asteraceae, Campanulaceae, Gesneriaceae, Lamiaceae, Verbenaceae, Bignoniaceae, Acanthaceae) (Fig 3).

Network analysis

Regarding connectivity distribution, the network of hummingbird clades and plant families was highly heterogeneous. The network had a few highly connected nodes (generalist), but the bulk of the nodes had few links (specialist). Considering only native plant species, 13 out of the 100 plant families were connected with representatives from all the nine hummingbird clades, and only three hummingbird clades were connected with more than 50 plant families. Additionally, the power-law distribution (AIC = 565.342) fit the observed probability distribution better than the exponential (AIC = 658.581) or truncated power-law (AIC = 656.354) distributions. The same heterogeneity was observed in the matrix including both native and non-native plant species (S2 Fig, S1 Appendix).

Table 2. Hummingbird clades, genera, and species included in the present study. For each of the nine clades (Clade) included in the network, we show the corresponding genera (Genus) and number of species (Species) per genus.

Clade*	Genus	Species	Clade*	Genus	Species
Bees	*Archilochus*	2	**Emeralds**	*Abeillia*	1
	Atthis	2		*Amazilia*	27
	Calliphlox	4		*Aphantochroa*	1
	Calothorax	2		*Campylopterus*	8
	Calypte	2		*Chalybura*	2
	Chaetocercus	6		*Chlorestes*	1
	Doricha	1		*Chlorostilbon*	14
	Eulidia	1		*Chrysuronia*	1
	Mellisuga	2		*Cyanophaia*	1
	Myrmia	1		*Cynanthus*	2
	Myrtis	1		*Damophila*	1
	Rhodopis	1		*Elvira*	2
	Selasphorus	6		*Eupetomena*	1
	Thaumastura	1		*Eupherusa*	4
	Tilmatura	1		*Goethalsia*	1
Brilliants	*Aglaeactis*	4		*Goldmania*	1
	Boissonnneaua	2		*Hylocharis*	7
	Clytolaema	1		*Klais*	1
	Coeligena	9		*Lepidopyga*	2
	Ensifera	1		*Leucippus*	4
	Eriocnemis	7		*Leucochloris*	1
	Haplophaedia	2		*Microchera*	1
	Heliodoxa	5		*Orthorhyncus*	1
	Lafresnaya	1		*Phaeochroa*	1
	Loddigesia	1		*Stephanoxis*	1
	Ocreatus	1		*Taphrospilus*	1
	Pterophanes	1		*Thalurania*	6
	Urochroa	1		*Trochilus*	2
	Urosticte	2	**Mountain Gems**	*Eugenes*	1
Coquettes	*Adelomyia*	1		*Heliomaster*	4
	Aglaiocercus	3		*Hylonympha*	1
	Chalcostigma	5		*Lampornis*	6
	Discosura	4		*Lamprolaima*	1
	Heliangelus	5		*Panterpe*	1
	Lesbia	2		*Sternoclyta*	1
	Lophornis	9	**Mangoes**	*Androdon*	1
	Metallura	7		*Anthracothorax*	7
	Opisthoprora	1		*Augastes*	2
	Oreonympha	1		*Avocettula*	1
	Oreotrochilus	5		*Chrysolampis*	1
	Oxypogon	1		*Colibri*	4
	Phlogophilus	2		*Doryfera*	2
	Polyonymus	1		*Eulampis*	2
	Ramphomicron	2		*Heliactin*	1
	Sappho	1		*Heliothryx*	2
	Sephanoides	2		*Polytmus*	3
	Taphrolesbia	1		*Schistes*	1

(*Continued*)

Table 2. (Continued)

Clade*	Genus	Species	Clade*	Genus	Species
Hermits	*Anopetia*	1			
	Eutoxeres	2	**Patagona**	*Patagona*	1
	Glaucis	2			
	Phaethornis	17	**Topazes**	*Florisuga*	2
	Ramphodon	1		*Topaza*	1
	Threnetes	3			

* Based on McGuire *et al.* [9, 29].

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When we ordered the nodes based on the connection number, considering only native plant species, the network was highly nested (NODF = 70.680), and hummingbirds and plants showed high NODF values (NODF hummingbirds = 81.050, NODF plants = 70.600) (Fig 2). Compared with the null models, the matrix was statistically different from the ER and CE models (NODF model ER = 43.950, $P < 0.001$, SES model ER = 14.372; NODF model CE = 51.890, $P < 0.001$, SES model CE = 9.443), but not from the FF model (NODF model FF = 69.700, $P = 0.935$, SES model FF = 2.387).

However, when we included phylogeny in the network construction, the nestedness of the network containing only native plants dropped dramatically (NODF = 43.270, NODF hummingbirds = 63.970, NODF plants = 43.120; Fig 3). The network was statistically different from randomly selected networks when using the ER and CC models (NODF model ER = 22.140, $P < 0.001$, SES model ER = 9.763; NODF model CE = 29.510, $P < 0.001$, SES model CE = 6.819) but not the FF model (NODF model FF = 40.829, $P = 0.835$, SES model FF = 5.499). The nestedness value of the matrix including both native and non-native plant species was similar to those described above (S1 Appendix).

The network was not significantly modular (M = 0.189 ± 0.004; M model ER = 0.204, $P = 0.97$, SES model ER = −3.085; M model FF = 0.214, $P = 0.957$, SES model FF = −5.028). Similarly, the network including both native and non-native plant species was not significantly modular (S1 Appendix). Most links were observed between species from different modules (73.4%), and the mean connectance among modules was high (42.9%). Although the networks were not modular, the analysis with only native plant species identified four (63%) to five (37%) modules. In these modules, the hummingbird clades were associated with several plant families in more than 90% of the repetitions, indicating shared preferences for plants (S3 Table). With the exception of Topazes, all hummingbird clades were frequently associated with plant families whose floral morphology was principally intermediate or non-ornithophilous (S3 Table). No hummingbird clade was associated with another hummingbird clade in more than 90% of the modularity repetitions. Specifically, Bees and Mountain Gems were in the same module in 78% of the repetitions, Brilliants and Coquettes in 70% of the repetitions, Hermits and Mangoes in 56% of the repetitions, and Hermits and Topazes in 42% of the repetitions. The Patagona clade had a variable position in the modules. In contrast, Emeralds were associated with plant nodes but not with any other hummingbird nodes in 76% of the repetitions. Based on the within-module degree z (i.e., the standardized number of links to other species in the same module) and the among-module connectivity c (i.e., the extent to which species in one module were linked to other modules), the plant and hummingbird nodes played different roles (Fig 4). Plant families acted as *peripheral* or *connector* nodes but were not *module hubs*. All hummingbird clades, except Topazes and Patagona, were "supergeneralist" nodes (*network hubs*), maintaining the cohesion of the network (green dots Fig 4).

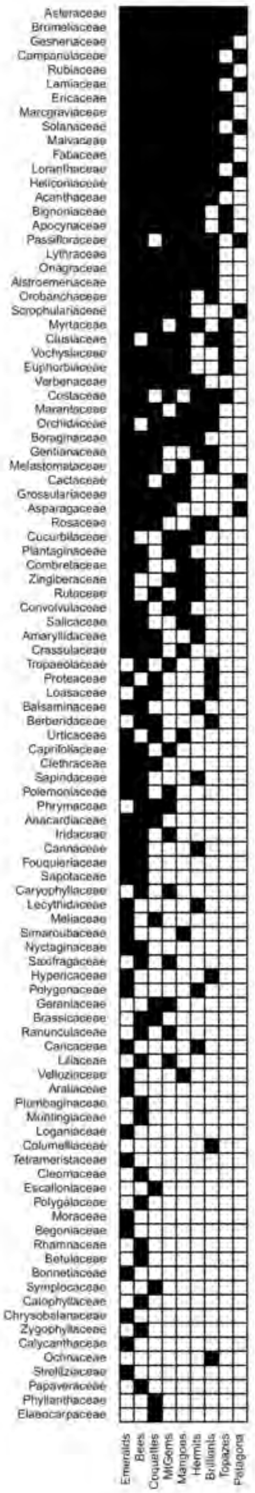
Asteraceae
Bromeliaceae
Gesneriaceae
Campanulaceae
Rubiaceae
Lamiaceae
Ericaceae
Marcgraviaceae
Solanaceae
Malvaceae
Fabaceae
Loranthaceae
Heliconiaceae
Acanthaceae
Bignoniaceae
Apocynaceae
Passifloraceae
Lythraceae
Onagraceae
Alstroemeriaceae
Orobanchaceae
Scrophulariaceae
Myrtaceae
Clusiaceae
Vochysiaceae
Euphorbiaceae
Verbenaceae
Costaceae
Marantaceae
Orchidaceae
Boraginaceae
Gentianaceae
Melastomataceae
Cactaceae
Grossulariaceae
Asparagaceae
Rosaceae
Cucurbitaceae
Plantaginaceae
Combretaceae
Zingiberaceae
Rutaceae
Convolvulaceae
Salicaceae
Amaryllidaceae
Crassulaceae
Tropaeolaceae
Proteaceae
Loasaceae
Balsaminaceae
Berberidaceae
Urticaceae
Caprifoliaceae
Clethraceae
Sapindaceae
Polemoniaceae
Phrymaceae
Anacardiaceae
Iridaceae
Cannaceae
Fouquieriaceae
Sapotaceae
Caryophyllaceae
Lecythidaceae
Meliaceae
Simaroubaceae
Nyctaginaceae
Saxifragaceae
Hypericaceae
Polygonaceae
Geraniaceae
Brassicaceae
Ranunculaceae
Caricaceae
Liliaceae
Velloziaceae
Araliaceae
Plumbaginaceae
Muntingiaceae
Loganiaceae
Columelliaceae
Tetrameristaceae
Cleomaceae
Escalloniaceae
Polygalaceae
Moraceae
Begoniaceae
Rhamnaceae
Betulaceae
Bonnetiaceae
Symplocaceae
Calophyllaceae
Chrysobalanaceae
Zygophyllaceae
Calycanthaceae
Ochnaceae
Strelitziaceae
Papaveraceae
Phyllanthaceae
Elaeocarpaceae
Emeralds
Bees
Coquettes
MtGems
Mangoes
Hermits
Brilliants
Topazes
Patagona

Fig 2. Matrix representation of the interaction network between hummingbirds and their nectar plants. Hummingbird clades are in columns and plant families in rows, and non-native plant species were excluded. Nodes were ordered by number of links exemplifying nestedness pattern, with most pairwise interactions located at the top left corner of the matrix.

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Morphological information

Using floral morphology (Table 1), we found that 50% of the 100 plant families did not have ornithophilous flowers, whereas 36% had intermediate flower morphology and 14% had flowers corresponding with the ornithophilous pollination syndrome (S1 Table). Hummingbirds intensively visited flowers of all morphologies (top right, S1 Fig, Fig 3), but plant families with

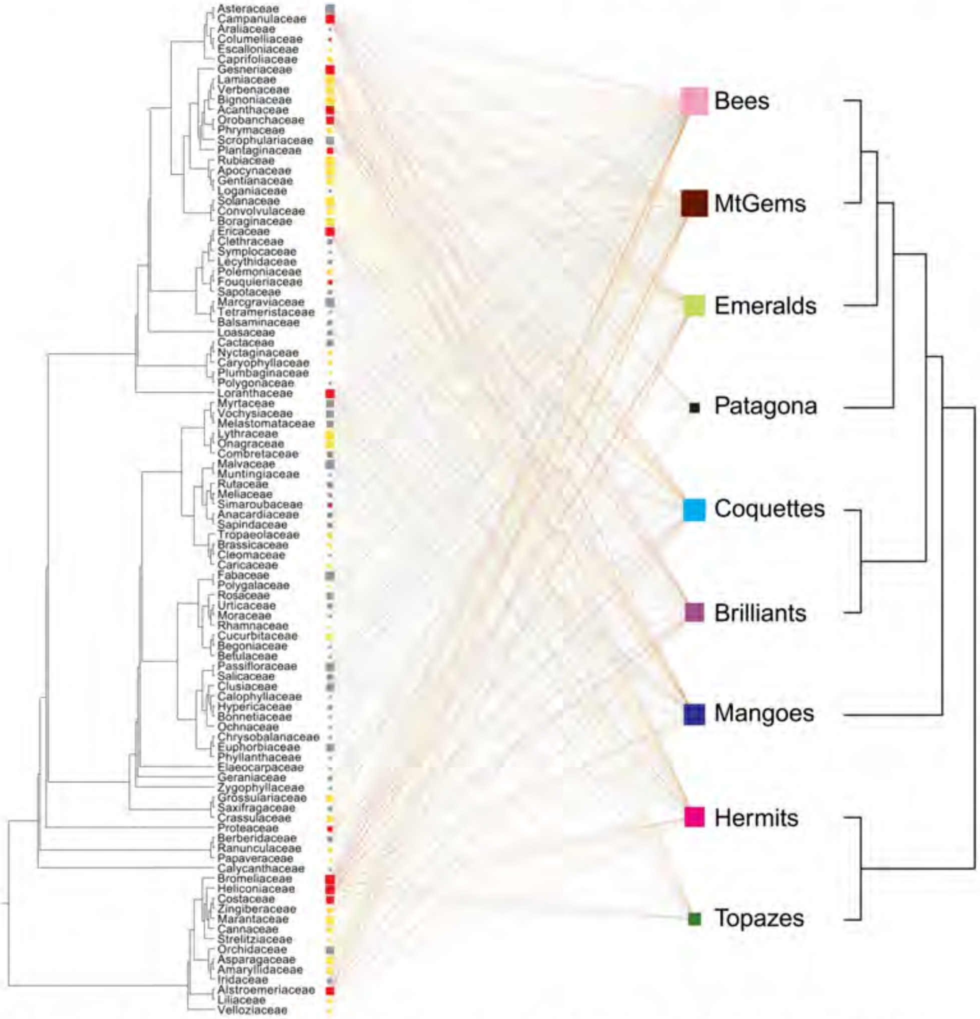

Fig 3. Network of hummingbirds and their nectar plants with nodes ordered phylogenetically. Ecological network of hummingbird clades (right) and plant families (left) (non-native plant species were excluded). Nodes were ordered phylogenetically, and their size was proportional to the number of species with which they interact. The lines represent the recorded 385 interactions. Plants were classified by floral morphology as ornithophilous (red), intermediate (yellow), or non-ornithophilous (gray) (Table 1).

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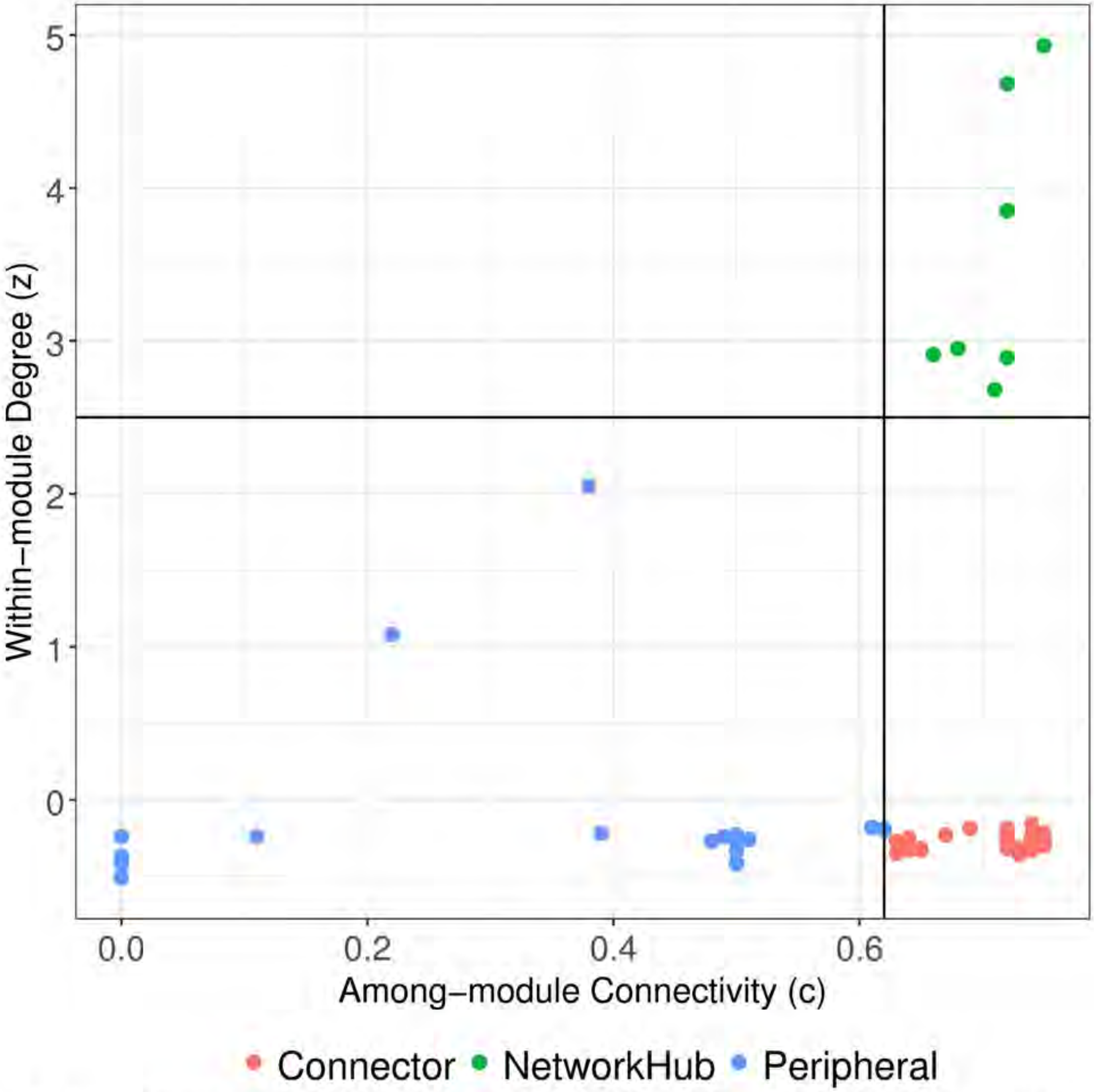

Fig 4. Plot classifying the ecological roles of hummingbirds and their floral nectar resources in a mutualistic network. The standardized within-module degree (*z*) measures how well connected a node is to other nodes in the same module (y-axis). The among-module connectivity (*c*) measures how each node is positioned with respect to all modules (x-axis). The values of 2.5 for *z* (horizontal line) and of 0.62 for *c* (vertical line) are cutoffs to defined node roles following Olesen *et al.*[58]. Peripheral node ($z \leq 2.5$, $c \leq 0.62$), connector node ($z \leq 2.5$ and $c \geq 0.62$), module hub ($z \geq 2.5$ and $c \leq 0.62$), and network hub ($z \geq 2.5$ and $c \geq 0.62$).

https://doi.org/10.1371/journal.pone.0211855.g004

ornithophilous pollination syndrome were generalist nodes and were intensively visited by representatives of all hummingbird clades (red squares in the top right of S1 Fig). These latter plant families were principally located at the extremes of the plant phylogeny (red squares in Fig 3).

Table 3. Hummingbird morphology at the clade level. For each morphological character, the number of records (n), mean, and standard deviation (mean ± s.d.) are shown. Clades are ordered phylogenetically.

	Exposed culmen (mm)		Wing chord (mm)		Weight (g)		Curvature[*]	
Clade	**n**	**Mean ± s.d.**	**n**	**Mean ± s.d.**	**n**	**Mean ± s.d.**	**n**	**Mean ± s.d.**
Bees	495	17.209 ± 2.192	487	42.620 ± 3.935	1715	2.874 ± 0.569	33	2 ± 0.485
Mountain Gems	301	25.021 ± 5.321	301	67.187± 5.453	315	6.408± 1.187	15	2 ± 0.488
Emeralds	3298	19.490 ± 2.596	2850	54.239 ± 6.069	1820	4.319 ± 1.390	96	2 ± 0.352
Patagona	1	40.7	1	126	3	20.567 ± 2.272	1	2 ± 0
Coquettes	440	14.787 ± 2.677	443	55.981 ± 11.017	206	4.949 ± 1.826	57	2 ± 0.350
Brilliants	426	27.174 ± 6.133	417	70.790 ± 6.502	211	7.009 ± 1.864	42	2 ± 0.407
Mangoes	429	25.809 ± 7.228	418	60.073 ± 6.543	258	5.654 ± 1.663	53	2 ± 0.644
Hermits	942	32.011 ± 6.334	840	55.939 ± 8.986	398	5.240 ± 1.934	183	4 ± 0.772
Topazes	27	11.305 ± 8.096	10	75.440 ± 3.790	19	9.287 ± 2.780	7	3 ± 0

[*] Curvature: 2, straight; 3, curved; 4, strongly curved.

https://doi.org/10.1371/journal.pone.0211855.t003

The analysis of hummingbird morphology at the clade level (Table 3) showed that the species in the Emerald and Bee clades, which corresponded with the most recent (Fig 1) and most generalist clades (Fig 2), respectively, had on average short-to-intermediate bills (17–25 mm), short wings (42–54 mm), small body sizes (2.9–4.3 g), and straight bills. In contrast, the species belonging to the oldest clades, Topazes and Hermits, had curved and long and strongly curved beaks, respectively (Table 1).

Biogeographical distribution and center of diversification

Two hundred and seventy (92.5%) of the hummingbird species included in our data set were distributed in the Neotropical region (Fig 5, Table 4, S4 Table), while 13.0% of the hummingbird species (38 species) were distributed exclusively in the Nearctic (3 species) or in the Nearctic and Neotropical regions (35 species). Of these, 20 species are latitudinal migrants, and the remaining species are elevational migrants or sedentary species. Similarly, 9.3% of the hummingbird species in our data set (27 species) were completely (4 species) or partially (23 species) distributed in the Austral region, but only three of these (*Oreotrochilus leucopleurus*, *Patagona gigas*, and *Sephanoides sephanoides*) have latitudinal migrations in South America (S4 Table).

In general, the hummingbird clades had large latitudinal ranges, but clades with North America as their center of diversification showed smaller mean latitudinal ranges than their southern counterparts (Table 4). All of the clades are mainly distributed in the Neotropical biogeographical region, but a significant proportion of the species belonging to the three most recent hummingbird clades are distributed in the Nearctic region (Emeralds, Bees, and Mountain Gems; Fig 5A, Table 4). Some species in these latter three clades reach the northernmost latitude (60° N), while their minimum latitudinal range is around 0° N. Specifically, *Selasphorus rufus* and *Archilochus colubris* (Bee clade) reach 60° N during the breeding season (Fig 5A, S4 Table). In South America, only two species (*Sappho sparganura* and *Sephanoides sephanoides*) are located below the minimum latitudinal range of −39° S (−40° and −54° S, respectively; S4 Table); of these latter two species, only *S. sephanoides* migrates latitudinally. In contrast, the Brilliant clade has a restricted distribution evidenced by its low mean latitudinal range and standard deviation (Table 4). The oldest clades (Mangoes, Hermits, and Topazes) mainly have a Neotropical distribution and are widely distributed in South America (Fig 5A, Table 4).

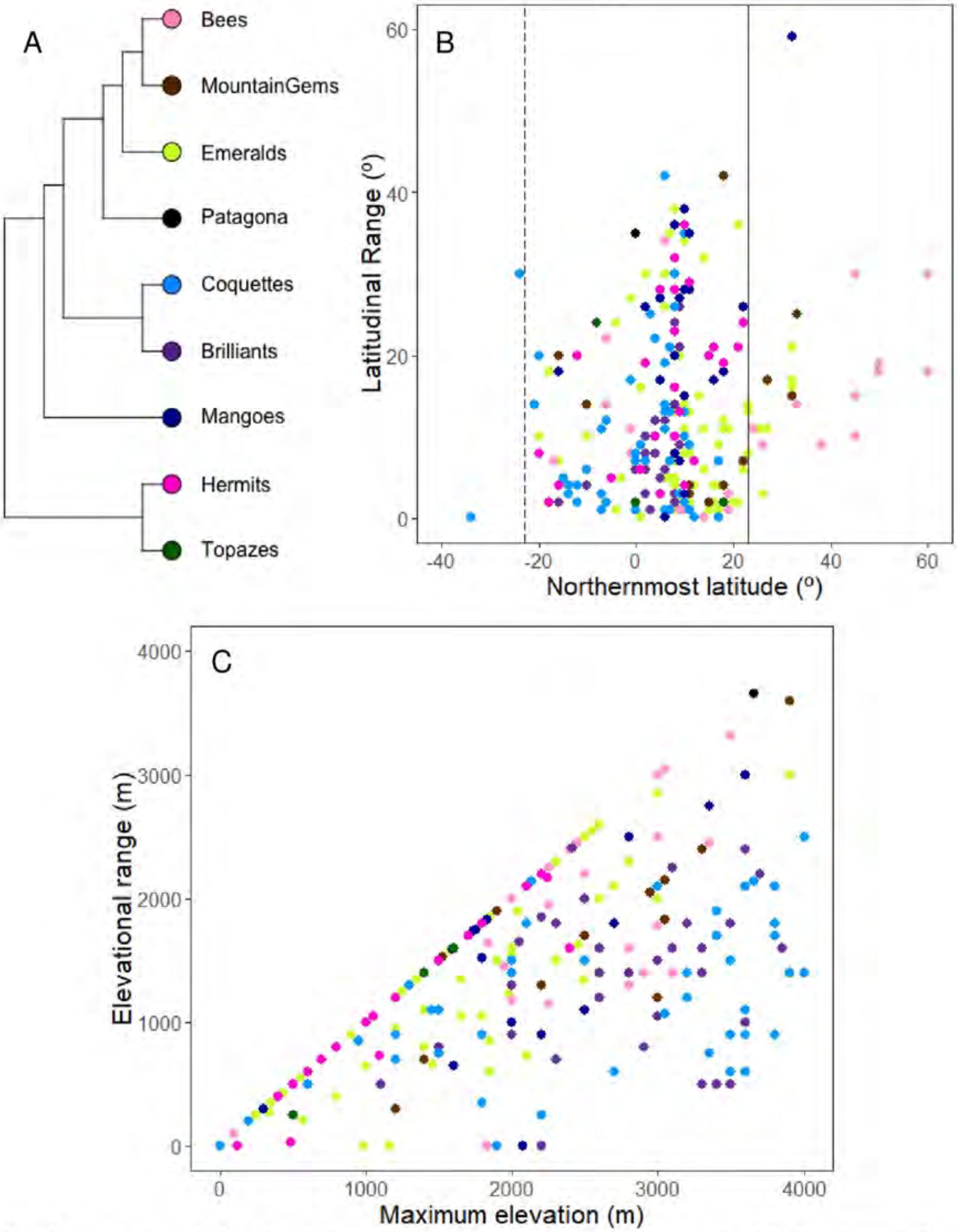

Fig 5. Hummingbird latitudinal and elevational ranges. (A) Phylogenetic tree representing the hummingbird clades. The colors next to the clades match the colors in the plots, identifying the clade to which each species belongs. (B) Latitudinal range of hummingbird species (dots); the x-axis shows the northernmost latitude and the y-axis the mean latitudinal range. The vertical lines cross at the approximate latitude of the Tropic of Cancer (23° N, continuous line) and Tropic of Capricorn (23° S, dashed line) representing an approximate delimitation between the

Nearctic, Neotropical and Austral biogeographical regions. For further details about biogeographical regions see text. (C) Elevational range of hummingbird species; the x-axis represents the maximum elevation and the y-axis the elevational range.

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Regarding elevational range, Patagona has the largest range, followed by the Bee and Mountain Gem clades, while the Brilliant, Mango, Coquette, and Emerald clades have intermediate ranges (around 1300 meters above sea level) (Table 4). Hermit and Topazes were restricted to lower elevations, in contrast with Brilliants and Coquettes, which were principally related with Andean high elevations (above 1600 meters above sea level; Fig 5B, Table 4).

The analysis of niche conservatism in hummingbirds revealed that the center of diversification had a significant effect on the transition of hummingbird species from one biogeographical region to another (Chi = 46.114, d.f. = 1, $P < 0.001$). The probability that a hummingbird species would colonize a different biogeographical region was higher for hummingbirds with a center of diversification in North America compared to those with a center of diversification in South America (GLM odds ratio = 9.080, Chi = 43.679, d.f. = 1, $P < 0.001$, Fig 6). Additionally, clade had a significant effect on current hummingbird distribution (Chi = 21.887, d.f. = 7, $P = 0.003$). In general, clades that diversified in North America had a higher proportion of species currently distributed in two biogeographical regions. However, a small proportion of species belonging to clades that diversified in South America (Coquettes, Hermits, and Mangoes) had a North American origin, although few of these species successfully dispersed in the Neotropical region (Fig 6).

Additionally, the two clades with species that exclusively diversified in South America (Brilliants and Topazes) did not colonize the Nearctic biogeographical region (Fig 6). Species in the Bee clade differed significantly from those in the Brilliant, Hermit, and Mango clades and also had a higher probability of colonizing new biogeographical regions (GLM odds ratio = 3.186, Chi = 9.462, d.f. = 1, $P = 0.002$; GLM odds ratio = 4.552, Chi = 8.910, d.f. = 1, $P = 0.003$; GLM odds ratio = 2.324, Chi = 4.297, d.f. = 1, $P = 0.038$, respectively; Fig 6). The same pattern was found for species of the Emerald and Mountain Gem clades, which had a higher probability of colonizing two biogeographical regions compared to those of the Brilliant clade (GLM odds ratio = 1.927, Chi = 3.904, d.f. = 1, $P = 0.048$; GLM odds ratio = 3.186, Chi = 6.870, d.f. = 1, $P = 0.009$, respectively; Fig 6). Finally, species in the Hermit clade had a lower probability of colonizing new biogeographical regions compared to those in the Emerald clade (GLM odds ratio = 2.752, Chi = 4.537, d.f. = 1, $P = 0.033$, Fig 6).

Discussion

The network between hummingbird clades and plant families at the continental scale was nested and heterogeneous, as expected, and behaved similarly to other mutualistic networks (e.g., [13, 89]). By incorporating phylogenetic, morphological, ecological and biogeographical information, we found that low niche conservatism, low specialized morphologies and recent diversification were the determinant factors that differentiate a generalist hummingbird clade node from a specialist hummingbird clade node. We detected large-scale biogeographical patterns indicative of both niche conservatism and evolution that support the higher biodiversity found near the equator [4].

Hummingbird-plant interaction network

Mutualistic networks have been shown to display universal patterns in architectural properties such as connectivity, nestedness and modularity. These facts imply that the mechanisms behind the establishment of plant-animal interactions are likely independent of species composition, place, and time [23–25].

Table 4. Biogeographical distribution and center of diversification for hummingbird clades. For each clade, the percentage of species distributed in the two biogeographical areas is shown. Additionally, the diversification center and the mean latitudinal (Lat) and mean elevational (Elev) range of each clade (mean ± standard deviation) were estimated. See text for details on biogeographical areas and center of diversification.

Clade	% Nearctic[a]	% Neotropical[a]	% Austral[a]	Diversification Center[b]	Mean Max Lat (°)[c]	Mean Min Lat (°)[c]	Mean Lat Range (°)	Mean Elev Min (m)[d]	Mean Elev Max (m)[d]	Mean Elev Range (m)
Bees	36.364	81.818	9.091	North America	19.300 ± 21.131	7.567 ± 19.772	11.733	551.833 ± 604.715	2327.333 ± 792.586	1775.500
Mountain Gems	40.000	100.000	0.000	North America	13.667 ± 13.308	2.667 ± 16.387	11.000	621.333 ± 548.216	2251.667 ± 922.848	1630.333
Emeralds	16.667	91.667	6.250	South America	9.878 ± 11.355	−0.011 ± 14.835	9.889	296.889 ± 408.318	1657.500 ± 874.586	1360.611
Patagona	0.000	100.000	100.000	South America	0	−35.000	35.000	0	3660	3660.000
Coquettes	1.887	94.340	24.528	South America	0.453 ± 11.360	−11.548 ± 13.929	12.000	1608.208 ± 1205.671	2807.453 ± 1344.139	1199.245
Brilliants	0.000	100.000	7.895	South America	3.579 ± 6.954	−6.895 ± 8.953	10.474	1640.789 ± 907.763	2973.947 ± 819.316	1333.158
Mangoes	7.407	81.481	3.704	South America	7.182 ± 11.839	−13.591 ± 12.308	20.773	427.500 ± 599.042	1674.318 ± 958.464	1246.818
Hermits	3.846	100.000	0.000	South America	4.538 ± 11.704	−11.923 ± 11.527	16.462	69.846 ± 186.879	1130.346 ± 648.366	1060.500
Topazes	0.000	100.000	0.000	South America	3.333 ± 13.317	18.000 ± 15.010	21.333	83.333 ± 144.338	1166.667 ± 585.946	1083.333

[a] ebird [73], del Hoyo *et al.* [74]

[b] McGuire *et al.*[9], [18]

[c] Ornelas [76]

[d] Arizmendi *et al.* [79], Bleiweiss [80], del Hoyo *et al.* [74]

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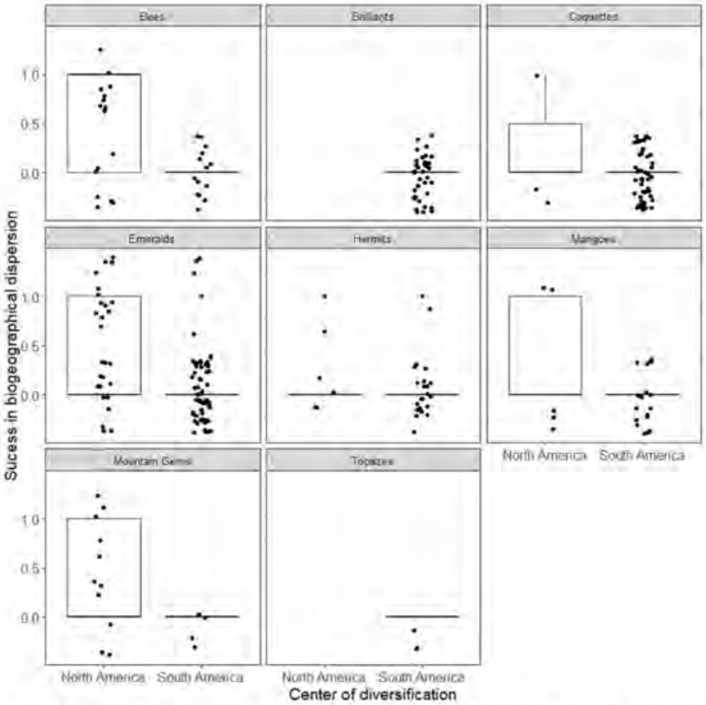

Fig 6. Hummingbird niche evolution and colonization. Relationship between the center of diversification and current distribution of hummingbirds in one (0 value on y axis) or in two or three (1 value on y axis) biogeographical regions. Each dot in the plots represents a hummingbird species, and these are faceting by clade. The Patagona clade was excluded because it contains only one South American species, *Patagona gigas*. The box encloses 50% of the data and is divided by the median (horizontal line); the upper and lower adjacent lines indicate the 0.95 and 0.05 quartiles, respectively.

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Some authors suggest that selecting a suite of null models allows inferring ecological mechanisms and their role in nestedness pattern because each null model excludes and/or constricts a specific factor of the original network [23, 55, 56]. We found that our hummingbird-plant network was significantly heterogeneous and nested depending on the null model. The nested pattern between hummingbird clades and plant families was explained by the overall connectivity and generalization pattern of hummingbirds and plants (significant CE null model) but not by the number of links per node nor plant and hummingbird phylogeny (no significant FF null model). Regarding the generalization pattern, this network has a core formed by generalist nodes composed of two hummingbird clades and 13 plant families (Fig 2, S1 Fig). Some of these nodes are remarkable for their high diversity and wide distribution. The Emerald clade is a large, taxonomically complex, and widely distributed hummingbird assemblage whose diversification in South America was favored by the Andean uplift [18, 29]. With respect to plants, the Asteraceae, Fabaceae, and Rubiaceae families are recognized for their high diversity and widespread distribution (25040, 19580, and 13150 species, respectively) [90]. Because the core concentrates a high number of interactions and contributes notably to the nestedness of the network, it possibly controls the selective forces acting on the specialist nodes and plays an important role in co-evolutionary processes and network persistence [23, 91]. Additionally, competition has been described as one of the principal mechanisms influencing the interaction between hummingbirds and plants [92–96]. Nestedness reduces interspecific competition and enhances the number of co-existing species [97]. The architecture of our network indicates that species co-existence and network persistence and stability are positively favored [91, 97, 98], allowing hummingbirds to be linked with an incredibly high number of plant species.

In contrast with our predictions about network structure, the hummingbird-flower network studied herein was not significantly modular (see Results), even though different studies on hummingbird-plant networks have detected significant modularity [20, 89, 99]. Previously, an inverse relationship between modularity and nestedness was described. A highly modular network is more specialized and less tolerant to lost connections [24]. However, because our hummingbird-plant network was constructed at a coarse scale (less than 50 nodes for hummingbirds) and the majority of connections were between modules (not intra modules), modularity was not detected [58]. One relevant finding was that, even at this scale, hummingbird nodes acted as module connectors, confirming that many hummingbirds have evolved the ability to interact with multiple plant partners [27, 100]. The hummingbird clades were associated at the same module with several plant families in more than 90% of the repetitions, indicating shared preferences for plants. It is possible that a more detailed analysis (at the species or genera level) would detect modules between hummingbirds and plants, offering a finer level of resolution to this mutualism.

By excluding exotic plant species from the analyses, we assumed that the original interactions in the network would remain intact. This assumption was not validated in previous studies on several plant communities where exotic species significantly changed the connections between the native nodes [101–105]. When we compared the architecture of the networks including or excluding exotic plant species, the network including exotic plant species connected the same nine hummingbird clades with the same 100 plant families, although we also recorded more connections with several plant families such as Myrtaceae, Rutaceae, and Strelitziaceae. However, the effects of non-native plants on network measurements such as nestedness and modularity were not statistically significant (see Results), probably because of the large scale used in our study (the hummingbird clade and plant family level).

Current ecological processes define the structure of ecological networks, although other factors such as the phylogenetic history and co-evolutionary dynamics of species interacting in a network are also important and measurable by network metrics such as nestedness and modularity [14, 27, 30, 58, 98]. When phylogeny was taken into account (i.e., the phylogenetic position of nodes was introduced into the network construction), network nestedness dropped dramatically. However, an interesting phylogenetic pattern emerged in the network: The hummingbird generalist nodes (Bees and Emeralds) are recent hummingbird lineages [9] that connect an important diversity of distantly-related plant families. Additionally, the oldest nodes, Hermits and Topazes, were strongly connected to both basal and more recent plant families (Fig 3). The decrease in the nestedness value agrees with a scenario in which subsets of nodes are highly connected internally, increasing network modularity [58]. In this respect, Martín Gonzalez *et al.* [13] studied 54 hummingbird-plant community networks across the Americas and found an association between network structure and phylogenetical signal node. Notably, complementary specialization and modularity also increased when closely related hummingbird species visited different sets of plant species, suggesting a close co-evolutionary relationship between hummingbirds and their plants. The results Martín Gonzalez *et al.* [13] in addition to the change in the connection pattern found in our network when phylogeny was considered suggests that both ecological and evolutionary processes are driving the mutualistic interactions between hummingbirds and their nectar resources. In particular, for Bee and Emerald hummingbirds, important peaks in speciation rates occurred during the last 5 MYA [9, 18, 81], and the Bee clade is the most recently derived and most rapidly diversifying group of hummingbirds [9]. Thus, in our network, the most recent hummingbird clades were generalist and connected with both old and recent plant families, exemplifying how recent hummingbirds evolved at a time when plant diversity was higher and likely used this diversity as an ecological advantage [106].

Additionally, from an evolutionary perspective, the generalist plant families in our network belonged to both recent and old plant lineages (Fig 3), suggesting that the interaction of hummingbirds and plants, over evolutionary time, promoted distinct patterns of plant diversification. For example, the old family Heliconiaceae is principally distributed in tropical America, and the mutualistic relationship between species in this family and hummingbirds has been well documented [107, 108]. Meanwhile, in the old family Bromeliaceae, only more recent lineages have adapted to hummingbird visitation [19, 109]. For recent cosmopolitan and generalist plant families such as Gesneriaceae, Campanulaceae, Lamiaceae, and Acanthaceae, different studies have suggested that hummingbird pollination triggered plant diversification, which is supported by the species diversity of Paleo vs. Neotropics lineages [19, 110–112]. Our findings additionally support Jordano's affirmation that the evolution of super-generalist nodes allows for the connection of diverse blocks that build the architecture of ecological services and biodiversity [27].

Morphological information

Besides the aforementioned phylogenetic history, the architecture of complex networks also relies on inherited traits [14, 22]. In the particular case of hummingbird-plant networks, hummingbird traits (bill length, tongue extension, bill curvature, and body mass) and flower traits (length and curvature of corolla and nectar production) determine interaction frequencies and network structure [99, 113, 114]. We found a generalization gradient in hummingbird morphology in the studied interaction network. Hummingbirds of recent and generalist clades (Bees, Mountain Gems, and Emeralds; Fig 3) are less morphologically specialized than those of other clades, i.e., hummingbirds of generalist clades were medium-sized and had predominantly straight beaks of medium length. The opposite pattern was observed in southern and specialist clades such as Hermits, Mangoes, and Patagona, which contained larger hummingbirds with longer and more curved beaks (Table 3). With respect to floral morphology, hummingbirds intensively use plant families with floral morphologies exhibiting the ornithophilous syndrome but also visit flowers with morphologies that are not typically adapted for hummingbird pollination [100, 115] (Fig 3, Table 1). In some communities, the frequency of use of non-ornithophilous plant species reflects periods of scarcity of ornithophilous species [20]. However, some of the generalist plant nodes of this network have intermediate and non-ornithophilous flowers (such as Asteraceae, Rubiaceae, and Lamiaceae, Fig 3), and the inclusion of these nodes is consistent with their pattern and frequency of use.

It has been suggested that high phenotypic specialization in hummingbirds as well as morphological matches between plant and bird species explains the network architecture between hummingbird and flower communities at a global scale [89]. Our results partially support these suggestions. Plant species belonging to genera such as *Heliconia*, *Salvia*, *Palicourea*, and *Tillandsia* are reportedly pollinated by specialized hummingbirds [19, 110] and, as expected, many hummingbird species in our network have connections with them [116–120] (S1 Table), especially hummingbirds belonging to the oldest clades (Mangoes, Topazes, and Hermits) with curved or strongly curved beaks, as this character is related with high specificity in nectar resources [114] (Fig 1, Table 1). However, the pattern of hummingbird-plant interactions and the inclusion of plant families with a large diversity of shapes and sizes in the network (not exclusively limited to those with tubular flowers of the ornithophilous syndrome) was a consequence of the intermediate morphology of the more generalist hummingbird clades (Table 3).

This generalist behavior agrees with the findings of Vitória *et al.* [14] in the Atlantic Forest of Brazil where hummingbirds interacted with plants irrespective of plants' evolutionary history. In the case of the Bee clade, the observed morphology of these hummingbirds combined with the low variation in their body mass and wing morphology [121] was found to favor access to the nectar of flowers with and/or without hummingbird pollination adaptations, reducing the physiological restrictions imposed by size [18]. Finally, the interaction between plant species and hummingbirds with a broad range of morphologies can have important ecological implications, such as, for example, favoring the diversification of flower size, which was confirmed by Serrano-Serrano *et al.* [122] for the *Nematanthus* clade (Gesneriaceae).

Biogeographical distribution and center of diversification

The network between hummingbird clades and plant families offers relevant clues about the influential factors behind the continental hummingbird biodiversity pattern. Our results suggest that the connection pattern of this network was determined by phylogenetic history and morphology (as discussed before) but was also influenced by the biogeographical distribution and center of diversification of hummingbirds. The Tropical Niche Conservatism (TNC) hypothesis is one of the models used to explain large-scale biogeographical patterns and, in particular, the higher levels of biodiversity found near the equator [15]. The hummingbird diversity pattern that we found adjusted to this model, as higher hummingbird biodiversity is found in the Neotropics [7, 17]. An important assumption of the TNC model is that most extant clades originated in the tropics during the mid-Tertiary when the tropics had a greater extension compared to temperate regions. Consequently, the presence of hummingbirds for a long period of time in the tropics in conjunction with the comparatively greater area of the tropics favored a high rate of speciation in the tropics and the specialization of these species to tropical environments [15]. The niche concept is consistent with the TNC hypothesis, and tropical lineages usually present patterns of niche conservatism [16]. The stem group diversification of hummingbirds probably started in the Paleogene (around 65–22 MYA) [9, 81]. Then, the subsequent colonization of the Nearctic and/or Austral biogeographical regions by hummingbird species from northern and central South America is consistent with the prediction of niche evolution because the transition from Neotropical to Nearctic or Austral regions represents an environmental turnover from relatively constant temperatures to a seasonal environment [12, 15, 16].

The biogeographical patterns revealed for hummingbirds were also consistent at the clade level and with respect to latitudinal and elevational range. In this regard, niche conservatism is also relevant for understanding the observed connection patterns. In particular, the Bee and Mountain Gem clades, which diversified in North America in highly seasonal environments [9, 18], had a high probability of colonizing a different biogeographical area and significantly contributed to the high species diversity of North and South America (Fig 6, Table 4). Some authors have suggested that hummingbird evolution under drastic climatic conditions represents an evolutionary advantage that allowed hummingbirds to colonize and expand their distribution to places with less harsh environments such as the tropics [12, 16]. Interestingly, these latter two clades (Bees and Mountain Gems) evolved recently (Fig 3) and, as mentioned earlier, were connected with an important number of plant families favored by intermediate morphologies and low niche conservatism. As mentioned earlier, McGuire *et al.* [9] detected clade-specific processes in hummingbirds and, particularly for the Bee, Emerald, and Mountain Gem clades, reported accelerated speciation rates. These researchers concluded that the rapid rates of diversification in hummingbirds were consistent with classical examples of rapid adaptive radiation. Our data offer additional support for their conclusions: The generalist behavior of these clades, which successfully use all available nectar resources, along with their ability to colonize "new" areas such as Central America and the Andes Mountains, could have favored the recent and accelerated speciation of these clades. The recent colonization of these clades was supported also by Abrahamczyk & Renner [19], who reported that several Emerald and Mountain Gem species have extended their ranges in a northern direction during the last 100 years.

The hummingbird clades that diversified in tropical South America exhibited a lower probability of colonizing new biogeographical areas, generally had larger latitudinal ranges but smaller elevational ranges, and contributed very little to species diversity in temperate North America, with the exception of the Emerald clade (Figs 5 and 6, Table 4). The case of the South American Brilliant and Coquette clades is interesting because hummingbirds from these clades had a generalist morphology but had a small elevational and latitudinal distribution and were mainly restricted to high elevations in the Andes Mountains [7]. Our data suggested that, particularly for these species, specialization occurred at the habitat level (not morphologically), as these birds are highly adapted to high mountain ecosystems, which is consistent with the tropical niche conservatism hypothesis.

Licona-Vera & Ornelas [18] proposed that the colonization of North America and the radiation of Bee hummingbirds in this region were favored by the repeated evolution of long-distance seasonal migration in different lineages and by the availability of favorable habitats and climatic conditions related with the formation of mountain systems in Mexico and Central America. Most long-distance seasonal migrant hummingbirds belong to the Bee clade, and 11 hummingbird species with variable latitudinal ranges (from 660 km to 6000 km) migrate across the Nearctic and the Neotropical regions. Bee species such as *Archilochus colubris* make flights of around 3300 km from their wintering areas to reproduction areas, and *Selasphorus rufus* and *S. calliope* travel even greater distances of 6000 and 4500 km, respectively [74, 79]. Although migrant populations have been reported for six Emerald species, their latitudinal ranges are smaller compared to those of the five Bee species that migrate in the same area (S4 Table). Similarly, some species belonging to the Patagonia and Coquette clades migrate latitudinally in South America [18]. For these species, migrations of 2000 km for *Patagona gigas* and 1300 km for *Sephanoides sephanoides* were reported between wintering and summering lands in South America. Notably, for *Oreotrochilus leucopleurus*, records suggest that this species migrates elevationally, but recent records in Bolivia during the Austral winter suggest that it latitudinally migrates [74]. Abrahamczyk & Renner [19] stated that the interaction between migratory vertebrates and nectar resources is likely not the result of co-evolution, which was supported by our results: Generalist clades with long-distance migrant species and populations (such as the Bee and Emerald hummingbirds) visited a diverse array of plants during migration [94, 123, 124].

Our study provided new insight into the factors influencing the interaction between hummingbirds and their nectar resources at a continental scale. Besides their recognized and relevant role as pollinators, from a network perspective, hummingbirds play an important role in the structure and maintenance of ecosystem services and biodiversity, acting as generalist and super-generalist nodes that connect with an amazingly high number of plant species [27, 100]. Given the current rates of habitat modification and the predicted changes in the distributional range of many species as a result of climate change, the loss of species as well as the mutualistic interactions that maintain different processes in natural ecosystems seems inevitable [36]. Understanding the pattern of contemporary specialization between hummingbirds and plants used by hummingbirds as nectar resources at a continental scale can provide insight into how hummingbird lineages with different biogeographical and evolutionary histories might respond to the biodiversity crisis and how the connection pattern between hummingbirds and their nectar resources might be affected by habitat modification and climate change.

It is relevant to further explore the approximations proposed herein at a smaller scale (genus, species), as the necessary information is currently available. Future studies can use quantitative matrices and dated phylogenies for hummingbirds and plants to explore plant niche evolution and to measure phylogenetic signaling in hummingbirds and plants with respect to morphological traits in order to disentangle the evolutionary, colonization, and connection patterns of hummingbird-plant mutualisms in greater detail.

Supporting information

S1 Fig. Network of hummingbirds and their floral nectar resources with nodes ordered by number of links. Ecological network of hummingbird clades (left) and plant families (right) (non-native plant species were excluded). Nodes were ordered by intensity, with the generalist nodes at the top and the specialist nodes at the bottom. Node size is proportional to the number of species with which each species interacts. Plants and interactions (lines) were classified by floral morphology as ornithophilous (red), intermediate (yellow), or non-ornithophilous (gray).
(TIF)

S2 Fig. Degree distribution for the number of interactions. This graph shows the cumulative frequency distribution (P (*k*)) of the number of links (*k*) in the hummingbird-plant network (without non-native plant species). The graph in the log-log plot combines plant and hummingbird interactions. The original data (circles) were adjusted to three distributions: (1) power-law function (pow.), (2) exponential (exp.), and (3) truncated power-law (pow.trun.). The network has the best fit with the power-law function (AIC exp. = 658.581, AIC pow. = 565.342, AIC pow.trun. = 656.354).
(TIFF)

S1 Table. Plant families and genera visited by hummingbirds. Plant species were grouped by family (FAMILY) and genus (GENUS). For each family, the number of recorded interactions (total number of 1s in the qualitative matrix for each family) (INTER.FAM), visiting hummingbird species (HUMM.FAM), and visiting hummingbird clades (CLAD.FAM) is indicated. For each genus, the number of species used by hummingbirds (SPECIES) and recorded interactions (total number of 1s in the qualitative matrix for each genus) (INTER.GEN) is indicated. Depending on the morphology of the plant species, we classified the pollination syndrome of each family (SYND) as ornithophilous (O), intermediate (I), or non-ornithophilous (NT). See Table 1 in the text for details on the characteristics of each category.
(DOCX)

S2 Table. Binary matrix of the interaction network between hummingbird clades and their nectar family plants. Hummingbird clades are in columns and plant families in rows; native and non-native plant species were included. In this binary matrix, 1 indicates an interaction between a hummingbird clade and a plant family, and 0 otherwise. Nodes are ordered by number of links.
(DOCX)

S3 Table. Plant families and hummingbird clades associated by modularity analysis. Plant families associated with hummingbird clades in more than 90% of the modularity analyses. We used the network with nodes ordered phylogenetically and only included native plant species. Numbers in parenthesis correspond to the number of analyses in which the plant family belonged to the same module as the hummingbird clade. The text color represents the pollination syndrome of each family: red (ornithophilous), blue (intermediate), and black (non-ornithophilous). See Table 2 in the text for details on the characteristics of each pollination syndrome category.
(DOCX)

S4 Table. Biogeographical, elevational, latitudinal, and morphological information and center of diversification for the hummingbird species included in this study. The source(s) of information for each category is (are) shown in the REF column and the Supplementary References section (see below). For the biogeographical distribution regions, the value 1 represents the presence of a hummingbird species in this (these) region(s); in contrast, 0 represents the lack of records. The latitudinal and elevational range columns are the difference between the minimum and maximum value for each category. The asterisk (*) in the Geographical Area column means that the center of diversification of these hummingbird species was indirectly inferred based on the closest sister species whose center of diversification has been explicitly detected. Also, the inference method used in the different studies to establish the center of diversification area is shown. For the definition of each biogeographical region and geographical area, see the text. For exposed culmen, weight, and wing morphological information, the mean and standard deviation (s.d.) of each hummingbird species are shown. The definition of each bill curvature category is explained in the text.
(DOCX)

S1 Appendix. Network analysis of the matrix including native and exotic plant species. Results for the degree distribution, nestedness, and modularity analyses of the mutualistic network of hummingbird clades and their nectar plants. In this network, we included all records independently of plant origin (native or exotic to the American continent).
(DOCX)

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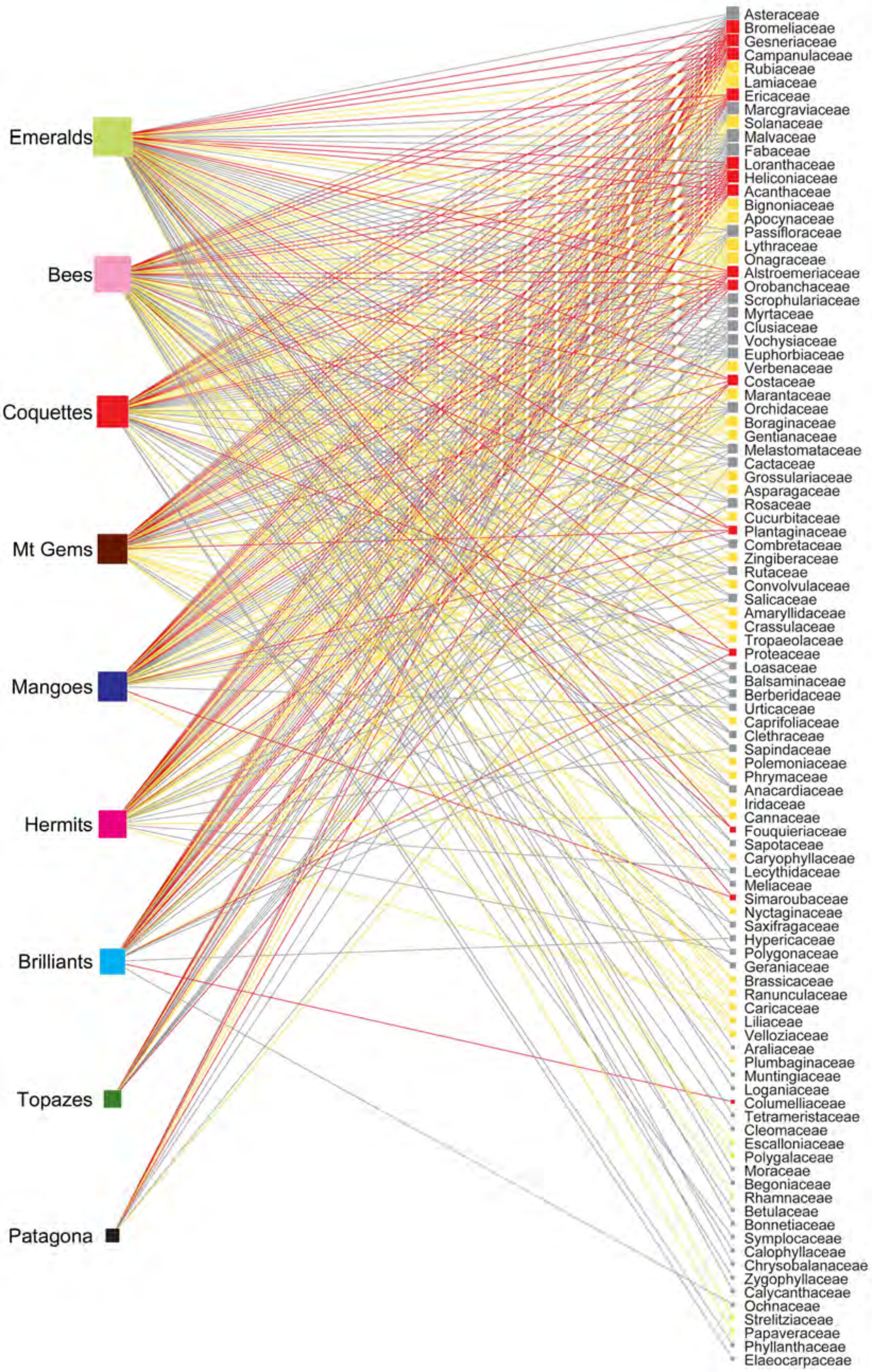
Supporting Information

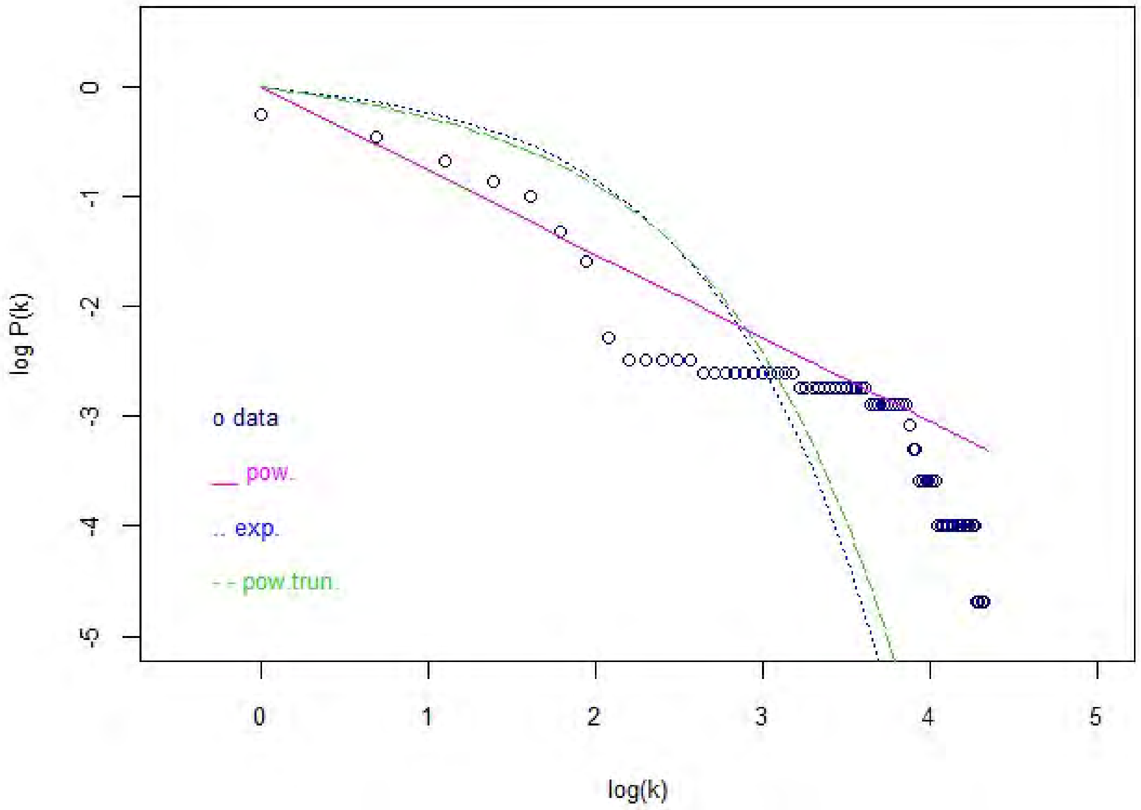
S1 Fig. Network of hummingbirds and their floral nectar resources with nodes ordered by number of links. Ecological network of hummingbird clades (left) and plant families (right) visited by hummingbirds (non-native plant species were excluded). Nodes were ordered by intensity, with the generalist nodes at the top and the specialist nodes at the bottom. Node size is proportional to the number of species with which each species interacts. Plants and interactions (lines) were classified by floral morphology as ornithophilous (red), intermediate (yellow), or non-ornithophilous (gray).

(TIFF)


Emeralds
Bees
Coquettes
Mt Gems
Mangoes
Hermits
Brilliants
Topazes
Patagona
Asteraceae
Bromeliaceae
Gesneriaceae
Campanulaceae
Rubiaceae
Lamiaceae
Ericaceae
Marcgraviaceae
Solanaceae
Malvaceae
Fabaceae
Loranthaceae
Heliconiaceae
Acanthaceae
Bignoniaceae
Apocynaceae
Passifloraceae
Lythraceae
Onagraceae
Alstroemeriaceae
Orobanchaceae
Scrophulariaceae
Myrtaceae
Clusiaceae
Vochysiaceae
Euphorbiaceae
Verbenaceae
Costaceae
Marantaceae
Orchidaceae
Boraginaceae
Gentianaceae
Melastomataceae
Cactaceae
Grossulariaceae
Asparagaceae
Rosaceae
Cucurbitaceae
Plantaginaceae
Combretaceae
Zingiberaceae
Rutaceae
Convolvulaceae
Salicaceae
Amaryllidaceae
Crassulaceae
Tropaeolaceae
Proteaceae
Loasaceae
Balsaminaceae
Berberidaceae
Urticaceae
Caprifoliaceae
Clethraceae
Sapindaceae
Polemoniaceae
Phrymaceae
Anacardiaceae
Iridaceae
Cannaceae
Fouquieriaceae
Sapotaceae
Caryophyllaceae
Lecythidaceae
Meliaceae
Simaroubaceae
Nyctaginaceae
Saxifragaceae
Hypericaceae
Polygonaceae
Geraniaceae
Brassicaceae
Ranunculaceae
Caricaceae
Liliaceae
Velloziaceae
Araliaceae
Plumbaginaceae
Muntingiaceae
Loganiaceae
Columelliaceae
Tetrameristaceae
Cleomaceae
Escalloniaceae
Polygalaceae
Moraceae
Begoniaceae
Rhamnaceae
Betulaceae
Bonnetiaceae
Symplocaceae
Calophyllaceae
Chrysobalanaceae
Zygophyllaceae
Calycanthaceae
Ochnaceae
Strelitziaceae
Papaveraceae
Phyllanthaceae
Elaeocarpaceae

S2 Fig. Degree distribution for the number of interactions. This graph shows the cumulative frequency distribution (P (*k*)) of the number of links (*k*) in the hummingbird-plant network (without non-native plant species). The graph in the log-log plot combines plant and hummingbird interactions. The original data (circles) were adjusted to three distributions: (1) power-law function (pow.), (2) exponential (exp.), and (3) truncated power-law (pow.trun.). The network has the best fit with the power-law function (AIC exp. = 658.581, AIC pow. = 565.342, AIC pow.trun. = 656.354).

(TIFF)



S1 Table. Plant families and genera visited by hummingbirds. Plant species were grouped by family (FAMILY) and genus (GENUS). For each family, the number of recorded interactions (total number of 1s in the qualitative matrix for each family) (INTER.FAM), visiting hummingbird species (HUMM.FAM), and visiting hummingbird clades (CLAD.FAM) is indicated. For each genus, the number of species used by hummingbirds (SPECIES) and recorded interactions (total number of 1s in the qualitative matrix for each genus) (INTER.GEN) is indicated. Depending on the morphology of the plant species, we classified the pollination syndrome of each family (SYND) as ornithophilous (O), intermediate (I), or non-ornithophilous (NT). See Table 1 in the text for details on the characteristics of each category.

(DOC)

S1 Table

FAMILY	INTER.FAM	HUMM.FAM	CLAD.FAM	SYND	GENUS	SPECIES	INTER.GEN
Acanthaceae	152	81	7	O	*Anisacanthus*	6	16
					Aphelandra	4	14
					Asystasia	1	3
					Avicennia	1	1
					Barleria	1	3
					Beloperone	1	1
					Bravaisia	1	1
					Dicliptera	2	2
					Graptophyllum	1	1
					Habracanthus	1	3
					Hansteinia	1	1
					Jacobinia	1	1
					Justicia	8	23
					Mendoncia	2	2
					Odontonema	1	2
					Pachystachys	4	19
					Razisea	2	5
					Ruellia	4	7
					Sanchezia	3	10
					Strobilanthes	1	2
					Thunbergia	3	11
					Trichanthera	2	9
Alstroemeriaceae	44	37	7	O	*Alstroemeria*	3	6
					Bomarea	8	38
Amaryllidaceae	5	5	4	I	*Hippeastrum*	2	2
					Manfreda	1	1
Anacardiaceae	10	9	3	NT	*Anacardium*	2	6
					Toxicodendron	1	3
Apocynaceae	42	30	7	I	*Allamanda*	2	2
					Asclepias	3	10
					Mandevilla	6	13
					Nerium	1	1
					Prestonia	1	5
					Tabernaemontana	3	6
					Thevetia	1	1
					Urechites	1	2
Araliaceae	4	2	1	NT	*Dendropanax*	1	2
					Schefflera	1	2
Asparagaceae	65	29	5	I	*Agave*	15	60
					Bessera	1	1
					Dracaena	1	1
					Taetsia	1	1
					Yucca	1	1
Asteraceae	119	63	9	NT	*Ageratum*	1	1
					Aspilia	2	3
					Barnadesia	2	10
					Bidens	2	2
					Chuquiraga	3	5
					Cirsium	9	31
					Clibadium	1	1
					Dasyphyllum	2	4
					Dendroseris	2	2

S1 Table (continued)

FAMILY	INTER.FAM	HUMM.FAM	CLAD.FAM	SYND	GENUS	SPECIES	INTER.GEN
Asteraceae					*Eremanthus*	2	7
					Espeletia	2	5
					Gynoxys	1	1
					Heliomeris	1	1
					Hololepis	1	1
					Lagascea	1	2
					Lepidaploa	1	1
					Lessingianthus	1	1
					Mutisia	3	11
					Piptocarpha	2	2
					Roldana	1	5
					Stifftia	1	7
					Vernonanthura	1	5
					Vernonia	2	3
					Zinnia	1	1
Balsaminaceae	4	4	3	NT	*Impatiens*	2	4
Begoniaceae	1	1	1	NT	*Begonia*	1	1
Berberidaceae	9	9	3	NT	*Berberis*	2	9
Betulaceae	1	1	1	NT	*Alnus*	1	1
Bignoniaceae	128	47	7	I	*Arrabidaea*	1	2
					Bignonia	1	1
					Campsis	2	3
					Chilopsis	2	7
					Clytostoma	1	1
					Dolichandra	1	4
					Fridericia	1	2
					Handroanthus	2	8
					Jacaranda	1	2
					Memora	1	2
					Piriadacus	1	4
					Pleonotoma	1	1
					Pyrostegia	1	5
					Saritaea	1	2
					Setilobus	1	7
					Spathodea	2	20
					Tabebuia	11	39
					Tecoma	3	9
					Zeyheria	1	1
Bonnetiaceae	1	1	1	NT	*Bonnetia*	1	1
Boraginaceae	48	32	6	I	*Bourreria*	2	3
					Cordia	12	35
					Cynoglossum	1	1
					Ehretia	2	2
					Hydrophyllum	1	1
					Lithospermum	1	1
					Macromeria	1	1
					Mertensia	1	1
					Phacelia	1	1
					Turricula	1	1
					Wigandia	1	1
Brassicaceae	6	6	2	I	*Draba*	2	2
					Nasturtium	1	1

S1 Table (continued)

FAMILY	INTER.FAM	HUMM.FAM	CLAD.FAM	SYND	GENUS	SPECIES	INTER.GEN
					Stanleya	1	3
Bromeliaceae	244	113	9	O	*Aechmea*	7	29
					Billbergia	4	7
					Bromelia	2	8
					Canistrum	1	1
					Dyckia	1	1
					Guzmania	15	46
					Hohenbergia	3	5
					Mezobromelia	1	1
					Neoregelia	2	3
					Nidularium	2	4
					Orthophytum	1	2
					Pitcairnia	9	21
					Puya	2	16
					Quesnelia	3	7
					Racinaea	2	2
					Tillandsia	16	46
					Vriesea	9	20
					Werauhia	1	1
Cactaceae	64	39	5	NT	*Carnegiea*	1	1
					Cereus	1	1
					Cylindropuntia	2	2
					Echinocereus	1	4
					Lemaireocereus	2	7
					Melocactus	2	9
					Neobuxbaumia	1	4
					Opuntia	7	26
					Stenocereus	2	2
Calophyllaceae	1	1	1	NT	*Calophyllum*	1	1
Calycanthaceae	1	1	1	NT	*Beureria*	1	1
Campanulaceae	121	75	8	O	*Burmeistera*	5	5
					Centropogon	12	56
					Lobelia	5	37
					Siphocampylus	7	17
Cannaceae	9	7	3	I	*Canna*	2	8
Caprifoliaceae	19	10	3	I	*Lonicera*	7	15
					Symphoricarpos	3	4
Caricaceae	4	4	2	I	*Carica*	1	4
Caryophyllaceae	8	5	2	I	*Silene*	5	8
Chrysobalanaceae	1	1	1	NT	*Hirtella*	1	1
Cleomaceae	5	4	1	NT	*Cleome*	2	3
					Peritoma	2	2
Clethraceae	5	5	3	NT	*Clethra*	2	5
Clusiaceae	40	33	6	NT	*Clusia*	4	27
					Symphonia	2	13
Columelliaceae	1	1	1	O	*Desfontainia*	1	1
Combretaceae	22	18	4	NT	*Combretum*	5	18
					Laguncularia	2	4
Convolvulaceae	51	32	4	I	*Bonamia*	1	1
					Convolvulus	1	2
					Exogonium	1	3

S1 Table (continued)

FAMILY	INTER.FAM	HUMM.FAM	CLAD.FAM	SYND	GENUS	SPECIES	INTER.GEN
					Ipomoea	10	39
					Jacquemontia	1	2
Costaceae	51	34	6	O	*Costus*	8	51
Crassulaceae	13	12	4	I	*Dudleya*	2	2
					Echeveria	4	6
					Kalanchoe	3	4
Cucurbitaceae	30	19	4	I	*Gurania*	5	30
Elaeocarpaceae	5	5	1	NT	*Vallea*	1	5
Ericaceae	238	95	8	O	*Agarista*	2	2
					Arbutus	3	4
					Arctostaphylos	4	8
					Bejaria	1	5
					Cavendishia	9	61
					Comarostaphylis	1	1
					Disterigma	1	8
					Gaultheria	6	10
					Gaylussacia	1	1
					Killipiella	1	2
					Macleania	4	37
					Menziesia	1	1
					Pernettya	1	2
					Psammisia	5	26
					Sarcodes	1	1
					Satyria	2	8
					Sphyrospermum	1	2
					Thibaudia	4	10
					Vaccinium	3	9
Escalloniaceae	1	1	1	I	*Escallonia*	1	1
Euphorbiaceae	26	20	6	NT	*Acalypha*	2	3
					Croton	3	3
					Euphorbia	7	13
					Jatropha	1	1
					Manihot	1	1
					Pedilanthus	1	2
					Poinsettia	1	1
Fabaceae	482	174	8	NT	*Abarema*	1	3
					Acacia	3	5
					Acrocarpus	1	2
					Anneslia	1	1
					Bauhinia	6	27
					Brownea	2	4
					Caesalpinia	4	21
					Cajanus	2	3
					Calliandra	14	55
					Calopogonium	1	1
					Camptosema	1	1
					Canavalia	2	5
					Caragana	1	1
					Cassia	1	2
					Centrosema	2	3
					Cercidium	1	1
					Cercis	2	2

S1 Table (continued)

FAMILY	INTER.FAM	HUMM.FAM	CLAD.FAM	SYND	GENUS	SPECIES	INTER.GEN
					Chaetocalyx	1	1
					Chloroleucon	1	2
					Clathrotropis	1	2
					Clitoria	1	1
					Collaea	2	2
					Crotalaria	3	6
					Dahlstedtia	2	8
					Delonix	2	13
					Dioclea	2	3
					Dipteryx	1	1
					Ebenopsis	1	1
					Erythrina	12	85
					Gliricidia	1	3
					Havardia	1	1
					Hymenolobium	1	1
					Inga	10	109
					Leucaena	2	2
					Lonchocarpus	1	2
					Lotus	1	1
					Lupinus	3	7
					Mimosa	2	4
					Mucuna	2	3
					Neorudolphia	1	4
					Olneya	2	2
					Parkinsonia	1	1
					Periandra	1	2
					Phaseolus	2	14
					Pithecellobium	1	7
					Prosopis	2	3
					Robinia	2	3
					Sabinea	2	4
					Samanea	2	10
					Sophora	1	1
					Strongylodon	1	1
					Tachigali	1	1
					Tamarindus	2	4
					Vicia	1	2
					Vigna	1	1
Fouquieriaceae	18	9	2	O	*Fouquieria*	5	18
Gentianaceae	15	12	5	I	*Chelonanthus*	1	3
					Gentiana	1	2
					Lisianthius	1	1
					Macrocarpaea	3	5
					Swertia	1	1
					Symbolanthus	2	3
Geraniaceae	2	2	2	NT	*Geranium*	2	2
Gesneriaceae	240	81	8	O	*Alloplectus*	1	9
					Besleria	8	56
					Columnea	9	37
					Drymonia	8	24
					Gasteranthus	2	3
					Gesneria	1	1

S1 Table (continued)

FAMILY	INTER.FAM	HUMM.FAM	CLAD.FAM	SYND	GENUS	SPECIES	INTER.GEN
					Glossoloma	3	12
					Heppiella	1	4
					Kohleria	8	45
					Moussonia	1	1
					Nematanthus	4	10
					Paliavana	1	4
					Rechsteineria	1	1
					Reldia	1	2
					Rhytidophyllum	1	1
					Sinningia	4	7
Grossulariaceae	24	14	5	I	*Escallonia*	1	1
					Ribes	7	23
Heliconiaceae	183	83	8	O	*Heliconia*	34	176
Hypericaceae	2	2	2	NT	*Vismia*	1	2
Iridaceae	9	8	3	NT	*Gladiolus*	1	1
					Iris	2	2
					Tigridia	1	6
Lamiaceae	204	83	8	I	*Aegiphila*	2	3
					Amasonia	1	3
					Clinopodium	1	1
					Coleus	1	2
					Condea	1	2
					Cornutia	2	2
					Holmskioldia	2	2
					Hyptis	1	2
					Leonotis	3	9
					Leonurus	2	3
					Lepechinia	1	1
					Leptohyptis	1	2
					Monarda	4	4
					Monardella	1	1
					Origanum	1	1
					Plectranthus	1	1
					Prunella	1	5
					Rhabdocaulon	1	1
					Salvia	28	121
					Satureja	1	1
					Scutellaria	2	2
					Stachys	4	19
					Trichostema	3	3
					Vitex	4	8
Lecythidaceae	3	3	2	NT	*Bertholletia*	1	2
					Couroupita	1	1
Liliaceae	6	3	2	I	*Erythronium*	1	2
					Lilium	2	2
Loasaceae	7	6	3	NT	*Caiophora*	1	3
					Eucnide	1	1
					Loasa	1	3
Loganiaceae	1	1	1	NT		0	1
Loranthaceae	93	70	8	O	*Aetanthus*	2	5
					Gaiadendron	2	4
					Phrygilanthus	1	1

S1 Table (continued)

FAMILY	INTER.FAM	HUMM.FAM	CLAD.FAM	SYND	GENUS	SPECIES	INTER.GEN
Loranthaceae					*Psittacanthus*	9	56
					Struthanthus	1	1
					Tripodanthus	1	1
					Tristerix	2	6
Lythraceae	28	23	7	I	*Cuphea*	7	23
					Lafoensia	2	2
					Lagerstroemia	2	2
					Punica	1	1
Malvaceae	201	102	8	NT	*Abutilon*	2	10
					Bombax	1	1
					Byttneria	1	2
					Ceiba	2	9
					Chiranthodendron	1	1
					Dombeya	2	7
					Goethea	1	1
					Hampea	2	5
					Helicteres	4	18
					Hibiscus	4	47
					Luehea	2	2
Malvaceae					*Malva*	1	1
					Malvaviscus	3	47
					Melochia	1	1
					Pachira	1	2
					Pavonia	3	12
					Pseudobombax	2	2
					Quararibea	1	5
					Trichospermum	1	1
					Triumfetta	1	1
					Urena	1	2
Marantaceae	20	15	6	I	*Calathea*	5	5
					Ischnosiphon	2	2
					Maranta	1	1
					Monotagma	2	2
					Saranthe	1	1
					Thalia	2	5
Marcgraviaceae	37	25	8	NT	*Marcgravia*	8	16
					Marcgraviastrum	1	1
					Norantea	2	10
					Sarcopera	1	5
Melastomataceae	53	35	5	NT	*Brachyotum*	3	14
					Conostegia	2	2
					Heterotrichum	1	1
					Huilaea	2	3
					Mecranium	1	1
					Meriania	3	4
					Miconia	6	19
					Tibouchina	1	2
Meliaceae	6	6	3	NT	*Cedrela*	1	1
					Guarea	2	2
					Melia	1	3
Moraceae	1	1	1	NT	*Ficus*	1	1
Muntingiaceae	2	2	1	NT	*Muntingia*	1	2

S1 Table (continued)

FAMILY	INTER.FAM	HUMM.FAM	CLAD.FAM	SYND	GENUS	SPECIES	INTER.GEN
Musaceae	32	30	6	O	*Musa*	4	29
Myrtaceae	79	60	9	NT	*Callistemon*	2	4
					Eucalyptus	3	36
					Eugenia	2	8
					Myrciaria	1	1
					Psidium	2	3
					Syzygium	3	15
Nyctaginaceae	10	10	2	I	*Bougainvillea*	3	5
					Mirabilis	2	5
Ochnaceae	1	1	1	NT	*Tyleria*	1	1
Oleaceae	2	1	1	I	*Nyctanthes*	2	2
Onagraceae	82	53	7	I	*Epilobium*	4	10
					Fuchsia	12	67
					Ludwigia	1	1
					Zauschneria	1	1
Orchidaceae	27	18	6	NT	*Dilomilis*	1	1
					Elleanthus	4	15
					Epidendrum	1	2
					Odontoglossum	1	1
					Prosthechea	1	1
					Rhynchostele	1	1
					Spiranthes	1	1
					Stenorrhynchos	1	3
Orobanchaceae	75	34	6	O	*Agalinis*	1	1
					Bartsia	1	1
					Castilleja	18	59
					Esterhazya	2	2
					Lamourouxia	4	7
					Macranthera	2	2
					Pedicularis	2	3
Papaveraceae	1	1	1	I	*Corydalis*	1	1
Passifloraceae	59	41	7	NT	*Passiflora*	19	51
Phrymaceae	18	8	3	I	*Diplacus*	2	4
					Erythranthe	1	1
					Mimulus	5	13
Phyllanthaceae	1	1	1	NT	*Phyllanthus*	1	1
Pittosporaceae	3	3	2	NT	*Pittosporum*	1	3
Plantaginaceae	95	39	4	O	*Digitalis*	2	2
					Keckiella	3	4
					Linaria	2	2
					Maurandya	1	1
					Penstemon	17	64
					Plantago	1	1
					Russelia	3	21
Plumbaginaceae	4	3	2	I	*Plumbago*	2	4
Polemoniaceae	18	11	3	I	*Gilia*	1	3
					Ipomopsis	2	7
					Loeselia	1	7
					Polemonium	1	1
Polygalaceae	2	1	1	I	*Securidaca*	2	2
Polygonaceae	4	4	2	NT	*Antigonon*	2	3

S1 Table (continued)

FAMILY	INTER.FAM	HUMM.FAM	CLAD.FAM	SYND	GENUS	SPECIES	INTER.GEN
Polygonaceae					*Coccoloba*	1	1
Proteaceae	7	6	4	O	*Embothrium*	2	5
					Grevillea	1	1
Ranunculaceae	33	12	2	I	*Aconitum*	1	1
					Aquilegia	6	15
					Delphinium	7	17
Rhamnaceae	1	1	1	I	*Ceanothus*	1	1
Rosaceae	27	22	5	NT	*Eriobotrya*	1	1
					Hesperomeles	1	2
					Polylepis	1	2
					Prunus	1	2
					Rubus	6	20
Rubiaceae	384	154	8	I	*Aegiphila*	1	2
					Augusta	1	1
					Bouvardia	2	18
					Calycophyllum	1	1
					Cinchona	1	1
					Coffea	2	9
					Coussarea	1	3
					Crusea	1	8
					Duggena	1	4
					Duroia	1	5
					Ernodea	1	1
					Faramea	2	7
					Genipa	2	14
					Hamelia	4	53
					Hillia	1	1
					Isertia	2	9
					Ixora	3	8
					Manettia	4	10
					Morinda	2	2
					Palicourea	16	111
					Pentas	1	1
					Posoqueria	1	1
					Psychotria	12	59
					Rondeletia	1	1
					Sabicea	2	3
					Simira	1	1
					Sommera	1	1
					Warszewiczia	2	13
Rutaceae	27	27	6	NT	*Citrus*	2	19
					Decagonocarpus	1	2
					Murraya	1	1
Salicaceae	6	6	4	NT	*Ryania*	1	4
					Salix	1	2
Sapindaceae	16	10	3	NT	*Aesculus*	3	4
					Paullinia	3	5
					Serjania	2	5
					Ungnadia	2	2
Sapotaceae	5	5	2	NT	*Bumelia*	1	5
Saxifragaceae	2	2	2	NT	*Heuchera*	2	2

S1 Table (continued)

FAMILY	INTER.FAM	HUMM.FAM	CLAD.FAM	SYND	GENUS	SPECIES	INTER.GEN
Scrophulariaceae	16	12	6	NT	*Buddleja*	4	12
					Scrophularia	3	4
Simaroubaceae	2	2	2	O	*Quassia*	1	2
Solanaceae	63	40	8	I	*Acnistus*	2	4
					Brugmansia	1	1
					Cestrum	5	13
					Datura	2	2
					Dunalia	1	2
					Dyssochroma	1	1
					Iochroma	1	1
					Lycium	5	6
					Nicotiana	4	26
					Salpichroa	1	2
					Sessea	1	1
					Solanum	2	2
					Streptosolen	1	1
					Witheringia	1	1
Strelitziaceae	2	2	2	I	*Strelitzia*	1	1
Symplocaceae	1	1	1	NT	*Symplocos*	1	1
Tetrameristaceae	4	3	1	NT	*Pelliciera*	2	4
Tropaeolaceae	5	5	3	I	*Tropaeolum*	1	5
Urticaceae	6	6	3	NT	*Cecropia*	2	5
Velloziaceae	7	3	2	I	*Barbacenia*	5	6
Verbenaceae	101	67	6	I	*Citharexylum*	1	1
					Duranta	3	9
					Holmskioldia	1	2
					Lantana	4	32
					Lippia	2	3
					Petrea	2	3
					Rhaphithamnus	2	2
					Stachytarpheta	6	36
Vitaceae	1	1	1	NT	*Cayratia*	1	1
Vochysiaceae	23	20	6	NT	*Vochysia*	4	13
Xanthorrhoeaceae	7	6	2	I	*Aloe*	2	4
					Kniphofia	1	2
					Phormium	1	1
Zingiberaceae	35	30	5	I	*Alpinia*	2	7
					Etlingera	1	2
					Hedychium	1	3
					Renealmia	3	16
Zygophyllaceae	2	1	1	NT	*Larrea*	2	2

Supporting References

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S2 Table. Binary matrix of the interaction network between hummingbird clades and their nectar family plants. Hummingbird clades are in columns and plant families in rows; native and non-native plant species were included. In this binary matrix, 1 indicates an interaction between a hummingbird clade and a plant family, and 0 otherwise. Nodes are ordered by number of links.

S2 Table

	Emeralds	Bees	Coquettes	MtGems	Mangoes	Hermits	Brilliants	Topazes	Patagona
Asteraceae	1	1	1	1	1	1	1	1	1
Bromeliaceae	1	1	1	1	1	1	1	1	1
Myrtaceae	1	1	1	1	1	1	1	1	1
Lamiaceae	1	1	1	1	1	1	1	0	1
Ericaceae	1	1	1	1	1	1	1	1	0
Campanulaceae	1	1	1	1	1	1	1	0	1
Fabaceae	1	1	1	1	1	1	1	1	0
Gesneriaceae	1	1	1	1	1	1	1	1	0
Loranthaceae	1	1	1	1	1	1	1	0	1
Solanaceae	1	1	1	1	1	1	1	0	1
Heliconiaceae	1	1	1	1	1	1	1	1	0
Malvaceae	1	1	1	1	1	1	1	1	0
Marcgraviaceae	1	1	1	1	1	1	1	1	0
Rubiaceae	1	1	1	1	1	1	1	1	0
Acanthaceae	1	1	1	1	1	1	1	0	0
Apocynaceae	1	1	1	1	1	1	0	1	0
Alstroemeriaceae	1	1	1	1	1	1	1	0	0
Passifloraceae	1	1	0	1	1	1	1	0	1
Bignoniaceae	1	1	1	1	1	1	0	1	0
Lythraceae	1	1	1	1	1	1	1	0	0
Onagraceae	1	1	1	1	1	1	1	0	0
Marantaceae	1	1	1	0	1	1	1	0	0
Boraginaceae	1	1	1	1	1	1	0	0	0
Euphorbiaceae	1	1	1	1	1	0	0	1	0
Clusiaceae	1	0	1	1	1	0	1	1	0
Vochysiaceae	1	1	1	1	1	0	0	1	0
Verbenaceae	1	1	1	1	1	1	0	0	0
Orobanchaceae	1	1	1	1	1	0	1	0	0
Costaceae	1	1	0	1	0	1	1	1	0
Rutaceae	1	1	1	0	1	1	1	0	0
Musaceae	1	1	0	1	1	1	1	0	0
Orchidaceae	1	0	1	1	1	1	1	0	0
Scrophulariaceae	1	1	1	1	1	0	0	0	1
Cactaceae	1	1	0	1	1	0	0	0	1
Zingiberaceae	1	0	0	1	1	1	1	0	0
Gentianaceae	1	1	1	0	0	1	1	0	0
Grossulariaceae	1	1	1	1	1	0	0	0	0
Rosaceae	1	1	1	0	0	1	1	0	0
Asparagaceae	1	1	1	1	0	0	0	0	1
Melastomataceae	1	1	1	0	1	0	1	0	0
Combretaceae	1	1	0	0	1	1	0	0	0
Convolvulaceae	1	1	0	1	1	0	0	0	0

S2 Table (continued)

	Emeralds	Bees	Coquettes	MtGems	Mangoes	Hermits	Brilliants	Topazes	Patagona
Cucurbitaceae	1	0	0	1	1	1	0	0	0
Crassulaceae	1	1	1	0	1	0	0	0	0
Proteaceae	1	1	1	0	0	0	1	0	0
Plantaginaceae	1	1	0	1	1	0	0	0	0
Amaryllidaceae	1	1	1	0	0	1	0	0	0
Salicaceae	1	1	0	0	1	1	0	0	0
Tropaeolaceae	0	1	0	1	0	0	1	0	0
Berberidaceae	0	1	1	0	0	0	1	0	0
Balsaminaceae	1	1	0	0	0	1	0	0	0
Loasaceae	0	1	1	0	0	0	1	0	0
Urticaceae	1	0	1	0	1	0	0	0	0
Caprifoliaceae	1	1	0	1	0	0	0	0	0
Anacardiaceae	1	1	1	0	0	0	0	0	0
Cannaceae	1	1	0	0	0	1	0	0	0
Iridaceae	1	1	0	1	0	0	0	0	0
Phrymaceae	0	1	1	1	0	0	0	0	0
Meliaceae	1	0	1	0	0	1	0	0	0
Clethraceae	1	1	1	0	0	0	0	0	0
Polemoniaceae	1	1	0	1	0	0	0	0	0
Sapindaceae	1	1	0	0	0	1	0	0	0
Caricaceae	1	0	0	0	0	1	0	0	0
Liliaceae	0	1	0	1	0	0	0	0	0
Ranunculaceae	0	1	0	1	0	0	0	0	0
Fouquieriaceae	1	1	0	0	0	0	0	0	0
Polygonaceae	1	0	0	0	0	1	0	0	0
Lecythidaceae	1	0	0	0	0	1	0	0	0
Nyctaginaceae	1	1	0	0	0	0	0	0	0
Simaroubaceae	1	0	0	0	1	0	0	0	0
Pittosporaceae	1	1	0	0	0	0	0	0	0
Hypericaceae	1	0	0	0	0	0	1	0	0
Plumbaginaceae	1	1	0	0	0	0	0	0	0
Sapotaceae	1	1	0	0	0	0	0	0	0
Geraniaceae	0	0	1	1	0	0	0	0	0
Strelitziaceae	1	1	0	0	0	0	0	0	0
Xanthorrhoeaceae	1	1	0	0	0	0	0	0	0
Caryophyllaceae	0	1	0	1	0	0	0	0	0
Brassicaceae	0	1	1	0	0	0	0	0	0
Saxifragaceae	0	1	0	1	0	0	0	0	0
Velloziaceae	1	0	0	0	1	0	0	0	0
Betulaceae	0	1	0	0	0	0	0	0	0

S2 Table (continued)

	Emeralds	Bees	Coquettes	MtGems	Mangoes	Hermits	Brilliants	Topazes	Patagona
Columelliaceae	0	0	0	0	0	0	1	0	0
Elaeocarpaceae	0	0	1	0	0	0	0	0	0
Araliaceae	1	0	0	0	0	0	0	0	0
Cleomaceae	0	1	0	0	0	0	0	0	0
Begoniaceae	1	0	0	0	0	0	0	0	0
Muntingiaceae	0	1	0	0	0	0	0	0	0
Bonnetiaceae	1	0	0	0	0	0	0	0	0
Calycanthaceae	1	0	0	0	0	0	0	0	0
Calophyllaceae	0	1	0	0	0	0	0	0	0
Loganiaceae	1	0	0	0	0	0	0	0	0
Moraceae	1	0	0	0	0	0	0	0	0
Symplocaceae	0	0	1	0	0	0	0	0	0
Oleaceae	0	1	0	0	0	0	0	0	0
Papaveraceae	0	1	0	0	0	0	0	0	0
Tetrameristaceae	1	0	0	0	0	0	0	0	0
Ochnaceae	0	0	0	0	0	0	1	0	0
Vitaceae	1	0	0	0	0	0	0	0	0
Rhamnaceae	0	1	0	0	0	0	0	0	0
Escalloniaceae	0	0	1	0	0	0	0	0	0
Phyllanthaceae	0	0	1	0	0	0	0	0	0
Polygalaceae	0	1	0	0	0	0	0	0	0
Zygophyllaceae	0	1	0	0	0	0	0	0	0
Chrysobalanaceae	1	0	0	0	0	0	0	0	0

S3 Table. Plant families and hummingbird clades associated by modularity analysis. Plant families associated with hummingbird clades in more than 90% of the modularity analyses. We used the network with nodes ordered phylogenetically and only included native plant species. Numbers in parenthesis correspond to the number of analyses in which the plant family belonged to the same module as the hummingbird clade. The text color represents the pollination syndrome of each family: red (ornithophilous), blue (intermediate), and black (non-ornithophilous). See Table 2 in the text for details on the characteristics of each pollination syndrome category.

(DOC)

Bees	Mountain Gems	Emeralds	Patagona	Coquettes	Brilliants	Mangoes	Hermits	Topazes
Betulaceae (50)	Asparagaceae (45)	Araliaceae (50)	Campanulaceae (50)	Berberidaceae (47)	Columelliaceae (50)			Ericaceae (50)
Caprifoliaceae (48)	Cactaceae (45)	Begoniaceae (50)	Lamiaceae (50)	Elaeocarpaceae (50)	Ochnaceae (50)			Fabaceae (50)
Caryophyllaceae (50)	Convolvulaceae (46)	Bonnetiaceae (50)	Loranthaceae (50)	Escalloniaceae (50)				Gesneriaceae (50)
Cleomaceae (50)	Grossulariaceae (46)	Calycanthaceae (50)	Passifloraceae (45)	Loasaceae (47)				Heliconiaceae (50)
Iridaceae (46)	Plantaginaceae (46)	Caricaceae (48)	Scrophulariaceae (45)	Melastomataceae (50)				Malvaceae (50)
Liliaceae (50)		Chrysobalanaceae (50)	Solanaceae (50)	Phyllanthaceae (50)				Marcgraviaceae (50)
Muntingiaceae (50)		Lecythidaceae (48)		Proteaceae (47)				Rubiaceae (50)
Papaveraceae (50)		Loganiaceae (50)		Symplocaceae (50)				
Phrymaceae (49)		Moraceae (50)						
Plumbaginaceae (50)		Polygonaceae (50)						
Polemoniaceae (47)		Strelitziaceae (50)						
Polygalaceae (50)		Tetrameristaceae (50)						
Ranunculaceae (50)								
Rhamnaceae (50)								
Saxifragaceae (50)								
Tropaeolaceae (48)								
Zygophyllaceae (50)								

S4 Table. Biogeographical, elevational, latitudinal, and morphological information and center of diversification for the hummingbird species included in this study. The source(s) of information for each category is (are) shown in the REF column and the Supplementary References section (see below). For the biogeographical distribution regions, the value 1 represents the presence of a hummingbird species in this (these) region(s); in contrast, 0 represents the lack of records. The latitudinal and elevational range columns are the difference between the minimum and maximum value for each category. The asterisk (*) in the Geographical Area column means that the center od diversification of these hummingbird species was indirectly inferred based on the closest sister species whose center of diversification has been explicitly detected. Also, the inference method used in the different studies to establish the center of diversification area is shown. For the definition of each biogeographical region and geographical area, see the text. For culmen, weight, and wing morphological information, the mean and standard deviation (s.d.) of each hummingbird species are shown. The definition of each bill curvature category is explained in the text. (DOC)

Clade	Species	Biogeographical Region					Latitude Distribution (°)				Elevation Distribution (m.a.s.l.)				Center of Diversification			Culmen (mm)		Weight (g)		Wing (mm)		Curvature	Morphology
		Neartic	Neotropical	Caribbean	Austral	REF	High	Low	Range	REF	Minimum	Maximum	Range	REF	Geographical Area*	Inference	REF	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	REF
Bees	*Archilochus alexandri*	1	1	0	0	[1, 2]	50	32	18	[3]	0	2000	2000	[4]	North America	Ancestral State Reconstruction	[5]	17.673	1.254	2.950	0.286	41.145	2.292	2	[6], [3], Núñez L. (unpublished data), Rodríguez-Flores (unpublished data)
Bees	*Archilochus colubris*	1	1	0	0	[1, 2]	60	30	30	[3]	0	2450	2450	[7]	North America	Ancestral State Reconstruction	[5]	17.763	1.384	2.977	0.493	43.269	2.249	2	[6], [3], Núñez L. (unpublished data)
Bees	*Atthis ellioti*	0	1	0	0	[1, 2]	14	14	0.2	[3]	900	3300	2400	[7]	North America	Ancestral State Reconstruction	[5]			2.300	0.424			2	[6]
Bees	*Atthis heloisa*	1	1	0	0	[1, 2]	26	17	9	[3]	1500	2900	1400	[7]	North America	Ancestral State Reconstruction	[5]	13.033	0.357	2.132	0.192	36.458	3.035	2	[6], [3], Núñez L. (unpublished data)
Bees	*Calliphlox amethystina*	0	1	0	0	[1, 2]	6	-28	34	[3]	0	1500	1500	[7]	South America	Ancestral State Reconstruction	[5]			2.400	0.141			2	[6]
Bees	*Calliphlox bryantae*	0	1	0	0	[1, 2]	10	9	1	[3]	1830	1830	0	[7]	South America	Ancestral State Reconstruction	[5]	19.900	0.300	3.343	0.067	41.700	0.300	2	[6], Núñez L. (unpublished data)
Bees	*Calliphlox evelynae*	0	0	1	0	[1, 2]	27	21	6	[3]	0	100	100	[2]	Caribbean	Ancestral State Reconstruction	[5]	15.750	0.350	2.850	0.370	40.050	0.750	3	[6], Núñez L. (unpublished data)
Bees	*Calliphlox mitchellii*	0	1	0	0	[1, 2]	9	0	9	[3]	0	1900	1900	[7]	South America	Ancestral State Reconstruction	[5]			3.150	0.212			2	[6]
Bees	*Calothorax lucifer*	1	1	0	0	[1, 2]	33	19	14	[3]	1100	2250	1150	[7]	North America	Ancestral State Reconstruction	[5]	12.350	0.050	3.275	0.287	36.350	1.350	3	[6], Núñez L. (unpublished data)
Bees	*Calothorax pulcher*	1	1	0	0	[1, 2]	19	16	3	[3]	1000	2000	1000	[7]	North America	Ancestral State Reconstruction	[5]			2.850	0.354			3	[6]
Bees	*Calypte anna*	1	0	0	0	[1, 2]	45	30	15	[3]	0	1800	1800	[7]	North America	Ancestral State Reconstruction	[5]	18.500	0.300	4.275	0.955	49.650	0.050	2	[6], Núñez L. (unpublished data)
Bees	*Calypte costae*	1	1	0	0	[1, 2]	38	29	9	[3]	0	1500	1500	[7]	North America	Ancestral State Reconstruction	[5]	18.160	0.755	2.783	0.361	42.984	2.372	2	[6], [3], Núñez L. (unpublished data)
Bees	*Chaetocercus astreans*	0	1	0	0	[1, 2]	11	10	1	[3]	825	2000	1175	[2]	South America*	Ancestral State Reconstruction	[8]							2	[6]
Bees	*Chaetocercus berlepschi*	0	1	0	0	[1, 2]	2	-5	7	[3]	0	500	500	[2]	South America*	Ancestral State Reconstruction	[8]							2	[6]
Bees	*Chaetocercus bombus*	0	1	0	0	[1, 2]	-1	-12	11	[3]	0	3000	3000	[2]	South America	Ancestral State Reconstruction	[5]							2	[6]
Bees	*Chaetocercus heliodor*	0	1	0	0	[1, 2]	10	0	10	[3]	500	3000	2500	[7]	South America*	Ancestral State Reconstruction	[8]							2	[6]
Bees	*Chaetocercus jourdanii*	0	1	0	0	[1, 2]	11	7	3	[3]	900	3000	2100	[7]	South America*	Ancestral State Reconstruction	[8]							2	[6]
Bees	*Chaetocercus mulsant*	0	1	0	0	[1, 2]	4	-18	22	[3]	1500	2800	1300	[7]	South America	Ancestral State Reconstruction	[5]			3.800				2	[6]
Bees	*Doricha eliza*	0	1	0	0	[1, 2]	19	18	1	[3]	300	2250	1950	[7]	North America	Ancestral State Reconstruction	[5]	21.850	0.550	2.475	0.150	37.900	0.800	4	[6]
Bees	*Eulidia yarrellii*	0	0	0	1	[1, 2]	-17	-24	7	[3]	200	1840	1640	[2]	South America	Ancestral State Reconstruction	[5]			2.450	0.212			2	[6]

Bees	*Mellisuga helenae*	0	0	1	0	[1, 2]	23	19	4	[3]	0	500	500	[7]	Caribbean*	Ancestral State Reconstruction	[5]			1.750	0.212			2	[6]
Bees	*Mellisuga minima*	0	0	1	0	[1, 2]	20	18	2	[3]	0	1600	1600	[2]	Caribbean	Ancestral State Reconstruction	[5]			3.000	0.424			2	[6], Núñez L. (unpublished data)
Bees	*Myrmia micrura*	0	1	0	0	[1, 2]	-1	-9	8	[3]	0	100	100	[7]	South America	Ancestral State Reconstruction	[5]			3.000	0.424			3	[6]
Bees	*Myrtis fanny*	0	1	0	0	[1, 2]	-1	-12	11	[3]	1200	2800	1600	[7]	South America	Ancestral State Reconstruction	[5]			2.375	0.087			2	[6], Núñez L. (unpublished data)
Bees	*Rhodopis vesper*	0	1	0	1	[1, 2]	-6	-28	22	[3]	0	3050	3050	[7]	South America	Ancestral State Reconstruction	[5]			3.900	0.424			3	[6]
Bees	*Selasphorus calliope*	1	1	0	0	[1, 2]	50	31	19	[3]	180	3500	3320	[7]	North America	Ancestral State Reconstruction	[5]	14.506	0.953	2.270	0.386	39.906	2.044	2	[6], [3], Núñez L. (unpublished data)
Bees	*Selasphorus flammula*	0	1	0	0	[1, 2]	11	8	3	[3]	1700	3100	1400	[7]	North America	Ancestral State Reconstruction	[5]	12.325	0.575	2.650	0.173	40.995	0.955	2	[6], Núñez L. (unpublished data)
Bees	*Selasphorus platycercus*	1	1	0	0	[1, 2]	45	15	30	[3]	900	3350	2450	[7]	North America	Ancestral State Reconstruction	[5]	18.233	1.503	2.909	0.431	45.828	4.038	2	[6], [3], Núñez L. (unpublished data)
Bees	*Selasphorus rufus*	1	1	0	0	[1, 2]	60	42	18	[3]	0	2250	2250	[7]	North America	Ancestral State Reconstruction	[5]	17.327	1.450	2.948	0.440	42.452	2.022	2	[6], [3], Núñez L. (unpublished data)
Bees	*Selasphorus sasin*	1	0	0	0	[1, 2]	45	35	10	[3]	300	2500	2200	[7]	North America	Ancestral State Reconstruction	[5]	16.233	1.167	3.134	0.468	38.800	2.007	2	[6], [3], Núñez L. (unpublished data)
Bees	*Selasphorus scintilla*	0	1	0	0	[1, 2]	9	8	1	[3]	1220	3000	1780	[7]	North America	Ancestral State Reconstruction	[5]	11.350	0.600	2.213	0.119	34.265	1.555	2	[6], Núñez L. (unpublished data)
Bees	*Thaumastura cora*	0	1	0	1	[1, 2]	-6	-20	14	[3]	0	2400	2400	[2]	South America	Ancestral State Reconstruction	[5]			2.250	0.354			2	[6]
Bees	*Tilmatura dupontii*	1	1	0	0	[1, 2]	24	13	11	[3]	500	1950	1450	[7]	North America	Ancestral State Reconstruction	[5]	14.700	1.200	2.650	0.472	34.650	0.950	2	[6], [3]
Brilliants	*Aglaeactis aliciae*	0	1	0	0	[1, 2]	-6	-8	2	[3]	3000	3500	500	[2]	South America*	Ancestral State Reconstruction	[8]			7.800	0.707			2	[6]
Brilliants	*Aglaeactis castelnaudii*	0	1	0	0	[1, 2]	-10	-14	4	[3]	3500	4300	800	[2]	South America	Ancestral State Reconstruction	[8]			7.750	0.612			2	[6], Núñez L. (unpublished data)
Brilliants	*Aglaeactis cupripennis*	0	1	0	0	[1, 2]	8	-16	24	[3]	2900	3400	500	[7]	South America	Ancestral State Reconstruction	[8]			7.517	0.426			2	[6], Núñez L. (unpublished data)
Brilliants	*Aglaeactis pamela*	0	1	0	0	[1, 2]	-16	-18	2	[3]	3000	3500	500	[2]	South America*	Ancestral State Reconstruction	[8]			7.625	0.675			2	[6], Núñez L. (unpublished data)
Brilliants	*Boissonneaua flavescens*	0	1	0	1	[1, 2]	9	0	9	[3]	1400	2800	1400	[7]	South America	Ancestral State Reconstruction	[8]	17.252	1.009	8.275	0.377	75.618	3.420	2	[6], [3], Núñez L. (unpublished data)
Brilliants	*Boissonneaua jardini*	0	1	0	1	[1, 2]	6	0	6	[3]	350	2200	1850	[7]	South America*	Ancestral State Reconstruction	[8]	18.450	0.250	8.615	0.580	73.800	2.800	2	[6], Núñez L. (unpublished data)
Brilliants	*Clytolaema rubricauda*	0	1	0	0	[1, 2]	-12	-32	20	[3]	0	2410	2410	[7]	South America*	Ancestral State Reconstruction	[8]			7.567	1.277			2	[6], Núñez L. (unpublished data)
Brilliants	*Coeligena bonapartei*	0	1	0	0	[1, 2]	9	6	3	[3]	1400	3200	1800	[7]	South America*	Ancestral State Reconstruction	[8]	29.003	1.957	6.650	0.354	71.738	3.037	2	[6], [3]
Brilliants	*Coeligena coeligena*	0	1	0	0	[1, 2]	10	-18	28	[3]	1000	2600	1600	[7]	South America	Ancestral State Reconstruction	[8]	29.807	1.565	6.975	0.888	70.910	3.286	2	[6], [3], Núñez L. (unpublished data)
Brilliants	*Coeligena helianthea*	0	1	0	0	[1, 2]	8	6	2	[3]	1900	3300	1400	[7]	South America*	Ancestral State Reconstruction	[8]	30.079	1.638	6.762	0.593	70.687	2.147	2	[6], [3], Núñez L. (unpublished data)
Brilliants	*Coeligena iris*	0	1	0	0	[1, 2]	0	-6	6	[3]	1700	3500	1800	[7]	South America*	Ancestral State Reconstruction	[8]	28.726	0.662	8.400	0.361	77.242	4.569	2	[6], [3]
Brilliants	*Coeligena lutetiae*	0	1	0	0	[1, 2]	4	-8	12	[3]	2600	3600	1000	[7]	South America	Ancestral State	[8]	32.462	2.718	6.680	0.342	73.099	3.302	2	[6], [3], Núñez L. (unpublished

																Reconstruction								data)
Brilliants	*Coeligena prunellei*	0	1	0	0	[1, 2]	8	5	3	[3]	1400	2600	1200	[7]	South America*	Ancestral State Reconstruction	[8]	27.325	1.952	6.800	0.283	70.797	0.894	2	[6], [3]
Brilliants	*Coeligena torquata*	0	1	0	1	[1, 2]	8	-18	26	[3]	1500	3000	1500	[7]	South America	Ancestral State Reconstruction	[8]	33.575	1.915	7.043	0.444	73.955	3.379	2	[6], [3], Núñez L. (unpublished data)
Brilliants	*Coeligena violifer*	0	1	0	0	[1, 2]	-14	-18	4	[3]	2800	3300	500	[2]	South America	Ancestral State Reconstruction	[8]	33.008	2.214	7.606	0.846	75.321	4.043	2	[6], [3], Núñez L. (unpublished data)
Brilliants	*Coeligena wilsoni*	0	1	0	0	[1, 2]	6	0	6	[3]	700	2000	1300	[7]	South America	Ancestral State Reconstruction	[8]	32.510	1.060	7.405	1.284	68.005	2.435	2	[6], Núñez L. (unpublished data)
Brilliants	*Ensifera ensifera*	0	1	0	0	[1, 2]	8	-18	26	[3]	1700	3300	1600	[7]	South America	Ancestral State Reconstruction	[8]			13.500	2.121			1	[6]
Brilliants	*Eriocnemis cupreoventris*	0	1	0	0	[1, 2]	8	6	2	[3]	1950	3000	1050	[7]	South America*	Ancestral State Reconstruction	[8]	17.785	0.105	5.303	0.335	58.400	1.130	2	[6], Núñez L. (unpublished data)
Brilliants	*Eriocnemis derbyi*	0	1	0	0	[1, 2]	6	0	6	[3]	2500	3600	1100	[7]	South America*	Ancestral State Reconstruction	[8]							2	[6]
Brilliants	*Eriocnemis luciani*	0	1	0	0	[1, 2]	2	-8	10	[3]	2800	4800	2000	[7]	South America	Ancestral State Reconstruction	[8]			6.075	0.457			2	[6], Núñez L. (unpublished data)
Brilliants	*Eriocnemis mirabilis*	0	1	0	0	[1, 2]	3	2	1	[3]	2200	2200	0	[7]	South America*	Ancestral State Reconstruction	[8]							2	[6]
Brilliants	*Eriocnemis mosquera*	0	1	0	0	[1, 2]	6	0	6	[3]	1200	3600	2400	[7]	South America	Ancestral State Reconstruction	[8]			5.500	0.424			2	[6]
Brilliants	*Eriocnemis nigrivestis*	0	1	0	0	[1, 2]	2	-5	7	[3]	2750	4700	1950	[7]	South America*	Ancestral State Reconstruction	[8]			4.450	0.212			2	[6]
Brilliants	*Eriocnemis vestita*	0	1	0	0	[1, 2]	8	-6	14	[3]	2250	3850	1600	[7]	South America	Ancestral State Reconstruction	[8]	18.610	0.930	4.660	0.368	56.505	0.855	2	[6], Núñez L. (unpublished data)
Brilliants	*Haplophaedia aureliae*	0	1	0	0	[1, 2]	9	-17	26	[3]	1500	3100	1600	[7]	South America	Ancestral State Reconstruction	[8]	17.855	0.115	5.003	1.020	56.985	1.765	2	[6], Núñez L. (unpublished data)
Brilliants	*Haplophaedia lugens*	0	1	0	0	[1, 2]	2	-1	3	[3]	1100	2000	900	[7]	South America	Ancestral State Reconstruction	[8]	20.250	0.250	5.500	0.707	63.500	1.600	2	[6], Núñez L. (unpublished data)
Brilliants	*Heliodoxa gularis*	0	1	0	0	[1, 2]	2	-4	6	[3]	600	1100	500	[7]	South America*	Ancestral State Reconstruction	[8]	25.298	1.135			61.093	3.033	3	[6], [3]
Brilliants	*Heliodoxa imperatrix*	0	1	0	0	[1, 2]	5	0	5	[3]	400	2050	1650	[7]	South America	Ancestral State Reconstruction	[8]	24.193	0.337	8.074	0.956	64.863	4.650	2	[6], [3], Núñez L. (unpublished data)
Brilliants	*Heliodoxa jacula*	0	1	0	0	[1, 2]	10	0	10	[3]	500	2300	1800	[7]	South America	Ancestral State Reconstruction	[8]	21.748	0.886	7.228	0.621	68.128	5.330	2	[6], [3], Núñez L. (unpublished data)
Brilliants	*Heliodoxa rubinoides*	0	1	0	0	[1, 2]	6	-6	12	[3]	1200	2600	1400	[7]	South America	Ancestral State Reconstruction	[8]	22.200	1.300	8.450	0.354	68.960	0.900	3	[6], Núñez L. (unpublished data)
Brilliants	*Heliodoxa xanthogonys*	0	1	0	0	[1, 2]	7	0	7	[3]	700	2000	1300	[7]	South America	Ancestral State Reconstruction	[8]	18.752	1.881	6.817	0.426	65.348	2.608	2	[6], [3]
Brilliants	*Lafresnaya lafresnayi*	0	1	0	0	[1, 2]	9	-12	21	[3]	1500	3700	2200	[7]	South America	Ancestral State Reconstruction	[8]			5.400	0.735			4	[6], Núñez L. (unpublished data)
Brilliants	*Loddigesia mirabilis*	0	1	0	0	[1, 2]	-6	-8	2	[3]	2100	2900	800	[2]	South America*	Ancestral State Reconstruction	[8]			3.000				2	[6]
Brilliants	*Ocreatus underwoodii*	0	1	0	0	[1, 2]	11	-18	29	[3]	850	3100	2250	[7]	South America	Ancestral State Reconstruction	[8]	13.495	0.335	2.850	0.253	41.325	1.025	2	[6], Núñez L. (unpublished data)
Brilliants	*Pterophanes cyanopterus*	0	1	0	0	[1, 2]	8	-18	26	[3]	2600	3600	1000	[7]	South America	Ancestral State Reconstruction	[8]			10.375	0.767			2	[6], Núñez L. (unpublished data)
Brilliants	*Urochroa bougueri*	0	1	0	0	[1, 2]	4	-4	8	[3]	500	2500	2000	[7]	South America	Ancestral State Reconstruction	[8]			8.850	0.495			2	[6]

Brilliants	*Urosticte benjamini*	0	1	0	0	[1, 2]	6	0	6	[3]	700	1500	800	[7]	South America	Ancestral State Reconstruction	[8]			4.000	0.283			2	[6]
Brilliants	*Urosticte ruficrissa*	0	1	0	0	[1, 2]	2	-6	8	[3]	1600	2300	700	[7]	South America*	Ancestral State Reconstruction	[8]			4.100	0.141			2	[6]
Coquettes	*Adelomyia melanogenys*	0	1	0	1	[1, 2]	10	-25	35	[3]	1000	2500	1500	[7]	South America	Ancestral State Reconstruction	[8]	13.815	0.025	4.100	0.625	51.175	2.075	2	[6], Núñez L. (unpublished data)
Coquettes	*Aglaiocercus berlepschi*	0	1	0	0	[1, 2]	12	12	0.2	[3]	1450	1800	350	[2]	South America*	Ancestral State Reconstruction	[8]			5.000	0.707			2	[6]
Coquettes	*Aglaiocercus coelestis*	0	1	0	0	[1, 2]	10	0	10	[3]	300	2100	1800	[7]	South America	Ancestral State Reconstruction	[8]	15.135	0.135	5.125	0.709	61.860	5.860	2	[6], Núñez L. (unpublished data)
Coquettes	*Aglaiocercus kingi*	0	1	0	0	[1, 2]	10	-18	28	[3]	900	3000	2100	[7]	South America	Ancestral State Reconstruction	[8]			5.540	0.639			2	[6], Núñez L. (unpublished data)
Coquettes	*Chalcostigma herrani*	0	1	0	0	[1, 2]	6	-7	13	[3]	2700	3600	900	[7]	South America	Ancestral State Reconstruction	[8]			5.950	0.636			2	[6]
Coquettes	*Chalcostigma heteropogon*	0	1	0	0	[1, 2]	7	6	1	[3]	2900	3500	600	[7]	South America*	Ancestral State Reconstruction	[8]			6.100	0.283			2	[6]
Coquettes	*Chalcostigma olivaceum*	0	1	0	0	[1, 2]	-12	-16	4	[3]	3600	4600	1000	[2]	South America*	Ancestral State Reconstruction	[8]			8.500	0.707			2	[6]
Coquettes	*Chalcostigma ruficeps*	0	1	0	0	[1, 2]	4	-18	22	[3]	2100	2700	600	[7]	South America	Ancestral State Reconstruction	[8]			3.600	0.424			2	[6]
Coquettes	*Chalcostigma stanleyi*	0	1	0	0	[1, 2]	-1	-18	17	[3]	3500	4500	1000	[7]	South America*	Ancestral State Reconstruction	[8]			5.350	1.202			2	[6]
Coquettes	*Discosura conversii*	0	1	0	0	[1, 2]	10	-3	13	[3]	0	1400	1400	[7]	South America	Ancestral State Reconstruction	[8]			3.000				2	[6]
Coquettes	*Discosura langsdorffi*	0	1	0	0	[1, 2]	3	-22	25	[3]	0	300	300	[7]	South America*	Ancestral State Reconstruction	[8]	11.550	0.350	2.733	0.503			2	[6], Núñez L. (unpublished data)
Coquettes	*Discosura longicaudus*	0	1	0	0	[1, 2]	8	-22	30	[3]	0	200	200	[7]	South America*	Ancestral State Reconstruction	[8]			3.350	0.495			2	[6]
Coquettes	*Discosura popelairii*	0	1	0	0	[1, 2]	6	-13	19	[3]	500	1200	700	[7]	South America	Ancestral State Reconstruction	[8]			2.500				2	[6]
Coquettes	*Heliangelus amethysticollis*	0	1	0	0	[1, 2]	9	-18	27	[3]	1800	3200	1400	[2]	South America	Ancestral State Reconstruction	[8]	17.901	0.730	5.550	0.590	64.714	3.096	2	[6], [3], Núñez L. (unpublished data)
Coquettes	*Heliangelus exortis*	0	1	0	0	[1, 2]	7	-6	13	[3]	1500	3400	1900	[7]	South America*	Ancestral State Reconstruction	[8]	15.672	0.761	4.240	0.611	60.635	4.422	2	[6], [3], Núñez L. (unpublished data)
Coquettes	*Heliangelus mavors*	0	1	0	0	[1, 2]	10	6	4	[3]	2000	3200	1200	[7]	South America*	Ancestral State Reconstruction	[8]	14.247	0.402	4.150	0.354	60.543	3.504	2	[6], [3]
Coquettes	*Heliangelus regalis*	0	1	0	0	[1, 2]	-6	-8	2	[3]	1950	2200	250	[7]	South America*	Ancestral State Reconstruction	[8]			4.000	0.707			2	[6]
Coquettes	*Heliangelus viola*	0	1	0	0	[1, 2]	0	-7	7	[3]	2000	3500	1500	[7]	South America*	Ancestral State Reconstruction	[8]	15.055	0.425	6.010	0.800	65.470	2.030	2	[6], [3]
Coquettes	*Lesbia nuna*	0	1	0	1	[1, 2]	8	-18	26	[3]	2000	3800	1800	[7]	South America	Ancestral State Reconstruction	[8]	17.050	0.450	3.800		53.750	2.150	2	[6], Núñez L. (unpublished data)
Coquettes	*Lesbia victoriae*	0	1	0	1	[1, 2]	7	-14	21	[3]	2600	4000	1400	[7]	South America	Ancestral State Reconstruction	[8]	18.900	0.200	4.900	0.346	57.600	2.300	2	[6], Núñez L. (unpublished data)
Coquettes	*Lophornis adorabilis*	0	1	0	0	[1, 2]	10	8	2	[3]	300	1200	900	[2]	North America*	Ancestral State Reconstruction	[8]	10.828	0.384	2.700		37.500	1.470	2	[6], [3]
Coquettes	*Lophornis brachylophus*	0	1	0	0	[1, 2]	17	17	0.2	[3]	900	1800	900	[2]	North America*	Ancestral State Reconstruction	[8]	9.967	0.499	2.667	0.306	44.700	2.112	2	[6], [3]
Coquettes	*Lophornis chalybeus*	0	1	0	0	[1, 2]	6	-36	42	[3]	100	600	500	[7]	South America*	Ancestral State	[8]	13.334	0.756	2.800	0.346	41.898	1.905	2	[6], [3], Núñez L. (unpublished

																Reconstruction									data)
Coquettes	*Lophornis delattrei*	0	1	0	0	[1, 2]	8	-18	26	[3]	600	2000	1400	[7]	South America	Ancestral State Reconstruction	[8]	11.600	0.200	2.800	0.200	37.500	0.600	2	[6], Núñez L. (unpublished data)
Coquettes	*Lophornis helenae*	1	1	0	0	[1, 2]	17	10	7	[3]	350	1450	1100	[7]	North America*	Ancestral State Reconstruction	[8]	11.455	0.503	2.700	0.141	40.873	0.954	2	[6], [3]
Coquettes	*Lophornis magnificus*	0	1	0	0	[1, 2]	-15	-20	5	[3]	0	1000	1000	[2]	South America*	Ancestral State Reconstruction	[8]			3.000				2	[6]
Coquettes	*Lophornis ornatus*	0	1	0	0	[1, 2]	11	2	9	[3]	100	950	850	[7]	South America*	Ancestral State Reconstruction	[8]			2.550	0.354			2	[6]
Coquettes	*Lophornis pavoninus*	0	1	0	0	[1, 2]	6	5	1	[3]	500	2000	1500	[7]	South America	Ancestral State Reconstruction	[8]							2	[6]
Coquettes	*Lophornis stictolophus*	0	1	0	0	[1, 2]	6	-5	11	[3]	0	1300	1300	[7]	South America*	Ancestral State Reconstruction	[8]	10.230	0.784			36.118	1.319	2	[6], [3]
Coquettes	*Metallura aeneocauda*	0	1	0	0	[1, 2]	-14	-18	4	[3]	3000	3600	600	[2]	South America	Ancestral State Reconstruction	[8]			5.300	0.141			2	[6]
Coquettes	*Metallura baroni*	0	1	0	0	[1, 2]	2	-5	7	[3]	1900	1900	0	[7]	South America*	Ancestral State Reconstruction	[8]			4.350	0.212			2	[6]
Coquettes	*Metallura odomae*	0	1	0	0	[1, 2]	-7	-8	1	[3]	2600	3350	750	[2]	South America*	Ancestral State Reconstruction	[8]			5.000	0.283			2	[6]
Coquettes	*Metallura phoebe*	0	1	0	1	[1, 2]	-7	-18	11	[3]	1980	3050	1070	[7]	South America	Ancestral State Reconstruction	[8]			5.750	0.212			2	[6]
Coquettes	*Metallura theresiae*	0	1	0	0	[1, 2]	0	-8	8	[3]	2900	3800	900	[2]	South America*	Ancestral State Reconstruction	[8]			4.900	0.141			2	[6]
Coquettes	*Metallura tyrianthina*	0	1	0	1	[1, 2]	10	-18	28	[3]	1700	3800	2100	[7]	South America	Ancestral State Reconstruction	[8]			3.500	0.141			2	[6]
Coquettes	*Metallura williami*	0	1	0	0	[1, 2]	7	0	7	[3]	2100	3800	1700	[7]	South America	Ancestral State Reconstruction	[8]			4.525	0.247			2	[6], Núñez L. (unpublished data)
Coquettes	*Opisthoprora euryptera*	0	1	0	0	[1, 2]	6	-8	14	[3]	2500	3600	1100	[7]	South America	Ancestral State Reconstruction	[8]			6.300	0.416			3	[6]
Coquettes	*Oreonympha nobilis*	0	1	0	0	[1, 2]	-12	-14	2	[3]	2500	3900	1400	[2]	South America	Ancestral State Reconstruction	[8]			9.000				2	[6]
Coquettes	*Oreotrochilus adela*	0	0	0	1	[1, 2]	-16	-20	4	[3]	2600	4000	1400	[2]	South America*	Ancestral State Reconstruction	[8]			7.850	0.636			3	[6]
Coquettes	*Oreotrochilus chimborazo*	0	1	0	0	[1, 2]	0	-1	1	[3]	5300	5300	0	[7]	South America	Ancestral State Reconstruction	[8]			7.950	0.212			3	[6]
Coquettes	*Oreotrochilus estella*	0	1	0	1	[1, 2]	-6	-18	12	[3]	1830	4300	2470	[7]	South America	Ancestral State Reconstruction	[8]			8.400	0.566			3	[6]
Coquettes	*Oreotrochilus leucopleurus*	0	1	0	1	[1, 2]	-21	-35	14	[3]	1525	3660	2135	[7]	South America*	Ancestral State Reconstruction	[8]			8.150	0.354			3	[6]
Coquettes	*Oreotrochilus melanogaster*	0	1	0	1	[1, 2]	-12	-14	2	[3]	3500	4400	900	[2]	South America*	Ancestral State Reconstruction	[8]			8.400				3	[6]
Coquettes	*Oxypogon guerinii*	0	1	0	0	[1, 2]	9	6	3	[3]	3200	5200	2000	[7]	South America	Ancestral State Reconstruction	[8]			5.175	0.634			2	[6], Núñez L. (unpublished data)
Coquettes	*Phlogophilus harterti*	0	1	0	0	[1, 2]	-10	-16	6	[3]	750	1500	750	[2]	South America*	Ancestral State Reconstruction	[8]			2.450	0.204			2	[6], Núñez L. (unpublished data)
Coquettes	*Phlogophilus hemileucurus*	0	1	0	0	[1, 2]	1	-8	9	[3]	400	1500	1100	[7]	South America	Ancestral State Reconstruction	[8]			2.600	0.566			2	[6]
Coquettes	*Polyonymus caroli*	0	1	0	1	[1, 2]	-14	-17	3	[3]	1500	3600	2100	[2]	South America*	Ancestral State Reconstruction	[8]			5.350	0.354			2	[6]

Coquettes	*Ramphomicron dorsale*	0	1	0	0	[1, 2]	11	10	1	[3]	2000	4500	2500	[7]	South America*	Ancestral State Reconstruction	[8]			3.500				2	[6]
Coquettes	*Ramphomicron microrhynchum*	0	1	0	0	[1, 2]	8	-18	26	[3]	1700	3400	1700	[7]	South America	Ancestral State Reconstruction	[8]			3.500				2	[6]
Coquettes	*Sappho sparganura*	0	1	0	1	[1, 2]	-20	-40	20	[3]	1500	4000	2500	[2]	South America*	Ancestral State Reconstruction	[8]			5.550	0.495			2	[6]
Coquettes	*Sephanoides fernandensis*	0	0	0	1	[1, 2]	-34	-34	0.2	[3]	0	0	0	[7]	South America	Ancestral State Reconstruction	[8]	15.105	0.399	8.900	2.311	76.685	4.622	2	[6], [3], Núñez L. (unpublished data)
Coquettes	*Sephanoides sephanoides*	0	0	0	1	[1, 2]	-24	-54	30	[3]	0	2135	2135	[7]	South America	Ancestral State Reconstruction	[8]	15.524	0.929	5.225	0.457	60.580	2.597	2	[6], [3], Núñez L. (unpublished data)
Coquettes	*Taphrolesbia griseiventris*	0	1	0	0	[1, 2]	-7	-10	3	[3]	2600	3500	900	[2]	South America*	Ancestral State Reconstruction	[8]	2.200	0.000					2	[6]
Emeralds	*Abeillia abeillei*	0	1	0	0	[1, 2]	17	13	4	[3]	1000	1850	850	[7]	North America	Ancestral State Reconstruction	[5]	11.193	0.455	2.700	0.000	45.105	2.015	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia amabilis*	0	1	0	0	[1, 2]	13	-2	15	[3]	0	1580	1580	[7]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	18.241	0.939	3.886	0.225	51.568	2.887	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia amazilia*	0	1	0	1	[1, 2]	1	-15	16	[3]	0	2500	2500	[7]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	18.508	0.653	4.789	0.509	59.200	2.273	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia beryllina*	1	1	0	0	[1, 2]	32	15	17	[3]	0	3000	3000	[7]	North America	Ancestral State Reconstruction	[5]	19.273	1.062	4.434	0.453	53.903	2.620	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia boucardi*	0	1	0	0	[1, 2]	11	8	3	[3]	0	200	200	[2]	North America*	Ancestral State Reconstruction	[8]	19.280	0.875	4.500		52.581	1.745	2	[6], [3]
Emeralds	*Amazilia brevirostris*	0	1	0	0	[1, 2]	8	12	4	[3]	0	500	500	[7]	South America*	Ancestral State Reconstruction	[8]	18.923	1.240	4.500	0.115	49.066	2.846	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia candida*	1	1	0	0	[1, 2]	21	-15	36	[3]	0	800	800	[7]	North America	Ancestral State Reconstruction	[5]	17.011	0.990	3.758	0.503	50.031	2.423	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia castaneiventris*	0	1	0	0	[1, 2]	10	9	1	[3]	150	2045	1895	[7]	South America*	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]							2	[6]
Emeralds	*Amazilia chionogaster*	0	1	0	1	[1, 2]	-4	-28	24	[3]	450	2000	1550	[2]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	22.767	1.423	5.120	0.567	57.013	2.532	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia cyanifrons*	0	1	0	0	[1, 2]	8	3	5	[3]	400	2000	1600	[7]	South America*	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	17.436	0.730	5.000		52.771	1.880	2	[6], [3]
Emeralds	*Amazilia cyanocephala*	1	1	0	0	[1, 2]	23	15	8	[3]	0	2550	2550	[7]	North America	Ancestral State Reconstruction	[5]	20.086	1.047	5.462	0.717	57.632	2.803	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia cyanura*	0	1	0	0	[1, 2]	16	14	2	[3]	0	1050	1050	[7]	North America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	18.520	0.971	3.960	0.351	52.172	2.490	2	[6], [3]
Emeralds	*Amazilia decora*	0	1	0	0	[1, 2]	9	7	2	[3]	0	1200	1200	[2]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	21.470	0.955	3.950	0.212	51.334	2.272	2	[6], [3]
Emeralds	*Amazilia edward*	0	1	0	0	[1, 2]	9	8	1	[3]	0	1830	1830	[7]	North America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	18.066	0.731	4.700	0.424	51.496	2.159	2	[6], [3]
Emeralds	*Amazilia fimbriata*	0	1	0	0	[1, 2]	8	-30	38	[3]	0	1300	1300	[7]	South America	Bayesian dispersal–	[9]	19.212	0.991	4.767	0.201	52.720	2.444	2	[6], [3], Núñez L. (unpublished

															vicariance analysis (S-DIVA)										data)
Emeralds	*Amazilia franciae*	0	1	0	0	[1, 2]	6	-7	13	[3]	1000	2000	1000	[7]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	22.772	0.662	5.134	0.366	53.724	2.617	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia lactea*	0	1	0	0	[1, 2]	6	-24	30	[3]	300	1400	1100	[7]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	18.185	0.809	4.325	0.614	52.016	1.757	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia leucogaster*	0	1	0	0	[1, 2]	9	-11	20	[3]	0	250	250	[7]	South America*	Ancestral State Reconstruction	[8]	21.187	1.030	4.400	0.115	51.813	1.818	3	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia luciae*	0	1	0	0	[1, 2]	15	14	1	[3]	75	345	270	[7]	North America*	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]							2	[6]
Emeralds	*Amazilia rosenbergi*	0	1	0	0	[1, 2]	6	1	5	[3]	0	200	200	[7]	South America*	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	21.076	1.071	3.750	0.351	50.782	2.499	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia rutila*	1	1	0	0	[1, 2]	25	14	11	[3]	0	1350	1350	[7]	North America	Ancestral State Reconstruction	[5]	21.612	1.807	4.868	0.977	56.569	4.647	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia saucerrottei*	0	1	0	0	[1, 2]	12	8	4	[3]	0	3000	3000	[7]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	17.523	0.861	4.883	0.241	52.109	2.076	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia tobaci*	0	1	0	0	[1, 2]	11	8	3	[3]	0	1800	1800	[7]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	18.482	0.712	4.400	0.283	52.968	2.434	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia tzacatl*	1	1	0	0	[1, 2]	23	9	14	[3]	0	1800	1800	[7]	North America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	20.749	1.308	4.408	0.543	55.518	2.903	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia versicolor*	0	1	0	0	[1, 2]	7	-28	35	[3]	0	1700	1700	[7]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	16.762	0.764	3.519	0.398	48.247	1.962	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia violiceps*	1	1	0	0	[1, 2]	32	17	15	[3]	0	2250	2250	[7]	North America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	22.250	1.116	5.185	0.516	56.152	3.818	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia viridigaster*	0	1	0	0	[1, 2]	8	0	8	[3]	0	2100	2100	[7]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	17.852	0.577	3.913	0.566	51.530	1.618	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Amazilia yucatanensis*	1	1	0	0	[1, 2]	27	16	11	[3]	0	600	600	[7]	North America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	20.476	0.756	4.104	0.248	54.519	1.695	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Aphantochroa cirrochloris*	0	1	0	0	[1, 2]	-10	-20	10	[3]	800	1460	660	[7]	South America	Ancestral State Reconstruction	[8]			9.000				2	[6]
Emeralds	*Campylopterus curvipennis*	1	1	0	0	[1, 2]	22	16	6	[3]	0	350	350	[7]	South America*	Ancestral State Reconstruction	[8]	27.020	1.057	8.113	2.459	65.280	3.178	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Campylopterus ensipennis*	0	1	1	0	[1, 2]	11	10	1	[3]	700	2000	1300	[7]	South America*	Ancestral State Reconstruction	[8]	26.119	2.331	9.750	0.354	66.189	20.046	3	[6], [3], Núñez L. (unpublished data)
Emeralds	*Campylopterus falcatus*	0	1	0	0	[1, 2]	10	-1	11	[3]	900	3000	2100	[7]	South America*	Ancestral State Reconstruction	[8]	23.880	1.512	6.927	1.081	64.797	2.543	3	[6], [3], Núñez L. (unpublished data)
Emeralds	*Campylopterus hemileucurus*	0	1	0	0	[1, 2]	17	8	9	[3]	0	2450	2450	[7]	South America	Ancestral State Reconstruction	[8]	31.050	4.414	10.133	1.108	75.583	2.643	4	[6], [3], Núñez L. (unpublished data)

Emeralds	*Campylopterus largipennis*	0	1	0	0	[1, 2]	8	-15	23	[3]	0	550	550	[7]	South America	Ancestral State Reconstruction	[8]	26.695	1.287	8.529	1.443	72.914	2.632	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Campylopterus phainopeplus*	0	1	0	0	[1, 2]	10	2	8	[3]	1200	4800	3600	[7]	South America*	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]							3	[6]
Emeralds	*Campylopterus rufus*	0	1	0	0	[1, 2]	16	12	4	[3]	1250	1850	600	[7]	North America	Ancestral State Reconstruction	[5]	25.915	1.424	7.580	1.308	73.648	1.161	3	[6], [3], Núñez L. (unpublished data)
Emeralds	*Campylopterus villaviscensio*	0	1	0	0	[1, 2]	0	-1	1	[3]	400	1500	1100	[7]	South America	Ancestral State Reconstruction	[8]	27.950	0.950	7.400	1.435			2	[6], Núñez L. (unpublished data)
Emeralds	*Chalybura buffonii*	0	1	0	0	[1, 2]	9	-4	13	[3]	0	2000	2000	[7]	South America	Ancestral State Reconstruction	[8]	23.160	0.250	6.358	0.620	65.010	3.090	2	[6], Núñez L. (unpublished data)
Emeralds	*Chalybura urochrysia*	0	1	0	0	[1, 2]	14	8	6	[3]	0	900	900	[7]	South America	Ancestral State Reconstruction	[8]	23.135	0.445	6.348	0.934	72.940	3.610	2	[6], Núñez L. (unpublished data)
Emeralds	*Chlorestes notata*	0	1	0	0	[1, 2]	6	-20	26	[3]	0	1000	1000	[7]	South America	Ancestral State Reconstruction	[8]	17.450	0.950	5.838	2.785			2	[6], Núñez L. (unpublished data)
Emeralds	*Chlorostilbon alice*	0	1	0	0	[1, 2]	11	9	2	[3]	750	1800	1050	[7]	South America*	Ancestral State Reconstruction	[8]			3.500	0.707			2	[6]
Emeralds	*Chlorostilbon auriceps*	1	1	0	0	[1, 2]	26	15	11	[4]	0	1800	1800	[7]	North America*	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]			3.250	0.354			2	[6]
Emeralds	*Chlorostilbon canivetii*	1	1	0	0	[1, 2]	23	10	13	[3]	0	1850	1850	[7]	North America	Ancestral State Reconstruction	[5]	14.670	2.047	2.291	0.488	45.472	2.276	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Chlorostilbon gibsoni*	0	1	0	0	[1, 2]	10	6	4	[3]	0	2300	2300	[7]	South America*	Ancestral State Reconstruction	[8]			3.250	0.354			2	[6]
Emeralds	*Chlorostilbon lucidus*	0	1	0	1	[1, 2]	-16	-23	7	[3]	1160	1160	0	[7]	South America*	Ancestral State Reconstruction	[8]			4.000	0.707			2	[6]
Emeralds	*Chlorostilbon maugaeus*	0	0	1	0	[1, 2]	19	18	1	[3]	0	800	800	[2]	Caribbean	Ancestral State Reconstruction	[5]	13.500	0.500	3.275	0.411	47.700	0.800	2	[6], Núñez L. (unpublished data)
Emeralds	*Chlorostilbon melanorhynchus*	0	1	0	0	[1, 2]	7	2	5	[10]	600	2700	2100	[2]	South America	Ancestral State Reconstruction	[8]			3.250	0.354			2	[6]
Emeralds	*Chlorostilbon mellisugus*	0	1	0	0	[1, 2]	11	-2	13	[3]	0	2200	2200	[7]	South America	Ancestral State Reconstruction	[8]	15.650	0.550	2.938	0.419	43.400	0.500	2	[6], Núñez L. (unpublished data)
Emeralds	*Chlorostilbon olivaresi*	0	1	0	0	[1, 2]	1	1	0.2	[3]	360	570	210	[7]	South America*	Ancestral State Reconstruction	[8]			3.700	0.141			2	[6]
Emeralds	*Chlorostilbon poortmani*	0	1	0	0	[1, 2]	8	5	3	[3]	500	2800	2300	[7]	South America*	Ancestral State Reconstruction	[8]			5.500	2.380			2	[6], Núñez L. (unpublished data)
Emeralds	*Chlorostilbon ricordii*	0	0	1	0	[1, 2]	27	21	6	[3]	0	1300	1300	[2]	Caribbean	Ancestral State Reconstruction	[5]	17.600	0.500	3.598	0.642	51.500	0.800	2	[6], Núñez L. (unpublished data)
Emeralds	*Chlorostilbon russatus*	0	1	0	0	[1, 2]	10	6	4	[3]	600	2600	2000	[7]	South America*	Ancestral State Reconstruction	[8]			3.400	0.283			2	[6]
Emeralds	*Chlorostilbon stenurus*	0	1	0	0	[1, 2]	9	8	1	[3]	1000	3000	2000	[7]	South America*	Ancestral State Reconstruction	[8]			3.400	0.283			2	[6]
Emeralds	*Chlorostilbon swainsonii*	0	0	1	0	[1, 2]	20	18	2	[3]	500	2500	2000	[2]	Caribbean	Ancestral State Reconstruction	[5]			3.750	1.768			2	[6]
Emeralds	*Chrysuronia oenone*	0	1	0	0	[1, 2]	8	-5	13	[3]	0	1500	1500	[7]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	20.584	0.941	4.825	0.499	51.166	2.072	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Cyanophaia bicolor*	0	0	1	0	[1, 2]	19	12	7	[3]	800	1000	200	[2]	Caribbean*	Ancestral State Reconstruction	[8]			4.750	0.071			2	[6]

Emeralds	*Cynanthus latirostris*	1	1	0	0	[1, 2]	32	16	16	[3]	150	3000	2850	[7]	North America	Ancestral State Reconstruction	[5]	20.352	2.074	3.268	0.561	52.005	2.857	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Cynanthus sordidus*	1	1	0	0	[1, 2]	20	18	2	[3]	900	2200	1300	[7]	North America	Ancestral State Reconstruction	[5]	21.036	1.330	3.444	0.447	53.777	2.861	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Damophila julie*	0	1	0	0	[1, 2]	10	-4	14	[3]	0	1750	1750	[7]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	14.000	1.100	3.250	0.472	43.350	0.450	2	[6], Núñez L. (unpublished data)
Emeralds	*Elvira chionura*	0	1	0	0	[1, 2]	11	7	4	[3]	750	1980	1230	[7]	North America	Ancestral State Reconstruction	[8]			3.200	0.141			2	[6]
Emeralds	*Elvira cupreiceps*	0	1	0	0	[1, 2]	11	8	3	[3]	700	1500	800	[2]	North America	Ancestral State Reconstruction	[8]	17.785	0.105	3.250	0.173	58.400	1.130	3	[6], Núñez L. (unpublished data)
Emeralds	*Eupetomena macroura*	0	1	0	0	[1, 2]	-18	-20	2	[3]	0	1500	1500	[2]	South America*	Ancestral State Reconstruction	[8]			7.558	1.249			3	[6], Núñez L. (unpublished data)
Emeralds	*Eupherusa cyanophrys*	0	1	0	0	[1, 2]	17	16	1	[3]	1200	2600	1400	[7]	North America*	Ancestral State Reconstruction	[8]	19.064	0.889	4.473	0.487	58.424	3.406	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Eupherusa eximia*	1	1	0	0	[1, 2]	19	8	11	[3]	0	2500	2500	[7]	North America	Ancestral State Reconstruction	[8]	17.397	1.066	4.320	0.278	57.322	2.630	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Eupherusa nigriventris*	0	1	0	0	[1, 2]	11	7	4	[3]	1370	2100	730	[7]	North America	Ancestral State Reconstruction	[8]	15.450	0.050	3.500	0.231	48.000	1.500	2	[6], Núñez L. (unpublished data)
Emeralds	*Eupherusa poliocerca*	0	1	0	0	[1, 2]	17	16	1	[3]	800	2300	1500	[7]	North America*	Ancestral State Reconstruction	[8]	18.691	0.949	4.398	0.494	59.184	3.444	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Goethalsia bella*	0	1	0	0	[1, 2]	8	7	1	[3]	600	1650	1050	[7]	South America*	Ancestral State Reconstruction	[8]			3.500	0.707			2	[6]
Emeralds	*Goldmania violiceps*	0	1	0	0	[1, 2]	8	7	1	[3]	600	1400	800	[7]	South America*	Ancestral State Reconstruction	[8]			3.950	0.636			2	[6]
Emeralds	*Hylocharis chrysura*	0	1	0	1	[1, 2]	-18	-36	18	[3]	400	800	400	[2]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	20.426	1.496	4.275	0.250	52.624	1.706	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Hylocharis cyanus*	0	1	0	0	[1, 2]	10	-24	34	[3]	0	1250	1250	[7]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	17.454	0.703	3.567	0.208	46.593	2.307	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Hylocharis eliciae*	0	1	0	0	[1, 2]	18	6	12	[3]	0	350	350	[7]	South America	Ancestral State Reconstruction	[8]	17.437	0.822	3.913	0.242	47.823	1.605	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Hylocharis grayi*	0	1	0	0	[1, 2]	8	1	7	[3]	0	2600	2600	[7]	South America	Ancestral State Reconstruction	[8]	21.535	0.776	6.200	0.465	58.091	2.352	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Hylocharis leucotis*	1	1	0	0	[1, 2]	32	11	21	[3]	900	3900	3000	[7]	North America	Ancestral State Reconstruction	[5]	17.154	0.942	3.274	0.379	53.751	3.707	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Hylocharis sapphirina*	0	1	0	0	[1, 2]	2	-28	30	[3]	0	500	500	[7]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	19.256	0.667	4.200	0.210	50.331	1.849	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Hylocharis xantusii*	1	0	0	0	[1, 2]	26	23	3	[3]	0	1500	1500	[7]	North America*	Ancestral State Reconstruction	[8]	17.382	0.692	3.258	0.809	50.648	1.582	2	[6], [3]
Emeralds	*Klais guimeti*	0	1	0	0	[1, 2]	14	-18	32	[3]	400	1900	1500	[7]	South America	Ancestral State Reconstruction	[8]	11.450	0.150	2.838	0.111	47.250	2.350	2	[6], Núñez L. (unpublished data)
Emeralds	*Lepidopyga coeruleogularis*	0	1	0	0	[1, 2]	10	6	4	[3]	0	100	100	[7]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]			4.100	0.283			2	[6]
Emeralds	*Lepidopyga goudoti*	0	1	0	0	[1, 2]	11	10	1	[3]	0	1600	1600	[7]	South America*	Ancestral State Reconstruction	[8]	18.505	1.025	3.818	0.269	46.925	0.355	2	[6], Núñez L. (unpublished data)

Emeralds	*Leucippus baeri*	0	1	0	0	[1, 2]	-4	-5	1	[3]	0	1300	1300	[2]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	20.050	0.750	4.375	0.171			2	[6], Núñez L. (unpublished data)
Emeralds	*Leucippus chlorocercus*	0	1	0	0	[1, 2]	0	-1	1	[3]	0	430	430	[7]	South America*	Ancestral State Reconstruction	[8]	17.700	0.000	5.367	0.603			2	[6], Núñez L. (unpublished data)
Emeralds	*Leucippus fallax*	0	1	0	0	[1, 2]	11	10	1	[3]	0	800	800	[7]	South America*	Ancestral State Reconstruction	[8]	21.013	0.994			59.297	1.682	2	[6], [3]
Emeralds	*Leucippus taczanowskii*	0	1	0	1	[1, 2]	-6	-8	2	[3]	350	1000	650	[2]	South America	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	24.171	1.360	6.950	0.714	67.386	2.106	3	[6], [3], Núñez L. (unpublished data)
Emeralds	*Leucochloris albicollis*	0	1	0	1	[1, 2]	-20	-28	8	[3]	825	2455	1630	[7]	South America*	Bayesian dispersal–vicariance analysis (S-DIVA)	[9]	22.096	0.971	5.125	0.946	57.990	2.062	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Microchera albocoronata*	0	1	0	0	[1, 2]	14	8	6	[3]	300	1650	1350	[2]	North America	Ancestral State Reconstruction	[8]			2.550	0.071	2.535	0.015	2	[6], Núñez L. (unpublished data)
Emeralds	*Orthorhyncus cristatus*	0	0	1	0	[1, 2]	19	12	7	[3]	0	500	500	[2]	South America	Ancestral State Reconstruction	[8]	10.200	0.700	3.275	0.591	46.650	0.150	2	[6], Núñez L. (unpublished data)
Emeralds	*Phaeochroa cuvierii*	0	1	0	0	[1, 2]	18	7	11	[3]	0	350	350	[7]	South America*	Ancestral State Reconstruction	[8]	20.050	0.250	9.000	0.906			2	[6], Núñez L. (unpublished data)
Emeralds	*Stephanoxis lalandi*	0	1	0	0	[1, 2]	-20	-30	10	[3]	1150	2490	1340	[7]	South America*	Ancestral State Reconstruction	[8]	14.143	0.960	2.817	0.508	47.685	1.238	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Taphrospilus hypostictus*	0	1	0	0	[1, 2]	-1	-28	27	[3]	500	1200	700	[7]	South America	Ancestral State Reconstruction	[8]	22.498	0.918	7.000	0.308	63.568	1.303	3	[6], [3]
Emeralds	*Thalurania colombica*	0	1	0	0	[1, 2]	14	3	11	[3]	0	1900	1900	[7]	South America	Ancestral State Reconstruction	[8]	18.752	0.955	4.255	0.293	52.793	3.497	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Thalurania fannyi*	0	1	0	0	[1, 2]	11	3	8	[10]	0	1900	1900	[2]	South America*	Ancestral State Reconstruction	[8]			4.450	0.354			2	[6]
Emeralds	*Thalurania furcata*	0	1	0	0	[1, 2]	6	-28	34	[3]	0	1900	1900	[7]	South America	Ancestral State Reconstruction	[8]	20.322	0.717	4.236	0.448	53.919	2.489	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Thalurania glaucopis*	0	1	0	0	[1, 2]	-20	-28	8	[3]	980	980	0	[7]	South America*	Ancestral State Reconstruction	[8]	18.607	0.933	4.500	0.548	54.587	3.159	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Thalurania ridgwayi*	1	1	0	0	[1, 2]	21	19	2	[3]	250	1200	950	[7]	North America*	Ancestral State Reconstruction	[8]			3.733	0.404			2	[6]
Emeralds	*Thalurania watertonii*	0	1	0	0	[1, 2]	-3	-8	5	[3]	0	500	500	[2]	South America*	Ancestral State Reconstruction	[8]			4.800	0.163			2	[6], Núñez L. (unpublished data)
Emeralds	*Trochilus polytmus*	0	0	1	0	[1, 2]	19	18	1	[3]	0	1000	1000	[2]	Caribbean*	Ancestral State Reconstruction	[8]	20.397	1.065	4.729	0.390	59.895	4.366	2	[6], [3], Núñez L. (unpublished data)
Emeralds	*Trochilus scitulus*	0	0	1	0	[1, 2]	18	17	1	[10]	0	1000	1000	[2]	Caribbean*	Ancestral State Reconstruction	[8]			4.800	0.707			2	[6]
Hermits	*Anopetia gounellei*	0	1	0	0	[1, 2]	-5	-10	5	[3]	455	485	30	[7]	South America*	Ancestral State Reconstruction	[8]			3.000	0.000			4	[6]
Hermits	*Eutoxeres aquila*	0	1	0	0	[1, 2]	9	-4	13	[3]	0	2100	2100	[7]	South America	Ancestral State Reconstruction	[8]	27.300	0.080	10.467	1.595	84.515	2.965	5	[6], Núñez L. (unpublished data)
Hermits	*Eutoxeres condamini*	0	1	0	0	[1, 2]	2	-17	19	[3]	0	700	700	[7]	South America	Ancestral State Reconstruction	[8]	27.400	0.500	10.250	1.475			5	[6], Núñez L. (unpublished data)
Hermits	*Glaucis aeneus*	0	1	0	0	[1, 2]	15	-5	20	[3]	0	800	800	[7]	North America	Ancestral State Reconstruction	[8]	29.491	0.786	5.465	0.374	52.783	3.508	4	[6], [3], Núñez L. (unpublished data)
Hermits	*Glaucis hirsutus*	0	1	0	0	[1, 2]	10	-26	36	[3]	0	1000	1000	[7]	North America	Ancestral State Reconstruction	[8]	28.478	1.854	6.235	0.624	58.820	3.720	4	[6], [3], [11], Núñez L. (unpublished data)

Hermits	*Phaethornis anthophilus*	0	1	0	0	[1, 2]	10	6	4	[3]	0	1200	1200	[7]	South America	Ancestral State Reconstruction	[8]	34.599	2.187	4.820	0.560	55.439	2.175	3	[6], [3], Núñez L. (unpublished data)
Hermits	*Phaethornis atrimentalis*	0	1	0	0	[1, 2]	1	-5	6	[3]	0	1200	1200	[2]	South America	Ancestral State Reconstruction	[8]	24.191	0.959	2.572	0.146	38.973	1.134	3	[6], [11], Núñez L. (unpublished data)
Hermits	*Phaethornis bourcieri*	0	1	0	0	[1, 2]	8	-2	10	[3]	0	400	400	[7]	South America	Ancestral State Reconstruction	[8]	28.690	1.567	4.119	0.488	54.465	2.579	2	[6], [3], [11], Núñez L. (unpublished data)
Hermits	*Phaethornis eurynome*	0	1	0	0	[1, 2]	-20	-28	8	[3]	76	2242	2166	[7]	South America*	Ancestral State Reconstruction	[8]	32.752	3.781	4.883	0.708	58.612	4.587	3	[6], [3], Núñez L. (unpublished data)
Hermits	*Phaethornis guy*	0	1	0	0	[1, 2]	11	-18	29	[3]	0	2200	2200	[2]	South America	Ancestral State Reconstruction	[8]	41.343	2.360	5.421	1.275	60.683	1.941	4	[6], [3], Núñez L. (unpublished data)
Hermits	*Phaethornis hispidus*	0	1	0	0	[1, 2]	8	-15	23	[3]	0	1000	1000	[7]	South America	Ancestral State Reconstruction	[8]	31.273	1.556	5.209	0.254	55.339	3.126	4	[6], [3], [11], Núñez L. (unpublished data)
Hermits	*Phaethornis idaliae*	0	1	0	0	[1, 2]	-12	-32	20	[3]	121	121	0	[7]	South America*	Ancestral State Reconstruction	[8]			2.250	0.354			4	[6]
Hermits	*Phaethornis longirostris*	1	1	0	0	[1, 2]	8	-8	16	[3]	0	1000	1000	[7]	North America	Ancestral State Reconstruction	[8]	37.930	0.710	5.692	1.234	61.170	1.290	4	[6], Núñez L. (unpublished data)
Hermits	*Phaethornis longuemareus*	0	1	0	0	[1, 2]	21	0	21	[3]	0	1700	1700	[7]	South America	Ancestral State Reconstruction	[8]	21.673	0.858	3.039	0.577	38.275	2.215	4	[6], [3], Núñez L. (unpublished data)
Hermits	*Phaethornis malaris*	0	1	0	0	[1, 2]	8	-20	28	[3]	0	600	600	[2]	South America	Ancestral State Reconstruction	[8]	38.003	2.483	5.935	0.458	59.129	2.706	4	[6], [3], [11], Núñez L. (unpublished data)
Hermits	*Phaethornis nattereri*	0	1	0	0	[1, 2]	-16	-20	4	[3]	0	500	500	[2]	South America*	Ancestral State Reconstruction	[8]			2.750	0.354			4	[6]
Hermits	*Phaethornis pretrei*	0	1	0	0	[1, 2]	-18	-20	2	[3]	364	1091	727	[7]	South America*	Ancestral State Reconstruction	[8]	30.252	1.108	4.200	0.251	57.478	2.105	3	[6], [3], Núñez L. (unpublished data)
Hermits	*Phaethornis ruber*	0	1	0	0	[1, 2]	8	-24	32	[3]	0	500	500	[7]	South America	Ancestral State Reconstruction	[8]	22.053	1.404	2.625	0.558	33.309	4.383	3	[6], [3], [11], Núñez L. (unpublished data)
Hermits	*Phaethornis striigularis*	0	1	0	0	[1, 2]	18	-1	19	[3]	0	1800	1800	[7]	South America*	Ancestral State Reconstruction	[8]			2.550	0.497			3	[6], Núñez L. (unpublished data)
Hermits	*Phaethornis superciliosus*	0	1	0	0	[1, 2]	22	-2	24	[3]	0	1800	1800	[7]	South America*	Ancestral State Reconstruction	[8]	41.720	2.757	6.187	0.505	64.913	4.161	4	[6], [3], Núñez L. (unpublished data)
Hermits	*Phaethornis syrmatophorus*	0	1	0	0	[1, 2]	4	-6	10	[3]	800	2400	1600	[7]	South America	Ancestral State Reconstruction	[8]	39.802	2.594	5.750	0.870	58.774	2.554	4	[6], [3], Núñez L. (unpublished data)
Hermits	*Phaethornis yaruqui*	0	1	0	0	[1, 2]	12	5	7	[3]	0	1500	1500	[7]	South America	Ancestral State Reconstruction	[8]	40.307	2.505	5.450	1.285	57.916	3.161	3	[6], [3], Núñez L. (unpublished data)
Hermits	*Ramphodon naevius*	0	1	0	0	[1, 2]	-12	-32	20	[3]	0	500	500	[2]	South America*	Ancestral State Reconstruction	[8]	33.125	1.536	7.100	1.327	68.668	4.351	3	[6], [3], Núñez L. (unpublished data)
Hermits	*Threnetes leucurus*	0	1	0	0	[1, 2]	5	-23	28	[3]	0	1000	1000	[7]	North America	Ancestral State Reconstruction	[8]	27.775	1.683	5.262	0.761	58.422	3.434	3	[6], [3], [11], Núñez L. (unpublished data)
Hermits	*Threnetes niger*	0	1	0	0	[1, 2]	5	2	3	[3]	0	500	500	[2]	South America*	Ancestral State Reconstruction	[8]	28.471	1.074	5.875	1.031	59.114	3.439	3	[6], [3]
Hermits	*Threnetes ruckeri*	0	1	0	0	[1, 2]	16	-5	21	[3]	0	1050	1050	[7]	North America	Ancestral State Reconstruction	[8]	28.628	0.701	6.047	0.419	55.565	4.095	3	[6], [3], Núñez L. (unpublished data)
Mangoes	*Androdon aequatorialis*	0	1	0	0	[1, 2]	10	-5	15	[3]	0	1590	1590	[7]	South America	Ancestral State Reconstruction	[8]	37.968	1.862	7.460	1.091	65.165	3.099	1	[6], [3], Núñez L. (unpublished data)
Mangoes	*Anthracothorax dominicus*	0	0	1	0	[1, 2]	20	18	2	[3]	0	1500	1500	[2]	Caribbean*	Ancestral State Reconstruction	[8]			6.250	1.708			3	[6]
Mangoes	*Anthracothorax mango*	0	0	1	0	[1, 2]	19	18	1	[3]	900	1500	600	[2]	Caribbean	Ancestral State Reconstruction	[8]			8.500				3	[6]
Mangoes	*Anthracothorax nigricollis*	0	1	0	0	[1, 2]	10	-28	38	[3]	0	1750	1750	[7]	North America	Ancestral State	[8]	23.450	0.750	6.940	0.377	65.295	1.025	3	[6], Núñez L. (unpublished

																Reconstruction									data)
Mangoes	*Anthracothorax prevostii*	1	1	0	0	[1, 2]	22	-4	26	[3]	0	1500	1500	[7]	North America*	Ancestral State Reconstruction	[8]	26.418	0.573	6.633	0.404	66.765	7.284	3	[6], [3], Núñez L. (unpublished data)
Mangoes	*Anthracothorax veraguensis*	0	1	0	0	[1, 2]	10	7	3	[3]	0	700	700	[7]	North America*	Ancestral State Reconstruction	[8]			7.000				3	[6]
Mangoes	*Anthracothorax viridigula*	0	1	0	0	[1, 2]	9	2	7	[3]	0	500	500	[2]	South America*	Ancestral State Reconstruction	[8]			7.200	1.151			3	[6], Núñez L. (unpublished data)
Mangoes	*Anthracothorax viridis*	0	0	1	0	[1, 2]	19	18	1	[3]	800	1200	400	[2]	Caribbean*	Ancestral State Reconstruction	[8]	24.465	1.238	7.000		61.298	0.987	3	[6], [3]
Mangoes	*Augastes lumachella*	0	1	0	0	[1, 2]	-18	-20	2	[3]	950	1600	650	[7]	South America*	Ancestral State Reconstruction	[8]			4.400	0.566			2	[6]
Mangoes	*Augastes scutatus*	0	1	0	0	[1, 2]	-18	-20	2	[3]	1000	2000	1000	[7]	South America*	Ancestral State Reconstruction	[8]			4.250	1.061			2	[6]
Mangoes	*Avocettula recurvirostris*	0	1	0	0	[1, 2]	8	0	8	[3]	0	800	800	[2]	South America*	Ancestral State Reconstruction	[8]	16.685	0.055	4.250	0.071	57.950	0.030	1	[6], [3]
Mangoes	*Chrysolampis mosquitus*	0	1	0	0	[1, 2]	11	-24	35	[3]	0	1740	1740	[7]	South America	Ancestral State Reconstruction	[8]	11.685	0.935	4.035	0.676	52.640	1.090	2	[6], Núñez L. (unpublished data)
Mangoes	*Colibri coruscans*	0	1	0	1	[1, 2]	8	-28	36	[3]	600	3600	3000	[7]	South America	Ancestral State Reconstruction	[8]	22.625	1.205	7.475	0.726	72.885	3.815	2	[6], Núñez L. (unpublished data)
Mangoes	*Colibri delphinae*	0	1	0	0	[1, 2]	16	-1	17	[3]	300	2800	2500	[7]	North America	Ancestral State Reconstruction	[8]	17.350	1.050	6.375	0.854	68.700	1.900	2	[6], Núñez L. (unpublished data)
Mangoes	*Colibri serrirostris*	0	1	0	0	[1, 2]	-16	-34	18	[3]	2075	2075	0	[7]	South America*	Ancestral State Reconstruction	[8]	21.236	1.402	6.200	0.490	68.098	4.367	2	[6], [3], Núñez L. (unpublished data)
Mangoes	*Colibri thalassinus*	1	1	0	0	[1, 2]	32	-27	59	[3]	600	3350	2750	[7]	North America	Ancestral State Reconstruction	[8]	20.833	1.461	4.772	0.647	62.836	3.192	3	[6], [3], Núñez L. (unpublished data)
Mangoes	*Doryfera johannae*	0	1	0	0	[1, 2]	8	-12	20	[3]	280	1800	1520	[7]	South America	Ancestral State Reconstruction	[8]	27.443	2.155	4.653	1.019	53.024	3.950	1	[6], [3], Núñez L. (unpublished data)
Mangoes	*Doryfera ludovicae*	0	1	0	0	[1, 2]	11	-17	28	[3]	900	2700	1800	[7]	South America	Ancestral State Reconstruction	[8]	32.477	1.821	5.875	0.604	57.040	1.943	1	[6], [3], Núñez L. (unpublished data)
Mangoes	*Eulampis holosericeus*	0	0	1	0	[1, 2]	23	12	11	[3]	0	500	500	[2]	Caribbean	Ancestral State Reconstruction	[8]			5.975	1.068			3	[6], Núñez L. (unpublished data)
Mangoes	*Eulampis jugularis*	0	0	1	0	[1, 2]	19	12	7	[3]	800	1200	400	[2]	Caribbean	Ancestral State Reconstruction	[8]	23.200	3.400	9.300	1.760	72.600	3.000	4	[6], Núñez L. (unpublished data)
Mangoes	*Heliactin bilophus*	0	1	0	0	[1, 2]	2	-24	26	[3]	0	500	500	[2]	South America	Ancestral State Reconstruction	[8]			2.150	0.286			2	[6], Núñez L. (unpublished data)
Mangoes	*Heliothryx auritus*	0	1	0	0	[1, 2]	5	-22	27	[3]	0	400	400	[2]	South America*	Ancestral State Reconstruction	[8]			5.500	0.546			2	[6], Núñez L. (unpublished data)
Mangoes	*Heliothryx barroti*	0	1	0	0	[1, 2]	18	0	18	[3]	0	1830	1830	[7]	South America	Ancestral State Reconstruction	[8]	16.755	0.105	5.463	0.315	74.385	0.415	2	[6], Núñez L. (unpublished data)
Mangoes	*Polytmus guainumbi*	0	1	0	0	[1, 2]	9	-18	27	[3]	0	600	600	[7]	South America	Ancestral State Reconstruction	[8]	21.848	4.391	4.883	0.356	59.433	3.244	3	[6], [3], Núñez L. (unpublished data)
Mangoes	*Polytmus milleri*	0	1	0	0	[1, 2]	6	6	0.2	[3]	1300	2200	900	[7]	South America*	Ancestral State Reconstruction	[8]	2.500	0.000	5.000	0.829			3	[6]
Mangoes	*Polytmus theresiae*	0	1	0	0	[1, 2]	5	-12	17	[3]	0	300	300	[7]	South America	Ancestral State Reconstruction	[8]	17.769	4.865	3.575	0.218	54.935	1.558	3	[6], [3], Núñez L. (unpublished data)
Mangoes	*Schistes geoffroyi*	0	1	0	0	[1, 2]	10	-18	28	[3]	1400	2500	1100	[7]	South America	Ancestral State Reconstruction	[8]			3.800	0.424			2	[6]
Mountain Gems	*Eugenes fulgens*	1	1	0	0	[1, 2]	33	8	25	[3]	900	3300	2400	[7]	North America	Ancestral State Reconstruction	[5]	29.791	6.885	7.078	0.683	69.006	4.452	2	[6], [3], Núñez L. (unpublished data)

Mountain Gems	*Heliomaster constantii*	1	1	0	0	[1, 2]	27	10	17	[3]	0	1500	1500	[7]	North America	Ancestral State Reconstruction	[5]	34.512	1.298	7.168	0.509	63.136	1.579	2	[6], [3], Núñez L. (unpublished data)
Mountain Gems	*Heliomaster furcifer*	0	1	0	0	[1, 2]	-16	-36	20	[3]	0	1500	1500	[7]	South America	Ancestral State Reconstruction	[5]			5.750	0.612			3	[6], Núñez L. (unpublished data)
Mountain Gems	*Heliomaster longirostris*	1	1	0	0	[1, 2]	18	-24	42	[3]	0	1525	1525	[7]	North America	Ancestral State Reconstruction	[5]	34.533	0.464	6.380	0.708	60.617	1.562	2	[6], [3], Núñez L. (unpublished data)
Mountain Gems	*Heliomaster squamosus*	0	1	0	0	[1, 2]	-10	-24	14	[3]	0	800	800	[2]	South America	Ancestral State Reconstruction	[5]			5.750	0.612			2	[6], Núñez L. (unpublished data)
Mountain Gems	*Hylonympha macrocerca*	0	1	0	0	[1, 2]	11	10	1	[3]	900	1200	300	[7]	South America*	Ancestral State Reconstruction	[8]			7.250	0.645			3	[6]
Mountain Gems	*Lampornis amethystinus*	1	1	0	0	[1, 2]	22	15	7	[3]	900	3050	2150	[7]	North America	Ancestral State Reconstruction	[5]	21.980	1.667	5.863	0.827	65.245	4.073	3	[6], [3], Núñez L. (unpublished data)
Mountain Gems	*Lampornis calolaemus*	0	1	0	0	[1, 2]	11	8	3	[10]	800	2500	1700	[2]	North America	Ancestral State Reconstruction	[5]			5.425	0.660			2	[6]
Mountain Gems	*Lampornis castaneoventris*	0	1	0	0	[1, 2]	11	7	4	[3]	1220	3050	1830	[7]	North America	Ancestral State Reconstruction	[8]	21.800	0.500	5.425	0.610	62.150	3.650	2	[6], Núñez L. (unpublished data)
Mountain Gems	*Lampornis clemenciae*	1	1	0	0	[1, 2]	32	17	15	[3]	300	3900	3600	[7]	North America	Ancestral State Reconstruction	[5]	26.225	2.519	7.193	1.218	72.492	4.680	3	[6], [3], Núñez L. (unpublished data)
Mountain Gems	*Lampornis hemileucus*	0	1	0	0	[1, 2]	11	7	4	[3]	700	1400	700	[2]	North America	Ancestral State Reconstruction	[5]	20.750	0.650	5.650	0.635	61.350	3.050	2	[6], Núñez L. (unpublished data)
Mountain Gems	*Lampornis viridipallens*	0	1	0	0	[1, 2]	15	13	2	[3]	900	2200	1300	[7]	North America	Ancestral State Reconstruction	[5]	20.609	0.885	5.349	1.331	63.232	4.167	2	[6], [3], Núñez L. (unpublished data)
Mountain Gems	*Lamprolaima rhami*	1	1	0	0	[1, 2]	18	14	4	[3]	900	2950	2050	[7]	North America	Ancestral State Reconstruction	[5]	16.800	0.000	6.900	1.212	72.000	0.000	2	[6], [3]
Mountain Gems	*Panterpe insignis*	0	1	0	0	[1, 2]	11	7	4	[3]	1800	3000	1200	[7]	North America	Ancestral State Reconstruction	[5]			5.558	0.592			2	[6], Núñez L. (unpublished data)
Mountain Gems	*Sternoclyta cyanopectus*	0	1	0	0	[1, 2]	11	8	3	[3]	0	1900	1900	[7]	South America	Morphology	[12]			9.275	0.797			3	[6]
Patagona	*Patagona gigas*	0	1	0	1	[1, 2]	0	-35	35	[3]	0	3660	3660	[7]	South America*	Ancestral State Reconstruction	[8]			20.567	2.272			2	[6]
Topazes	*Florisuga fusca*	0	1	0	0	[1, 2]	-8	-32	24	[3]	0	1400	1400	[2]	South America*	Ancestral State Reconstruction	[8]			8.000	1.414			3	[6]
Topazes	*Florisuga mellivora*	0	1	0	0	[1, 2]	18	-20	2	[3]	0	1600	1600	[7]	South America	Ancestral State Reconstruction	[8]	18.310	0.430	6.850	0.444	75.440	2.680	3	[6], Núñez L. (unpublished data)
Topazes	*Topaza pella*	0	1	0	0	[1, 2]	0	-2	2	[3]	250	500	250	[7]	South America	Ancestral State Reconstruction	[8]	4.300	0.000	11.752	2.075			3	[6], Núñez L. (unpublished data)

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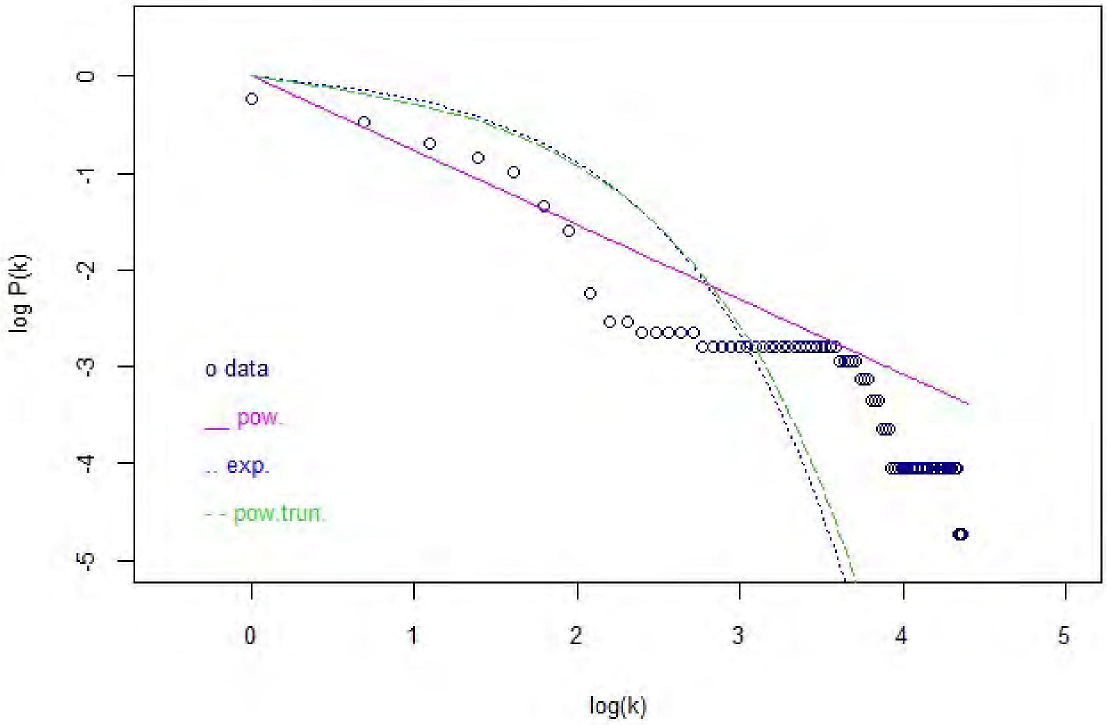
S1 Appendix. **Network analysis of the matrix including native and exotic plant species.** Results for the degree distribution, nestedness, and modularity analyses of the mutualistic network of hummingbird clades and their nectar plants. In this network, we included all records independently of plant origin (native or exotic to the American continent).



This graph shows the cumulative frequency distribution (P (*k*)) of the number of links (*k*) for the network between hummingbirds and their floral nectar resources. The graph in a log-log scale combines plant and hummingbird interactions. The original data (circles) was adjusted to three distributions: (1) power-law function (pow.), (2) exponential (exp.), and (3) truncated power-law (pow.trun.). The hummingbird-plant interaction network has a better fit to the power-law function (AIC exp. = 678.193, AIC pow. = 586.747, AIC pow.trun. = 676.967).

When the nodes are ordered based on the connection number, this net was highly nested (NODF = 72.160), and hummingbirds and plants got high NODF value (NODF hummingbirds = 82.320, NODF plants = 72.090). Compared with the null models, this matrix was statistically different from a randomly selected network using ER and CE models (NODF model ER = 44.220, *P* < 0.001, SES model ER = 15.022; NODF model CE = 52.260, *P* < 0.001, SES model CE = 10.001), but not using FF model (NODF model FF = 71.500, *P* = 0.938, SES model FF = 1.803).

When phylogeny was accounted for, the nestedness of the network diminished (NODF = 42.600, NODF hummingbirds = 64.650, NODF plants = 42.450). Nonetheless, the network remained statistically different from randomly selected networks with ER and CC models (NODF model ER = 22.120, *P* < 0.001, SES model ER = 9.356; NODF model CE = 29.170, *P* < 0.001, SES model CE = 6.693), but not from networks with FF model (NODF model FF = 40.487, *P* = 0.873, SES model FF = 5.579).

Respect modularity, the network were not significantly modular (M = 0.183 ± 0.002, M model ER = 0.222 (*P* = 0.944, SES model ER = -7.655), M model FF = 0.210 (*P* = 0.953, SES model FF = -5.657).

CAPÍTULO 3

MECANISMOS HISTÓRICOS POTENCIALES ESTRUCTURADORES DE LAS COMUNIDADES DE COLIBRÍES EN MÉXICO

MECANISMOS HISTÓRICOS POTENCIALES ESTRUCTURADORES DE LAS COMUNIDADES DE COLIBRÍES EN MÉXICO

INTRODUCCIÓN

Las especies biológicas presentan un patrón de distribución discontinuo a nivel global con zonas de alta y baja diversidad (Moreau & Bell 2013). Una de las hipótesis que explica el origen y mantenimiento de la diversidad sugiere que existen zonas “museo” y zonas “cuna” (Stenseth 1984, Moreau & Bell 2013). En las zonas museo los taxa son antiguos, tienen bajas tasas de extinción y tienen rangos de distribución amplios, mientras que en las zonas cuna se observan tasas de especiación altas y son centros de diversificación biológica (Dagallier *et al.* 2020).

Asimismo, las especies biológicas están ensambladas en comunidades a partir de un conjunto regional de especies (e.g. Fox 1987, Leibold 1997, Blackburn & Gaston 2001). Esto sugiere que las comunidades están saturadas al azar (Cornell & Lawton 1992), y la posterior coexistencia de estas especies por periodos largos ocurre por la ocupación de nichos diferentes que disminuye la competencia por los recursos (“habitat partitioning”, Wisheu 1998).

Diferentes fuerzas ecológicas actúan simultáneamente durante los procesos de estructuración de las comunidades ecológicas. Por un lado, especies con requerimientos ecológicos similares tenderán a ser incluidas dentro del mismo nicho (atracción fenotípica), mientras que los individuos de especies que ocupan el mismo nicho y/o hábitat interactuarán negativamente (repulsión fenotípica). Esta interacción negativa será intensa entre las especies más similares ecológicamente, pudiendo alterar el nicho realizado y/o la distribución de los taxones en subnichos dentro del nicho fundamental, o pudiendo llegar hasta la clásica exclusión competitiva. Es importante recalcar que el efecto de dichas interacciones negativas puede llevar a la exclusión de especies a la escala de individuo sin llevar a la exclusión de la comunidad (Chesson 2000, Webb *et al.* 2002).

Con la aparición de los estudios filogenéticos fue factible poner a prueba hipótesis que infieren los mecanismos de coexistencia actuales. A medida que aparecieron mejores hipótesis filogenéticas en muchos grupos de organismos y técnicas para el análisis de dichas filogenias, los estudios de ecología de comunidades empezaron a contar con una dimensión de información adicional, con la que ahora se pueden explicar las relaciones evolutivas de las especies que componen una comunidad, el papel de la competencia y el mantenimiento de la diversidad (Webb *et al.* 2002).

La mayor parte de los estudios que han integrado el enfoque filogenético con el de ecología de comunidades buscan responder preguntas sobre ensamble, organización y ocurrencia de especies en una comunidad (Webb *et al.* 2002). Al establecer la estructura filogenética de una comunidad se está describiendo la forma en la que las especies de dicha comunidad se ubican en la filogenia de un grupo mayor de especies (p.ej. la filogenia de las especies de una región biogeográfica o política más amplia en el que se ubica esta comunidad). En general los taxones muestran tres patrones principales de distribución sobre una filogenia: las especies pueden estar filogenéticamente **agrupadas, sobredipersas** o al **azar**. Webb y colaboradores (Webb *et al.* 2002) propusieron un esquema simple que permite interpretar la ocurrencia de estos patrones de distribución en términos de los mecanismos contemporáneos de coexistencia mencionados anteriormente. Ellos propusieron que una distribución filogenética agrupada de las especies de una comunidad respecto al conjunto regional ("phylogenetic attraction" en inglés), indica que el uso del hábitat es un rasgo ecológico conservado dentro de la comunidad y que la atracción fenotípica domina sobre la repulsión. Por otro lado, la sobredispersión filogenética ("phylogenetic overdispersion" en inglés) puede ocurrir como resultado de dos condiciones: 1) cuando taxones relacionados en la similitud de nicho son localmente excluidos (repulsión fenotípica), observándose un traslape de nicho mínimo entre las especies que coexisten, ó 2) cuando taxones lejanamente relacionados convergen en un uso de nicho similar y son fenotípicamente atraídos. Cuando existe un sobrelape mínimo en rasgos ecológicos filogenéticamente convergentes, la distribución de los taxones de la comunidad en la filogenia general muestra un patrón aleatorio.

Al estudiar la riqueza y composición de especies en diversas comunidades, surge la pregunta de por qué hábitats similares en diferentes regiones difieren en su composición de especies. Varias de las posibles explicaciones a este fenómeno están relacionadas con aspectos filogenéticos: 1) la historia particular de cada área favorece la ocupación por diferentes clados (Latham & Ricklefs 1993, Schluter & Ricklefs 1993, Ricklefs 2005), 2) los diferentes clados varían respecto a sus potenciales de diversificación (Farrell *et al.* 1991, Sanderson & Donoghue 1996, Dodd *et al.* 1999, Gardezi & Silva 1999) y de extinción, y/o 3) las áreas difieren en la cantidad de tiempo que han sido ocupadas (Brown *et al.* 2000, Ricklefs 2005). Sin embargo, a pesar de la información proporcionada a partir del establecimiento de la estructura filogenética en una comunidad, ésta por sí sola no puede explicar completamente cómo las barreras geográficas, las interacciones bióticas, las restricciones fisiológicas y los procesos evolutivos han influenciado la composición de especies en las comunidades locales (Graham *et al.* 2009). Evaluar los cambios en la composición de especies y en la composición filogenética a lo largo de barreras biogeográficas o de gradientes ambientales, es una alternativa que brinda información sobre los mecanismos ecológicos y evolutivos que están estructurando dichas comunidades biológicas (Graham & Fine 2008).

Debido a su ubicación geográfica, su topografía compleja, y la historia dinámica tanto a nivel tectónico como a nivel climático principalmente en las tierras altas, México reúne características ideales para estudiar los patrones de cambio en la composición de especies a nivel espacial, debido a que dichas características han sido consideradas como algunas de las razones principales por las que el país posee una biota muy diversa (Challenger 2007, Bryson *et al.* 2011). Asimismo, los colibríes (Aves: Trochilidae) constituyen un modelo biológico ideal para poner a prueba hipótesis sobre exclusión competitiva, estructura filogenética y composición de especies en comunidades biológicas debido a varias razones: 1) la existencia de una taxonomía clara para la familia (McGuire *et al.* 2007, McGuire *et al.* 2009, McGuire *et al.* 2014); 2) la gran similitud morfológica entre las especies asociada al nicho alimenticio (Schuchmann 1999, Gutiérrez-Z. *et al.* 2004); 3) los altos niveles de competencia entre los individuos por el acceso al néctar (Feinsinger 1976, Gutiérrez-Z. *et al.* 2004); 4) la presencia de comunidades diversas donde pueden estar coexistiendo más de 10 especies simultáneamente (Arizmendi 2001, Lara 2006a); 5) su congruencia morfológica y filogenética (Stiles 2008); y 6) la susceptibilidad a los gradientes ambientales relacionada a la habilidad de vuelo y la especialización alimenticia y morfológica (Stiles *et al.* 2005, Graham *et al.* 2009, Abrahamczyk & Kessler 2015, Benham & Witt 2016). En particular, algunas características propias de las elevaciones altas como las bajas temperaturas, la baja densidad del aire y de la tensión de oxígeno, y una mayor exposición a la radiación ultravioleta imponen restricciones metabólicas y fisiológicas importantes a los colibríes (Altshuler *et al.* 2004, Projecto-Garcia *et al.* 2013, Appenzeller & Witt 2017, Lim *et al.* 2019), lo que ha desencadenado que solo algunos grupos particulares hayan logrado colonizar estas áreas (Stiles 2008, Graham *et al.* 2009).

En el presente trabajo, y por primera vez para México, se establecieron los mecanismos históricos potenciales que han modelado la estructura filogenética de las comunidades de colibríes en el país. Si la importancia de la competencia y del filtro ambiental como procesos estructuradores de estas comunidades depende de la altitud y de las barreras biogeográficas (Graham *et al.* 2009), se espera que las comunidades de colibríes ubicadas en las zonas bajas de México estén compuestas por especies filogenéticamente lejanas (sobredispersión filogenética), evidenciando el efecto de la exclusión competitiva; mientras que las especies en comunidades a mayores altitudes y en zonas áridas estuvieran emparentadas filogenéticamente (agrupamiento filogenético), debido al filtro ambiental impuesto por la elevación y la precipitación (Graham *et al.* 2009). Asimismo, dado que la historia geológica de las barreras biogeográficas como el Eje Neovolcánico Transversal, las Sierras Madre y el Itsmo de Tehuantepec han determinado los patrones de contracción y expansión de distintos biomas a lo largo del tiempo (Metcalfe 2006, Caballero *et al.* 2010, Ramírez-Barahona & Eguiarte 2013), y los patrones filogeográficos de los colibríes (Ornelas *et al.* 2013, Rodríguez-Gómez *et al.* 2013, Ornelas *et al.* 2015, Hernández-Baños *et al.* 2020), se esperaba que estas barreras influyeran en la estructura filogenética de las comunidades al limitar la dispersión de las especies y afectando la composición de las comunidades de colibríes.

MATERIALES Y MÉTODOS

En este trabajo defino comunidad ecológica como el conjunto de dos o más especies que compartieron el mismo gremio trófico y que co-ocurrieron espacialmente y temporalmente (Webb *et al.* 2002, Stroud *et al.* 2015), y hábitat como la ubicación espacial donde se congrega una combinación de niveles de recursos (Webb *et al.* 2002).

Composición de especies en las comunidades de colibríes.

Se hizo una recopilación de listados de especies de colibríes en diferentes áreas de México a partir de trabajos publicados, literatura gris y comunicaciones personales. Para cada área se estableció el listado y la ubicación geográfica (latitud, longitud y elevación). Solo se usó la información de comunidades compuestas por más de una especie, y en donde hubiese información filogenética para las especies que las componían (Anexo 1). Las áreas incluidas variaron marcadamente en extensión, con un promedio de 272,440.32 km2 (rango: 10-960000 km2). Respecto a la elevación, la altura promedio de los sitios fue 1399.44 msnm (rango: 0–3,351.5 msnm).

Taxones, secuencias y alineamiento.

Siguiendo la clasificación más reciente de la familia Trochilidae (Chesser *et al.* 2010, Remsen *et al.* 2011), se llevó a cabo una recopilación de secuencias genéticas disponibles. A partir del GenBank (Benson *et al.* 2009) se obtuvo al menos una secuencia de ADN para un gen nuclear y tres genes mitocondriales de 107 especies de colibrí. El gen nuclear incluido fue el intrón 5 del gen de la adenilato quinasa (AK1 con 608 pb), y los tres genes mitocondriales fueron las subunidades 2 y 5 de la NADH deshidrogenasa (ND2 y ND5 con 362 y 337 pb respectivamente) y el gen ribosomal 12S (12S con 554 pb). De las 107 especies incluidas en la filogenia, 48 se encuentran en México, correspondiendo al 82.76% de la diversidad de colibríes del país (Anexo 2). Las secuencias fueron descargadas y alineadas manualmente usando el programa SeAl v. 2.0a11 (Rambaut 2002), admitiendo la inclusión de espacios (gaps) y de información faltante (missing data).

Con el propósito de comparar el efecto de la escala sobre los procesos ecológicos y evolutivos que estructuraron dichas comunidades (Jablonski & Sepkoski 1996), se construyeron dos árboles filogenéticos que fueron usados como conjuntos regionales. El primer árbol, denominado *Escala Continental*, incluyó información para 107 especies de colibríes y representó adecuadamente la diversidad taxonómica de la familia, al incluir elementos de los nueve clados principales establecidos por McGuire *et al.* (2009). En la segunda hipótesis filogenética se incluyeron solamente las 49 especies reportadas en México, por lo que fue denominada *Escala México* (Anexo 2). Siguiendo a McGuire *et al.* (2007) se utilizaron especies de vencejos *Cypseloides rutilus* y *Streptoprocne zonaris* (Apodidae), el grupo hermano de los colibríes, como grupo externo.

Reconstrucción filogenética

La selección del mejor modelo de selección nucleotídica para cada locus y para las secuencias concatenadas se realizó en jMODELTEST v0.1.1 (Posada 2008), admitiendo siete esquemas de sustitución, frecuencias de bases iguales y desiguales, una proporción de sitios invariables, y tasa de variación entre los sitios. El mejor modelo de evolución para cada secuencia se seleccionó usando el Criterio de Información de Aikake (AIC). Para la hipótesis filogenética

Escala Continental los mejores modelos ajustados fueron: GTR+I+G (ND2), TPM1uf+I+G (ND5), TrN+I+G (12S), K80+G (AK1), TVM+I+G (ND2 + ND5), TIM1+I+G (genes mitocondriales), GTR+I+G (todos los genes concatenados). Para la hipótesis filogenética Escala México los modelos de substitución nucleotídica elegidos por el programa fueron los siguientes: GTR+I+G (ND2), TPM1uf+I+G (ND5), TrN+I+G (12S), TPM1uf+G (AK1), TVM+I+G (ND2 + ND5), GTR+I+G (genes mitocondriales), TVM+I+G (todos los genes concatenados).

Las relaciones filogenéticas fueron reconstruidas mediante Inferencia Bayesiana usando el programa MrBayes v3.12 (Ronquist & Huelsenbeck 2003) y CIPRES Science Gateway (Miller *et al.* 2010). Con el fin de incorporar la heterogeneidad en el modelo de evolución molecular y así incrementar precisión de las inferencias filogenéticas (Brown & Lemmon 2007), las secuencias para las especies de colibríes fueron analizadas mediante seis particiones:

1) Todos los genes simultáneamente (ND2+ND5+12S+AK1).
2) Discriminando cada uno de los genes (ND2, ND5, 12S, AK1).
3) Genes mitocondriales contra el gen nuclear (ND2+ND5+12S, AK1).
4) Discriminando los codones de los genes mitocondriales ND2 y ND5, con la posición 1 y 2 respecto a la posición 3 (ND2-posición 1 y 2, ND2-posición 3, ND5-posición 1 y 2, ND5-posición 3, 12S, AK1).
5) Discriminando los codones de los genes mitocondriales ND2 y ND5, con la posición 1 y 2 respecto a la posición 3, pero empleando los modelos de evolución obtenidos por el programa jModelTest, en esta partición se emplearon los modelos de

evolución propuestos por Shapiro *et al.* (2006): HKY+G para la posición 1 y 2, y el modelo GTR+G para la posición 3.

6) Discriminando los codones de los genes mitocondriales ND2 y ND5 (ND2-posición 1, ND2-posición 2, ND2-posición 3, ND5-posición 1, ND5-posición 2, ND5-posición 3, 12S, AK1).

Debido a que MrBayes solo admite modelos con 1, 2 y 6 tasas de sustitución, la implementación del mejor modelo de evolución nucleotídica encontrado mediante AIC requirió seleccionar entre algunos modelos con más o menos parámetros. Debido a las consecuencias negativas que tiene la subparametrización sobre la inferencia filogenética (subestimación de la longitud de las ramas, atracción de ramas largas) (Brown & Lemmon 2007, McGuire *et al.* 2007), siempre se seleccionó el modelo sobreparametrizado más cercano. Para cada partición se corrieron dos análisis independientes con 25 millones de generaciones, muestreando cada 2.000 generaciones, y descartando el primer 10% de los árboles generados. Los parámetros obtenidos en los dos análisis para cada partición fueron concatenados y visualizados con TRACER v1.6 (http://tree.bio.ed.ac.uk/software/tracer/), para probar si el periodo de calentamiento fue adecuado, si el tamaño de muestra efectivo era apropiado para todos los parámetros (ESS > 200), y para asegurar la convergencia entre corridas.

Para determinar si el aplicar modelos específicos para las distintas particiones mejoró significativamente la explicación de los datos, se estimaron los factores de Bayes (Bayes factor en inglés) usando la media armónica (harmonic mean en inglés) siguiendo el método propuesto por Ronquist & Huelsenbeck (2003). Este método es robusto para elegir entre modelos con distintas particiones, permite comparar modelos que no están anidados de manera jerárquica, y no necesita ser corregido en función del número de parámetros (Ronquist & Huelsenbeck 2003, Nylander *et al.* 2004, Brown & Lemmon 2007).

Estimación de los tiempos de divergencia

Tener estimados de las longitudes absolutas de las ramas en una filogenia incrementa notablemente la precisión en las inferencias sobre relación y similitud entre especies. Asimismo, una adecuada calibración de las hipótesis filogenéticas es fundamental en el proceso de reconstrucción de comunidades ancestrales y su asociación con eventos biogeográficos (Webb *et al.* 2002). Para esto se llevó a cabo un análisis Bayesiano de reloj molecular relajado en BEAST v2.4.4 (Drummond & Rambaut 2007) para el mejor modelo seleccionado por los Factores de Bayes. Se establecieron a los colibríes como grupo monofilético, al clado de las abejas (siguiendo a McGuire *et al.* 2014) y al género *Amazilia* "sensu lato" (siguiendo a Ornelas *et al.* 2014). Se empleó el modelo de substitución previamente establecido en jMODELTEST 0.1.1 (Posada 2008), discriminando las posiciones de los codones y con tasas de substitución no ligadas. Los tiempos de divergencia fueron estimados usando un modelo de reloj relajado no-correlacionado con distribución lognormal (uncorrelated lognormal relaxed clock model) (Drummond *et al.* 2006). Se estimaron los tiempos de divergencia usando el modelo evolutivo de especies de Yule y cuatro puntos de calibración: 1) la divergencia entre colibríes y vencejos (lognormal, promedio 0.01, SD 1.43, offset 30.5, rango 46.99–30.56 Ma) (Ornelas *et al.* 2014); 2) la separación entre los clados de las abejas y las gemas de montaña (normal, promedio 12.0, SD 1, rango 13.9–10.3 Ma) (Licona-Vera & Ornelas 2017); 3) la divergencia del género *Amazilia* "sensu lato" (normal, promedio 18.4, SD 2.9, rango 24–13.16 Ma); y 4) la calibración de la raíz del árbol (normal, promedio 65.37, SD 3.4, rango 72–58.71 Ma) (Pacheco *et al.* 2011). Se corrieron dos cadenas independientes de MCMC con 50 millones de generaciones, recopilando información cada 50000 generaciones. Los resultados fueron visualizados en TRACER v1.6 (http://tree.bio.ed.ac.uk/software/tracer/) para confirmar valores adecuados para los parámetros (ESS > 200) y verificar estacionalidad. Las dos cadenas fueron combinadas con TreeAnnotator v1.10.1 (http://beast.community/treeannotator), descartando el 25% de los árboles generados. El árbol resultante fue visualizado en FIGTREE v1.4.3 (http://tree.bio.ed.ac.uk/).

Variables ambientales

La información de las variables climáticas para cada comunidad de colibríes en México se obtuvo de la base de datos global Worldclim (Hijmans *et al.* 2005). De las 19 variables disponibles en esta base de datos, se seleccionaron las siguientes: temperatura promedio anual (bio 1), rango diurno promedio de la temperatura (bio 2), estacionalidad de la temperatura (bio 4), rango de la temperatura anual (bio 7), precipitación anual (bio 12), estacionalidad de la precipitación (bio 15), precipitación del cuatrimestre más caliente (bio 18), y precipitación del cuatrimestre más frío (bio 19). Estas variables han demostrado ser buenos descriptores del ambiente (Graham *et al.* 2009), principalmente de los valores medios y de su estacionalidad.

Los datos de detección remota obtenidos por distintos sensores satelitales proveen medidas de variables ambientales que están relacionadas con características del hábitat (Buermann *et al.* 2008). Los satélites Terra y Aqua de la NASA están equipados con Espectrorradiómetros de Imágenes de Media Resolución (MODIS por sus siglas en inglés), que ofrecen medidas ópticas globales de vegetación a resoluciones finas y a intervalos de tiempo. Empleando el paquete "MODISTools" (Tuck *et al.* 2014) en el programa estadístico R (R Development Core Team 2014), se descargaron para cada comunidad de colibríes dos productos de MODIS que permitieron caracterizar la vegetación:

1. La fracción de radiación activa fotosintética absorbida por la vegetación (FPAR) y el índice de área foliar (LAI) (Myneni *et al.* 2015). FPAR es la fracción de radiación incidente fotosintéticamente activa (400-700 nm) absorbida por los elementos verdes del dosel. LAI es un equivalente en términos de biomasa, definido como el área foliar verde de un solo lado por unidad de terreno en doseles de hoja ancha, y como la mitad del área de la superficie total de acículas por unidad de terreno en doseles de coníferas. Este algoritmo es medido en intervalos de 8 días en pixeles de 500 m de resolución. El nombre del conjunto de datos es MCD15A2H (Myneni *et al.* 2015)
2. Espacios con Vegetación Continua (VCF) (Dimiceli *et al.* 2015). Esta constituye una representación de la cobertura vegetal, estimada a partir de tres componentes: el porcentaje de cobertura arbórea, el porcentaje de cobertura no-arbórea, y el porcentaje de terreno sin cobertura. Esta estimación se realiza anualmente en pixeles de 250 m de resolución. El nombre del conjunto de datos es MOD44B (Dimiceli *et al.* 2015).

Con el fin de controlar las variaciones entre años, y dependiendo de la disponibilidad de la información en los conjuntos de datos MODIS, se estimaron valores promedio para cada variable conjuntando datos de 5 años. Específicamente, se seleccionaron para cada comunidad los datos que incluían el año en el que fue descrita la comunidad, más los dos años anteriores y posteriores. Para explorar las diferencias significativas entre la altitud y la estructura filogenética de las comunidades de colibríes, se ajustaron modelos lineales generalizados

(MLG) con distribución quasipoisson y función de enlace logaritmo. Los modelos se llevaron a cabo con el paquete "base" del programa estadístico R (R Development Core Team 2014).

Cálculo de la estructura filogenética de las comunidades de colibríes

Para establecer la estructura filogenética de las comunidades de colibríes en México respecto a cada una de las dos filogenias creadas (Escala Continental y Escala México), se calcularon el **índice de parentesco neto** y el **índice del taxón más cercano**, los cuales fueron desarrollados por Webb (2000) y modificados por Webb *et al.* (2002). En este análisis se incluyeron únicamente las 193 comunidades de colibríes que tuvieron 3 especies o más representadas en las filogenias.

El índice de parentesco neto (NRI) es una medida estandarizada de la distancia filogenética pareada de un grupo de especies en una muestra respecto a una poza regional, y cuantifica el agrupamiento general de dichas especies en un árbol filogenético. Se calculó según la siguiente fórmula (Webb *et al.*, 2002):

$$NRI = \left(\frac{(mn(X_{obs}) - mnX(n))}{sdX(n)}\right)$$

Donde:

X_{obs} = Distancia filogenética entre dos taxones (la suma de todas las longitudes de ramas que intervienen) en la filogenia de la poza regional empleada.

$mn(X_{obs})$ = es el promedio de todas las posibles parejas *n* de taxones.

$mnX(n)$ = Promedio esperado para *n* taxones distribuidos azarosamente en la filogenia de la poza regional.

sdX(n) = Desviación estándar esperada para n taxones distribuidos azarosamente en la filogenia de la poza regional.

El índice del taxón más cercano (NTI) (González *et al.*, 2011) es una media estandarizada de la distancia filogenética al taxón más cercano de cada especie en la muestra y cuantifica el grado de agrupamiento terminal del árbol, independientemente del agrupamiento en la parte basal de este. Se calculó de la siguiente manera (Webb *et al.*, 2002):

$$NTI = \left(\frac{(mn(Y_{obs}) - mnY(n))}{sdY(n)}\right)$$

Donde:

Y_{obs} = Distancia filogenética al taxón más cercano en la filogenia regional.

mn(Y_{obs}) = es el promedio de todas las posibles parejas n de taxones.

mnY(n) = Promedio esperado para n taxones distribuidos azarosamente en la filogenia de la poza regional.

sdY(n) = Desviación estándar esperada para n taxones distribuidos azarosamente en la filogenia de la poza regional.

Tanto NRI como NTI tienen valores negativos cuando hay agrupamiento filogenético entre especies, y valores positivos en casos de sobredispersión filogenética. Para establecer si la estructura filogenética observada (y por consiguiente la distribución de similitud entre las especies) en una comunidad de colibríes no es producto del azar, se ensamblaron 999 comunidades aleatorias a partir de la misma poza regional, para comparar los NRI y NTI obtenidos (Webb 2000). Se empleó el método de cambio independiente (independent swap method) para generar los modelos nulos (Gotelli & Entsminger 2003). El cálculo de NRI, NTI y los modelos nulos se llevó a cabo con los paquetes "ape" (Paradis & K. 2018) y "picante" (Kembel *et al.* 2010) del programa estadístico R (R Development Core Team 2014).

Se emplearon análisis de componentes principales (PCA) para explorar la ubicación de las comunidades de colibríes es un espacio ambiental multidimensional. En estos análisis, cada comunidad fue caracterizada en función de las 15 variables ambientales (ocho climáticas y siete de vegetación). La colinealidad entre componentes se estableció mediante el índice de Belsey. Los autovalores, autovectores y ordenaciones producto de estos análisis permitieron identificar cuáles de las variables ambientales originales fueron buenas indicadoras de diferencias entre comunidades en términos de su estructura filogenética. Posteriormente se llevaron a cabo análisis discriminantes lineales (LDA) con el fin de establecer en qué medida las variables ambientales fueron buenas predictoras de la estructura filogenética de las comunidades de colibríes. En estos análisis la variable respuesta fueron las comunidades clasificadas por su significancia y valor de NRI y NTI, y las variables explicativas fueron las variables ambientales y de vegetación que más aportaron en los análisis de PCA. Estos análisis se llevaron a cabo con los paquetes "vegan" (Oksanen *et al.* 2018) y "ggplot2" (Vu 2011) del programa estadístico R (R Development Core Team 2014).

Con el fin de establecer la relación existente entre las variables climáticas y de vegetación que más aportaron en los análisis de ordenamiento con los valores de NRI y NTI, se emplearon modelos aditivos generalizados (GAM). Se optó por este tipo de modelos, debido a que la relación entre los valores de estructura filogenética y las variables ambientales seleccionadas no fue lineal. Inicialmente se verificó la falta de colinealidad entre las siete variables ambientales seleccionadas estimando los factores de inflación de la varianza (VIF).

La cantidad óptima de suavizado del modelo se estimó usando máxima verosimilitud realizada (REML). Los análisis se llevaron a cabo usando los paquetes “mgvc” (Wood 2011) en R (R-Development-Core-Team 2010).

RESULTADOS

Composición de especies en las comunidades de colibríes.

Se recopiló información para un total de 205 comunidades de colibríes en el país, cubriendo las 32 entidades federativas. Los Estados con mayor número de registros fueron Oaxaca (24 comunidades), Chiapas (16), San Luis Potosí (12), Guerrero (11) y Sonora (10) (Figura 1, Anexo 1).

Reconstrucción filogenética

Los análisis bayesianos que incorporaron el gen nuclear y los tres genes mitocondriales resultaron en dos hipótesis filogenéticas bien soportadas para las especies de colibríes (Anexos 3 y 4). Empleando como criterios las probabilidades posteriores y los Factores de Bayes, se estableció que los resultados obtenidos en MrBayes para el régimen de partición 6 (ND2-posición 1, ND2-posición 2, ND2-posición 3, ND5-posición 1, ND5-posición 2, ND5-posición 3, 12S, AK1) fueron los más apropiados para estimar las relaciones filogenéticas entre las especies de colibríes. Esto se cumplió tanto para el set completo (Escala continental) como para el set que incluía solo las especies de México (Escala México) (Anexos 5-8). Estos dos árboles fueron usados como base para la estimación de los tiempos de divergencia (Figuras 2 y 3).

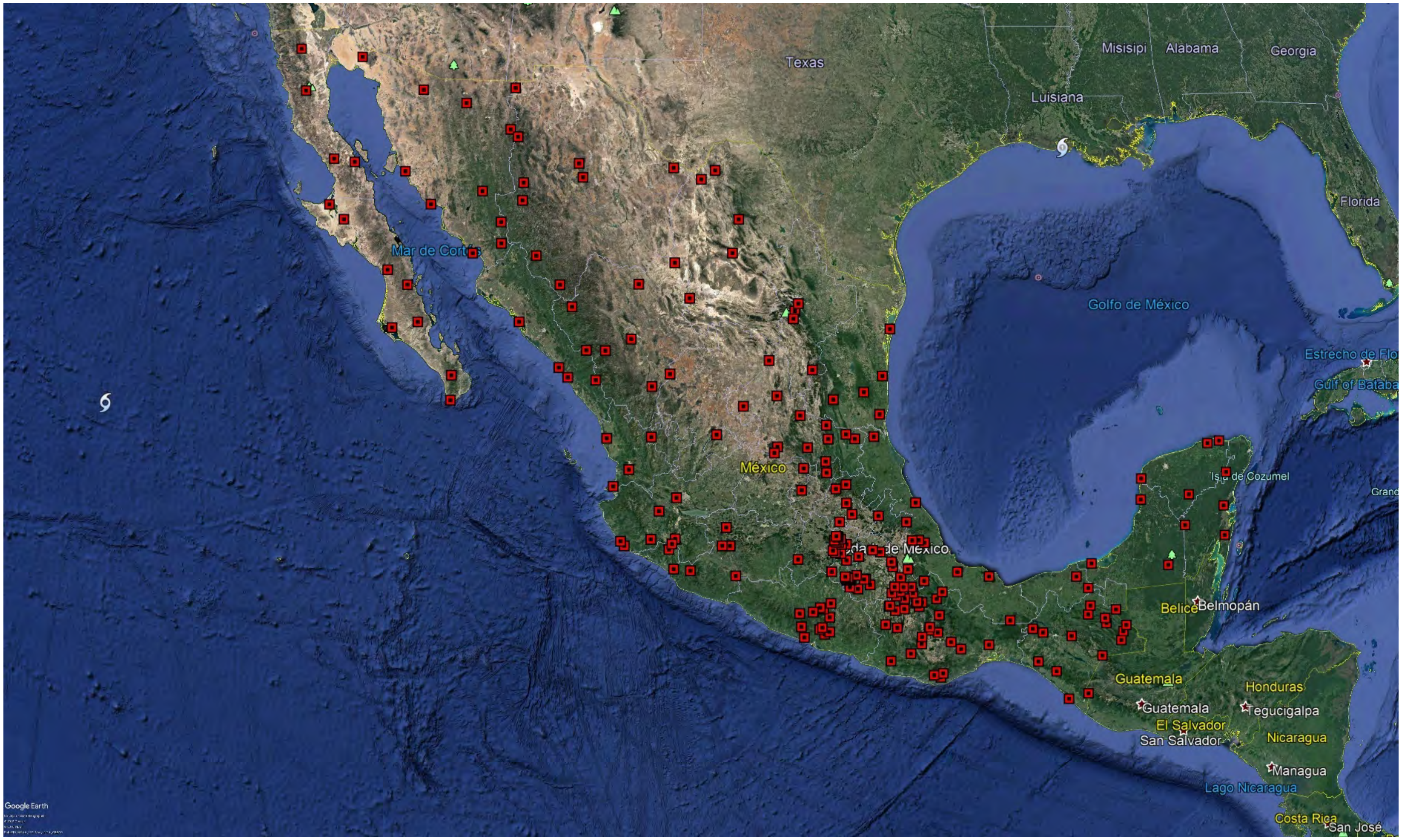


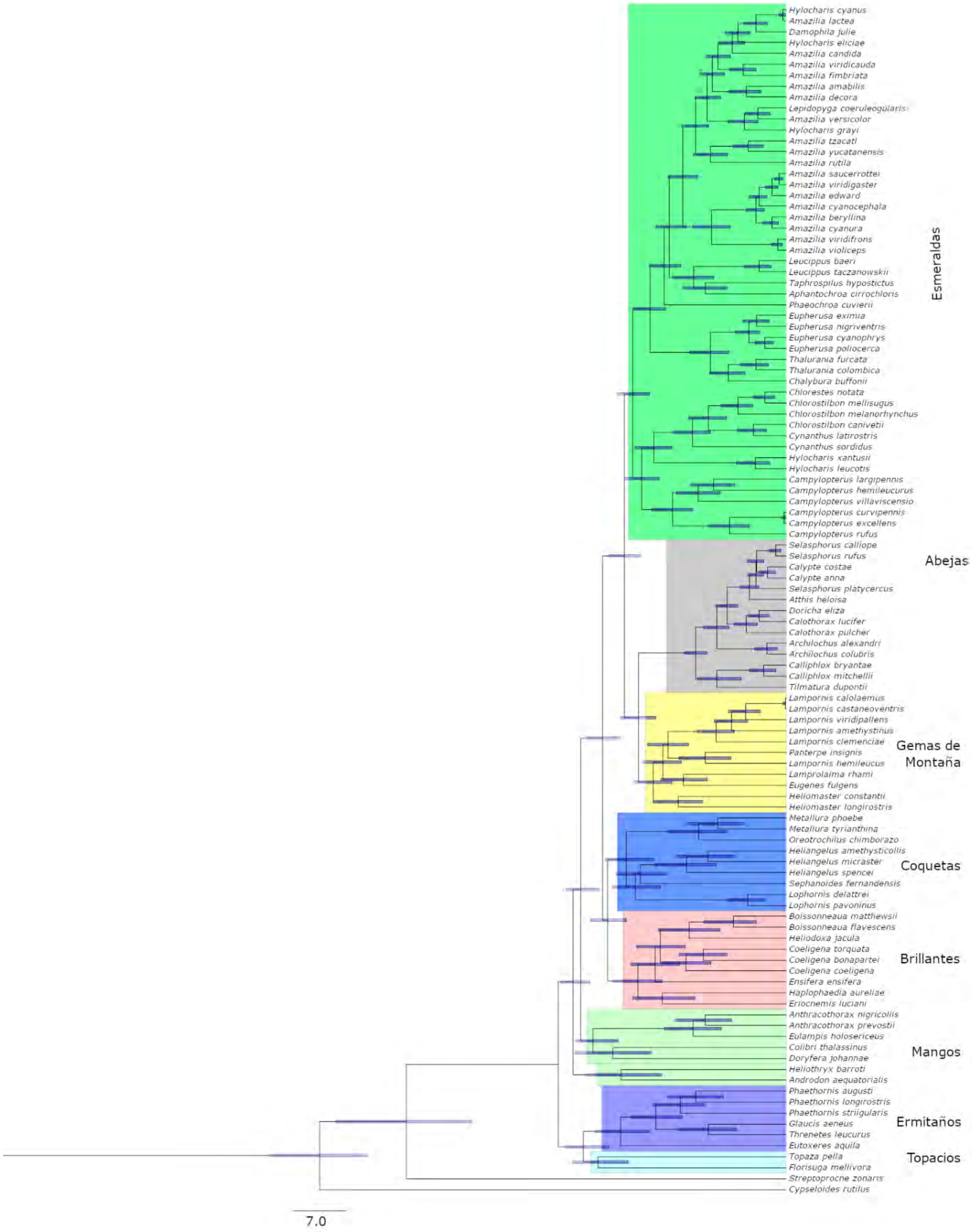
Figura 1: Mapa de México indicando en puntos rojos las comunidades de colibríes analizadas en el presente estudio. Fuente: Google Earth (2018).

Cálculo de la estructura filogenética de las comunidades de colibríes

Para el índice NRI, el cual estima la longitud de rama promedio para todas las combinaciones por pares de un conjunto de especie (Webb *et al.* 2002), de las 193 comunidades de colibríes analizadas, 13 a la escala continental (6.74%) y 16 (8.29%) a escala México tuvieron valores positivos estadísticamente significativas ($p > 0.95$) respecto a los modelos nulos (puntos rojos Figura 4), indicando sobredispersión filogenética (Kembel 2010). Por otro lado, 27 comunidades (13.99%) respecto a la filogenia continental y 26 (13.47%) respecto a la filogenia escala México tuvieron valores negativos de NRI estadísticamente significativos ($p < 0.05$) comparado con los modelos nulos (puntos azules Figura 4), indicando agregamiento filogenético (Kembel 2010). Las comunidades de colibríes con agrupamiento filogenético estuvieron localizadas principalmente al norte y centro del país, en las provincias fisiográficas de Desierto Chihuahuense, Sonora, Baja California, Sierra Madre Oriental, Tierras Bajas del Pacífico, Tamaulipas y Sierra Madre Occidental (latitud promedio 27° 04’ 37.5600’’) (Morrone *et al.* 2017, Morrone 2019) (Figura 4). Respecto al tipo de ecosistema en el que se ubican estas comunidades, la mayoría se localizaron en bosques de pino y pino encino (11 comunidades), matorrales xerófilos (11 comunidades), seguido de manglares y dunas costeras (4 comunidades), y bosques riparos (1 comunidad). Por su parte, las comunidades con sobredispersión filogenética se localizaron al sur del país principalmente, en las provincias Veracruzana, Tierras Altas de Chiapas, Sierra Madre del Sur y Península de Yucatán (latitud promedio 17° 25’ 30.6425’’) (Morrone *et al.* 2017, Morrone 2019); en selvas altas y medianas perennifolias (12 comunidades), manglares (1 comunidad), selva baja caducifolia (1 comunidad), bosque de coníferas (1 comunidad), y matorral espinoso (1 comunidad) (Figura 4).

En cuanto al índice NTI, el cuál estima la distancia promedio que separa cada especie de su relativo más cercano dentro de la comunidad (Webb *et al.* 2002), 15 comunidades (7.77%) a escala continental y 12 (6.22%) a escala México tuvieron valores positivos estadísticamente significativas respecto a los modelos nulos (Figura 5) indicando dispersión filogenética en la parte terminal del árbol (Kembel 2010). Por otro lado, 22 comunidades (11.40%) respecto a la filogenia continental y 21 (10.88%) respecto a la filogenia escala México tuvieron valores negativos de NTI estadísticamente significativos ($p < 0.05$) comparados con los modelos nulos indicando agrupamiento filogenético en la parte terminal del árbol (Kembel 2010) (Figura 5). Las comunidades de colibríes con agrupamiento filogenético respecto al índice NTI estuvieron ubicadas principalmente al norte y centro del país (latitud promedio 26° 09’ 56.2154’’), en las provincias biogeográficas de Baja California, Sonora, Desierto Chihuahuense, Sierra Madre Occidental, Sierra Madre del Sur, Sierra Madre Oriental, Tamaulipas (Morrone *et al.* 2017, Morrone 2019); en matorrales xerófilos (9 comunidades), bosques de pino-encino (7 comunidades), ecosistemas costeros (3 comunidades), selva baja caducifolia (1 comunidad) y bosque ripario (1 comunidad).

Figura 2: Hipótesis filogenética calibrada de todas las especies de colibríes (Escala continental) generada a partir del análisis Bayesiano de reloj molecular relajado usando el modelo evolutivo de especies de Yule y cuatro puntos de calibración. Se emplearon los datos combinados del intrón 5 del Adenilato Kinasa, la subunidad 2 y 5 de la NADH deshidrogenasa, y el gen 12S ribosomal. Las barras de color violeta indican el intervalo del 95% de densidad posterior más alta (HPD). Los colores agrupan las especies de colibríes por clados filogenéticos siguiendo a McGuire y colaboradores (2014).


Hylocharis cyanus
Amazilia lactea
Damophila julie
Hylocharis eliciae
Amazilia candida
Amazilia viridicauda
Amazilia fimbriata
Amazilia amabilis
Amazilia decora
Lepidopyga coeruleogularis
Amazilia versicolor
Hylocharis grayi
Amazilia tzacatl
Amazilia yucatanensis
Amazilia rutila
Amazilia saucerrottei
Amazilia viridigaster
Amazilia edward
Amazilia cyanocephala
Amazilia beryllina
Amazilia cyanura
Amazilia viridifrons
Amazilia violiceps
Leucippus baeri
Leucippus taczanowskii
Taphrospilus hypostictus
Aphantochroa cirrochloris
Phaeochroa cuvierii
Eupherusa eximia
Eupherusa nigriventris
Eupherusa cyanophrys
Eupherusa poliocerca
Thalurania furcata
Thalurania colombica
Chalybura buffonii
Chlorestes notata
Chlorostilbon mellisugus
Chlorostilbon melanorhynchus
Chlorostilbon canivetii
Cynanthus latirostris
Cynanthus sordidus
Hylocharis xantusii
Hylocharis leucotis
Campylopterus largipennis
Campylopterus hemileucurus
Campylopterus villaviscensio
Campylopterus curvipennis
Campylopterus excellens
Campylopterus rufus
Esmeraldas
Selasphorus calliope
Selasphorus rufus
Calypte costae
Calypte anna
Selasphorus platycercus
Atthis heloisa
Doricha eliza
Calothorax lucifer
Calothorax pulcher
Archilochus alexandri
Archilochus colubris
Calliphlox bryantae
Calliphlox mitchellii
Tilmatura dupontii
Abejas
Lampornis calolaemus
Lampornis castaneoventris
Lampornis viridipallens
Lampornis amethystinus
Lampornis clemenciae
Panterpe insignis
Lampornis hemileucus
Lamprolaima rhami
Eugenes fulgens
Heliomaster constantii
Heliomaster longirostris
Gemas de Montaña
Metallura phoebe
Metallura tyrianthina
Oreotrochilus chimborazo
Heliangelus amethysticollis
Heliangelus micraster
Heliangelus spencei
Sephanoides fernandensis
Lophornis delattrei
Lophornis pavoninus
Coquetas
Boissonneaua matthewsii
Boissonneaua flavescens
Heliodoxa jacula
Coeligena torquata
Coeligena bonapartei
Coeligena coeligena
Ensifera ensifera
Haplophaedia aureliae
Eriocnemis luciani
Brillantes
Anthracothorax nigricollis
Anthracothorax prevostii
Eulampis holosericeus
Colibri thalassinus
Doryfera johannae
Heliothryx barroti
Androdon aequatorialis
Mangos
Phaethornis augusti
Phaethornis longirostris
Phaethornis striigularis
Glaucis aeneus
Threnetes leucurus
Eutoxeres aquila
Ermitaños
Topaza pella
Florisuga mellivora
Topacios
Streptoprocne zonaris
Cypseloides rutilus
7.0

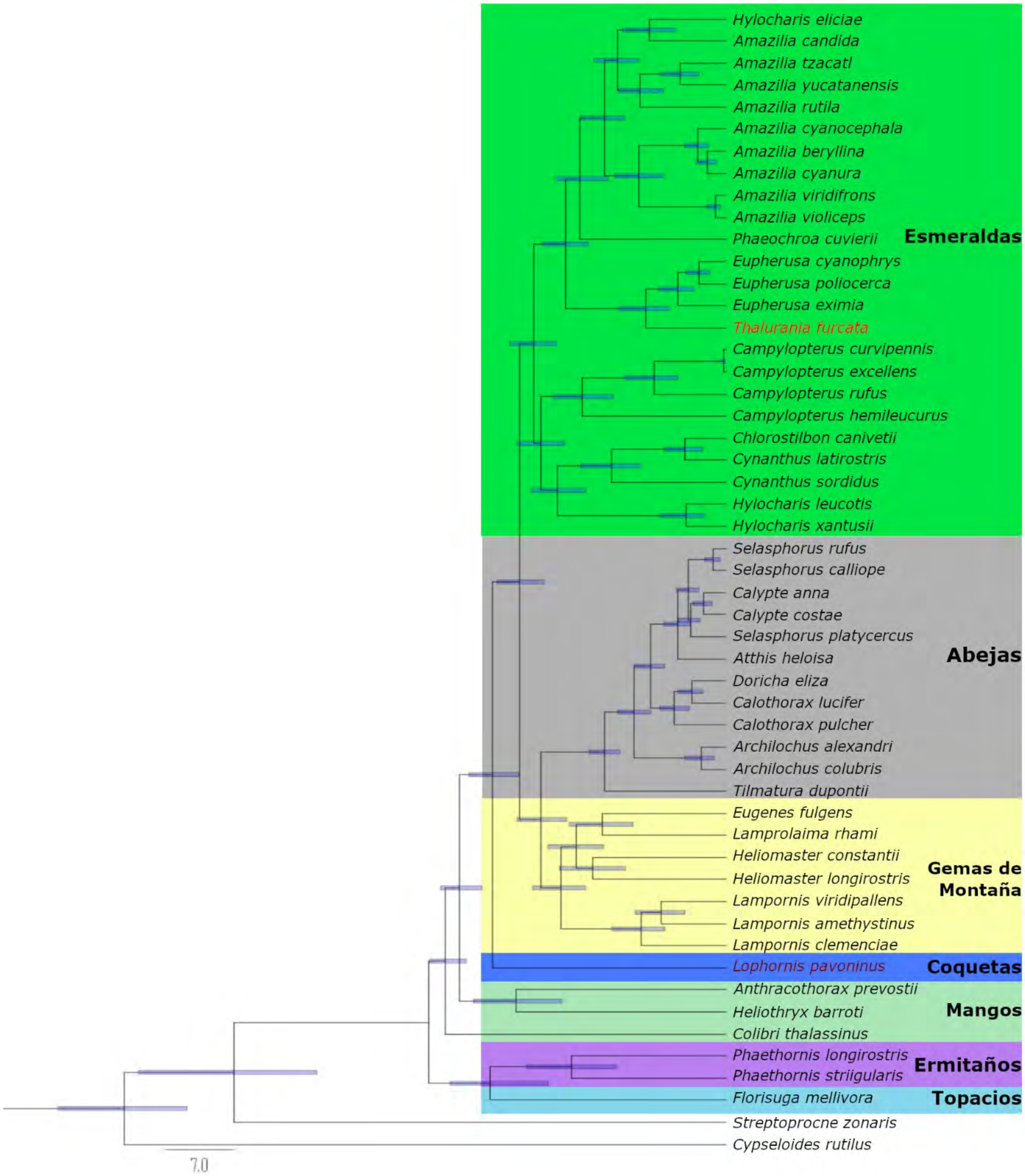


Figura 3: Hipótesis filogenética calibrada de las especies de colibríes en México (Escala México) generada a partir del análisis Bayesiano de reloj molecular relajado usando el modelo evolutivo de especies de Yule y cuatro puntos de calibración. Se emplearon los datos combinados del intrón 5 del Adenilato Kinasa, la subunidad 2 y 5 de la NADH deshidrogenasa, y el gen 12S ribosomal. Las barras de color violeta indican el intervalo del 95% de densidad posterior más alta (HPD). Los colores agrupan las especies de colibríes por clados filogenéticos siguiendo a McGuire y colaboradores (2014). Las especies *Lophornis pavoninus* y *Thalurania furcata* (en color rojo) se incluyeron como nodos substitutos a las especies mexicanas *Lophornis brachylopha* y *Thalurania ridgwayi* de las cuales no hay secuencias disponibles.

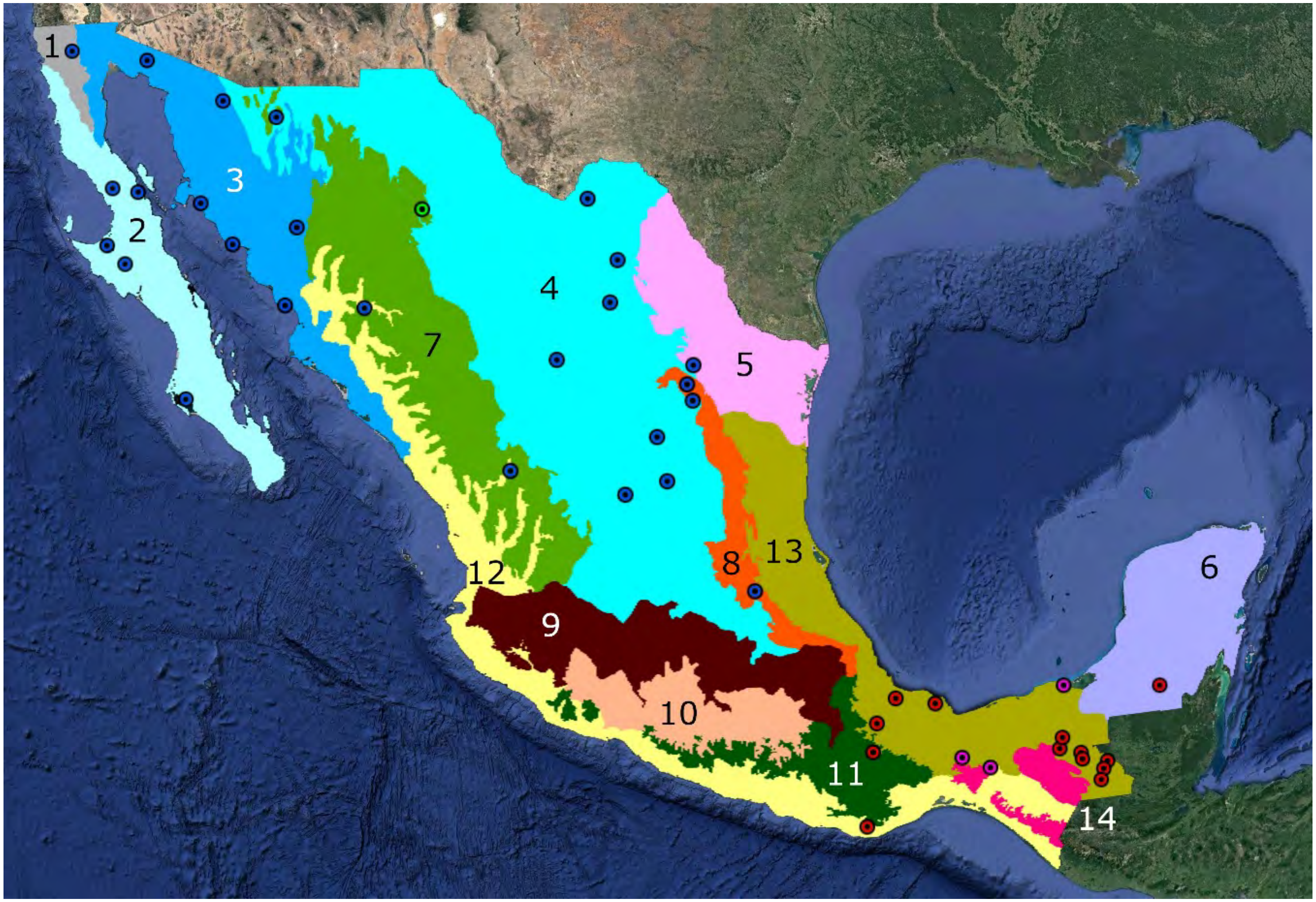


Figura 4: Mapa de México indicando las comunidades de colibríes donde el índice de parentesco neto (NRI) fue estadísticamente significativo. Los puntos azules indican las comunidades con agrupamiento filogenético ($p > 0.90$) en la filogenia a escala continental y a escala México. El punto verde es una comunidad con agrupamiento filogenético significativo exclusivamente en la escala continental. Los puntos rojos son las comunidades con sobredispersión filogenética ($p < 0.05$) en la escala continental y escala México. Los puntos morados son comunidades con sobredispersión filogenética exclusivamente en la escala México. Los colores en el mapa representan las Provincias biogeográficas de México (Morrone 2019) 1) Californiana; 2) Baja California; 3) Sonora; 4) Desierto Chihuahuense; 5) Tamaulipas; 6) Península de Yucatán; 7) Sierra Madre Occidental; 8) Sierra Madre Oriental; 9) Faja Volcánica Transmexicana; 10) Cuenca del Balsas; 11) Sierra Madre del Sur; 12) Tierras bajas del Pacífico; 13) Veracruzana; 14) Tierras Altas de Chiapas. Fuente: Google Earth (2018).

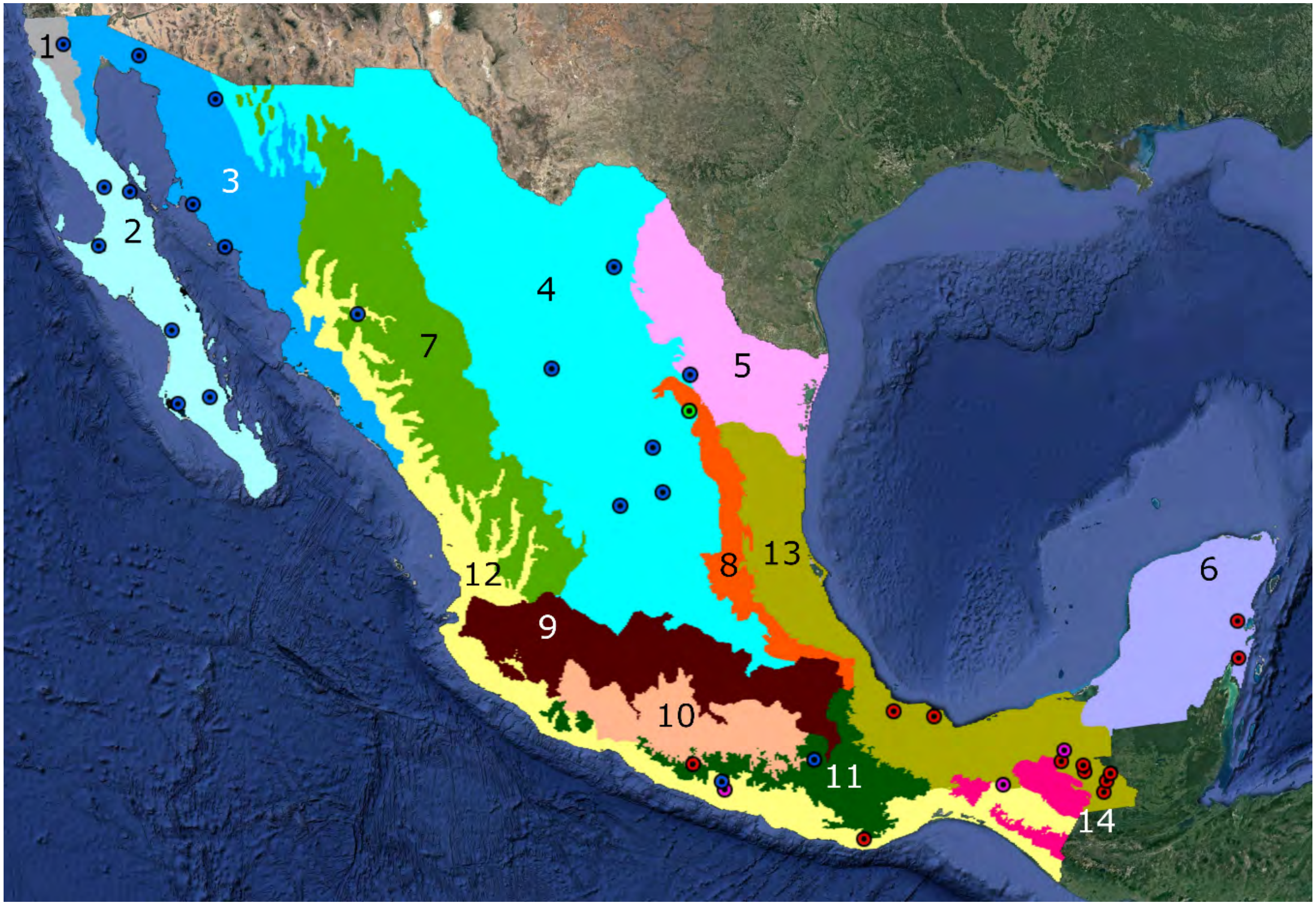


Figura 5: Mapa de México indicando las comunidades de colibríes donde el índice de taxón más cercano (NTI) fue estadísticamente significativo. Los puntos azules indican las comunidades con agrupamiento filogenético ($p > 0.90$) en la parte terminal del árbol de la filogenia a escala continental y a escala México. El punto verde es una comunidad con agrupamiento filogenético significativo exclusivamente en la escala continental. Los puntos rojos son las comunidades con sobredispersión filogenética ($p < 0.05$) en la parte terminal de los árboles en la escala continental y en la escala México. Los puntos morados son comunidades con sobredispersión filogenética exclusivamente en la escala continental. Los colores en el mapa representan las Provincias biogeográficas de México (Morrone 2019) 1) Californiana; 2) Baja California; 3) Sonora; 4) Desierto Chihuahuense; 5) Tamaulipas; 6) Península de Yucatán; 7) Sierra Madre Occidental; 8) Sierra Madre Oriental; 9) Faja Volcánica Transmexicana; 10) Cuenca del Balsas; 11) Sierra Madre del Sur; 12) Tierras bajas del Pacífico; 13) Veracruzana; 14) Tierras Altas de Chiapas. Fuente: Google Earth (2018).

Asimismo, las especies con sobredispersión filogenética respecto a este mismo índice se localizaron al sur del país, en las provincias Veracruzana, Tierras Altas de Chiapas, Sierra Madre del Sur, Península de Yucatán (Latitud promedio 17° 29´29.0907’’) (Morrone *et al.* 2017, Morrone 2019); en selvas altas perennifolias (8 comunidades), selvas medianas subcaducifolias (3 comunidades), selvas bajas caducifolias (2 comunidades), y matorral espinoso (1 comunidad) (Figura 5).

Veinticinco comunidades de colibríes tuvieron valores de NRI y NTI estadísticamente significativos, tanto para la filogenia a escala continental, como para la filogenia a escala México (Anexos 9 y 10). Nueve de ellas mostraron sobredispersión filogenética y 16 agrupamiento filogenético (Anexo 10).

Las comunidades con estructura filogenética aleatoria se localizaron en bosques de pino-encino (34.91%), bosques secos tropicales (18.94%), matorrales espinosos (16.57%), bosques mesófilos de montaña (7.10%), selvas altas perennifolias (7.10%), manglares (7.10%), selvas medianas (4.73%) y vegetación secundaria (3.55%). La mayoría de estas comunidades se ubicaron en la Zona de Transición Mexicana (56.67%); específicamente en las provincias Faja Volcánica Transmexicana, Sierra Madre del Sur, Sierra Madre Occidental, Sierra Madre Oriental y Tierras Altas de Chiapas. Las comunidades restantes se localizaron en la Zona Neotropical (33.33%) y en la Zona Neártica (10.00%), en las provincias de Tamaulipas, Baja California, Desierto Chihuahuense, Península de Yucatán, cuenca del Balsas, Veracruzana y Tierras bajas del Pacífico (Morrone 2019) (Anexo 12).

Estructura filogenética y elevación

En una exploración inicial sobre la relación entre la estructura filogenética de las comunidades de colibríes en México y la elevación, se observa que tanto para NRI como NTI los rangos altitudinales no difieren estadísticamente ($X^2 = 1.81$, g.l.= 2, $p = 0.12$ y $X^2 = 1.80$, g.l.= 2, $p = 0.11$ respectivamente), y hay un alto traslape entre las comunidades de las diferentes estructuras filogenéticas (Figura 6). Las comunidades con sobredispersión filogenética significativa respecto a NRI tuvieron una elevación promedio de 645.47 msnm (rango 0-1675 msnm), mientras que las comunidades con agrupamiento filogenético significativo tuvieron una elevación promedio de 1249.83 msnm (rango 2-2600 msnm). En el caso de las comunidades que tuvieron valores no significativos, su elevación promedio y rango altitudinal fueron mayores (sobredispersión filogenética: promedio 1346.11 msnm, rango 3–3300 msnm, agrupamiento filogenético: promedio 1605.26 msnm, rango 3.5–3351.5 msnm; Figura 6).

En el caso de NTI, el patrón fue prácticamente idéntico al descrito anteriormente para NRI. Las comunidades con sobredispersión filogenética significativa estuvieron situadas en menores elevaciones respecto a las comunidades con agrupamiento filogenético (sobredispersión: promedio 818.67 msnm, rango 10-1900 msnm; agrupamiento: promedio 1064.07 msnm, rango 2–2600 msnm). Asimismo, en el caso de las comunidades con estructura filogenética no significativa, la elevación promedio fue más alta y el rango de altitud más amplio (sobredispersión filogenética: promedio 1340.07 msnm, rango 0–3160 msnm; agrupamiento filogenético: promedio 1622.72 msnm, rango 3–3351.50 msnm, Figura 6).

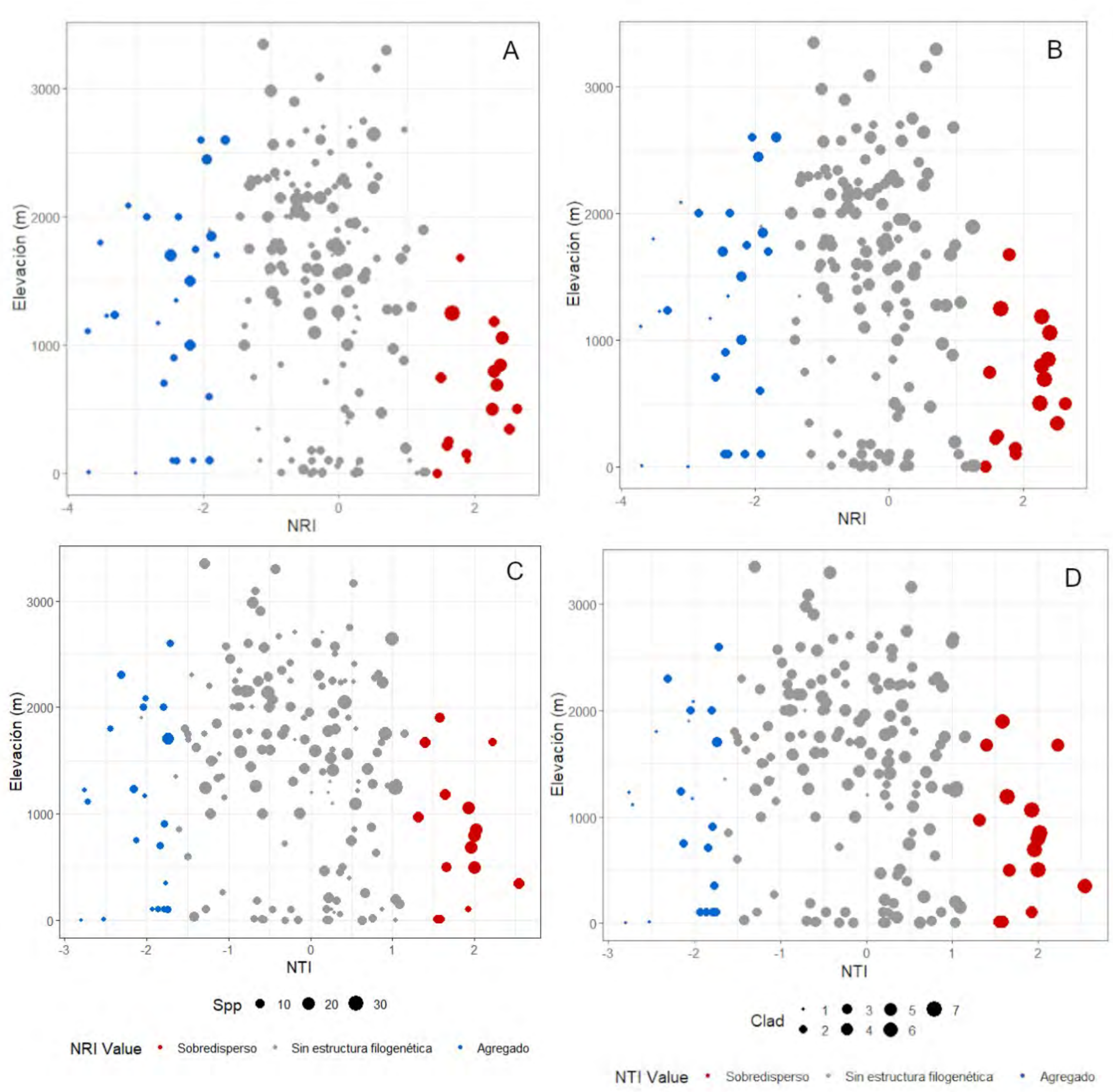


Figura 6: Gráfica de NRI (fila superior) y NTI (fila inferior) respecto la elevación. El tamaño del círculo es proporcional al número de especies (A y C) y número de clados filogenéticos (B y D) de colibríes en la comunidad.

Estructura y clados filogenéticos

Al correlacionar los resultados de estructura filogenética con la composición de las comunidades de colibríes en términos de clados (McGuire *et al.* 2014), se observó un patrón de riqueza y representatividad en las distintas comunidades. Específicamente, para NRI y NTI, el número de clados presentes en cada categoría disminuyó a medida que las comunidades pasaron de ser sobredispersas a agregadas. Tres clados filogenéticos (Esmeraldas, Abejas y Gemas de Montañas) fueron los únicos presentes en al menos una comunidad de cada categoría de estructura filogenética. Por su parte, las Coquetas, Ermitaños y Topacios fueron los clados que desaparecieron más rápidamente a medida que se incrementó el agrupamiento filogenético (Figuras 7 y 8). El número de especies promedio (números dentro de las barras de Figuras 7 y 8) cambió en función del clado y de la categoría de estructura filogenética. Las Esmeraldas estuvieron presentes en al menos el 50% de las comunidades de cada estructura filogenética, y el número de especies promedio por comunidad disminuyó de ocho a una a medida que se incrementó el agrupamiento filogenético (Figuras 7 y 8). El caso opuesto ocurrió con las Abejas, las cuales estuvieron presentes en el 80% de las comunidades estudiadas, y para las cuales el número de especies promedio por comunidad se relacionó negativamente con el agrupamiento filogenético (Figuras 7 y 8).

Estructura filogenética y variables ambientales

La información de las variables climáticas y de vegetación para las comunidades de colibríes en México se muestran en el Anexo 12. Los resultados del análisis de Componentes Principales (PCA) corroboraron la presencia de variables climáticas que están asociadas con la estructura filogenética. El primer componente estuvo asociado positivamente con la

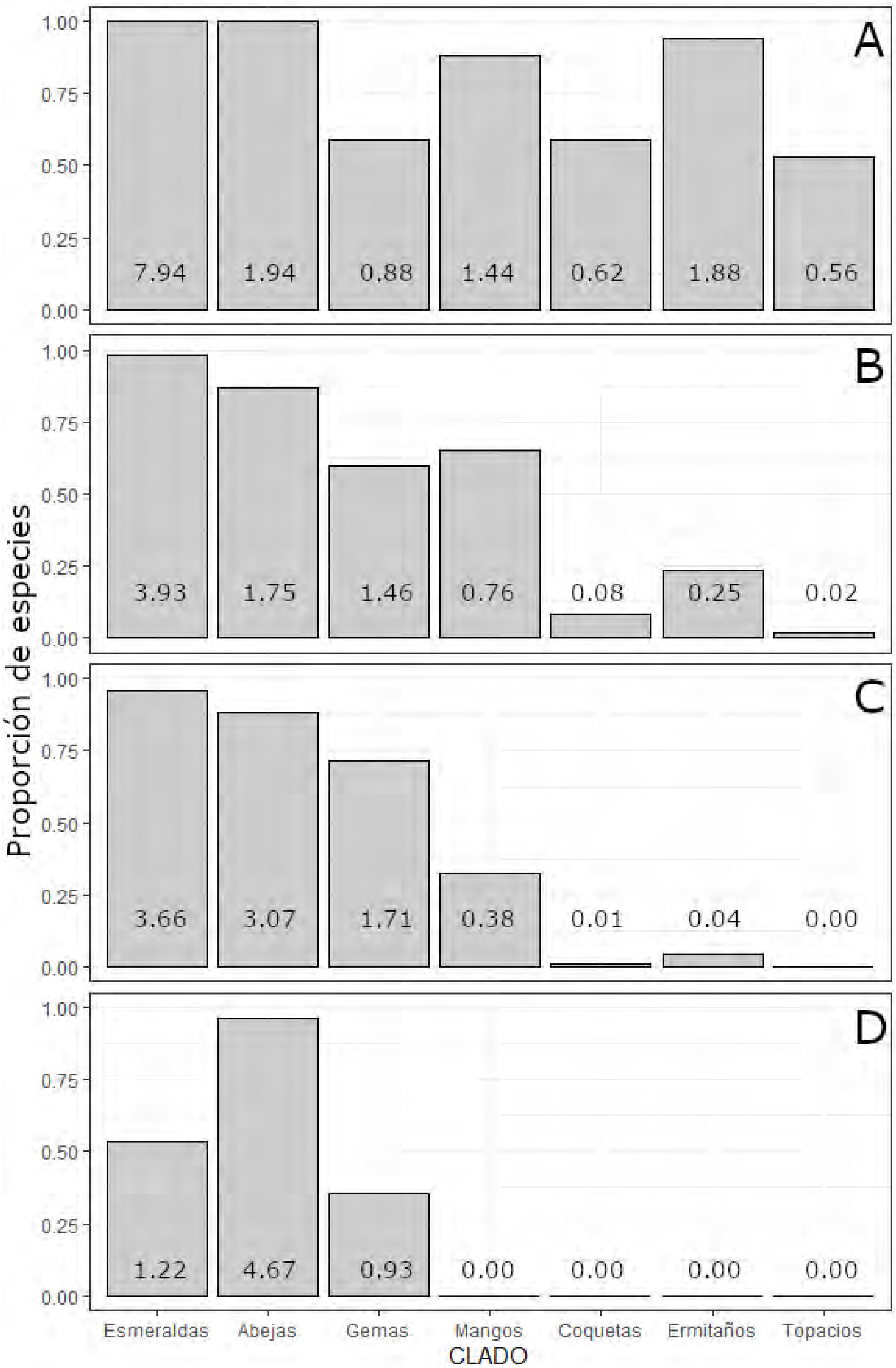


Figura 7: Representatividad de los distintos clados filogenéticos de colibríes respecto a la estructura filogenética estimada (índice NRI). (A) Comunidades con sobredispersión filogenética significativa; (B) comunidades con sobredispersión filogenética no significativa; (C) comunidades con agrupamiento filogenético no significativo; (D) comunidades con agrupamiento filogenético significativo. El eje de y representa la proporción de comunidades que tienen especies de un clado en particular, y los números en las barras respresentan el número de especies promedios por comunidad en esta categoría.

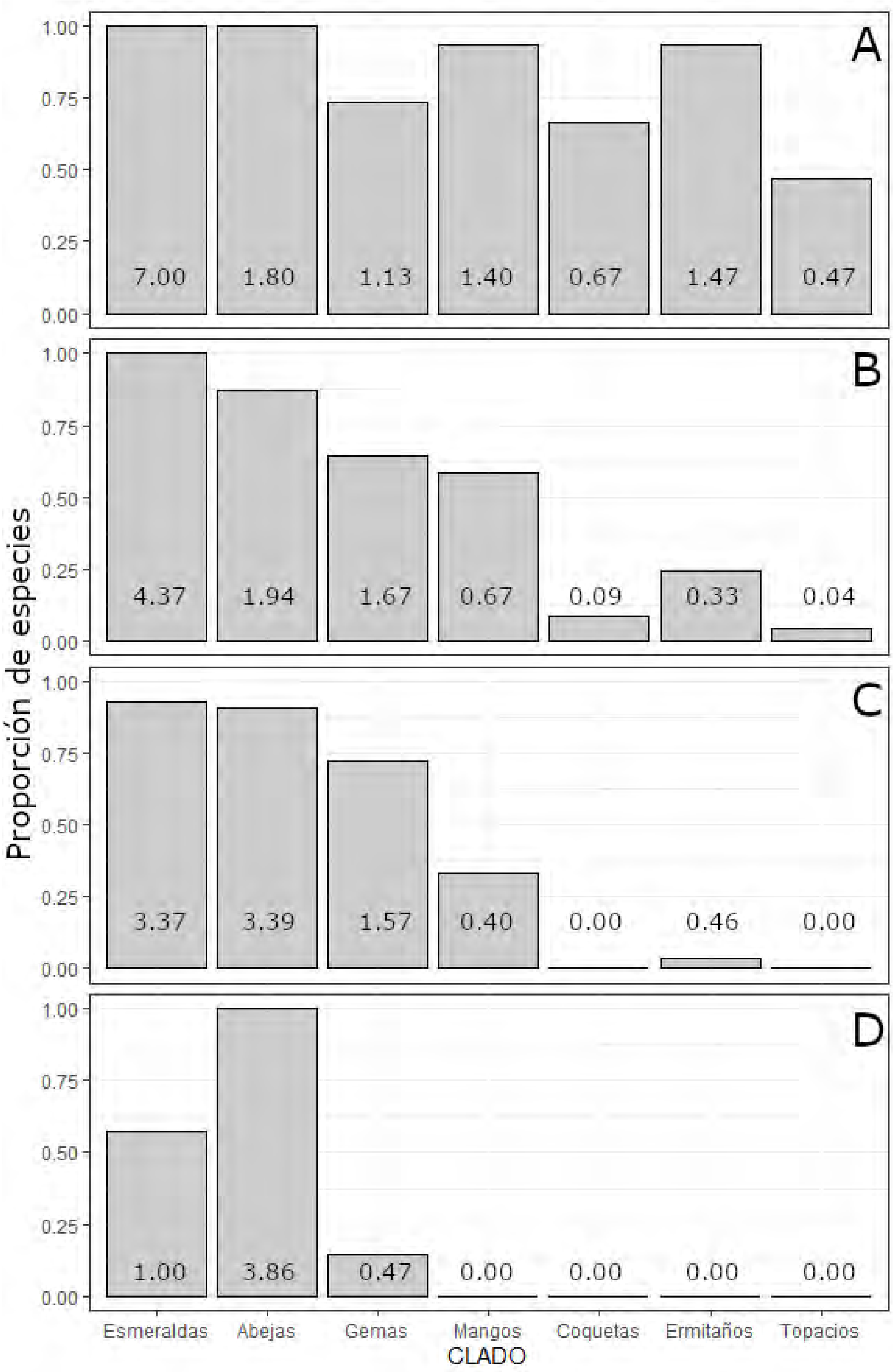


Figura 8: Representatividad de los distintos clados filogenéticos de colibríes respecto a la estructura filogenética estimada (índice NTI). (A) Comunidades con sobredispersión filogenética significativa; (B) comunidades con sobredispersión filogenética no significativa; (C) comunidades con agrupamiento filogenético no significativo; (D) comunidades con agrupamiento filogenético significativo. El eje de y representa la proporción de comunidades que tienen especies de un clado en particular, y los números en las barras respresentan el número de especies promedios por comunidad en esta categoría.

precipitación anual, la precipitación total durante los tres meses más cálidos y fríos del año, y negativamente con el rango de la temperatura anual y con el rango diurno promedio anual de la temperatura. Por su parte, el segundo componente estuvo relacionado positivamente con la estacionalidad de la precipitación y negativamente con la estacionalidad de la temperatura (Figura 9). Cuando se observa cómo se ubicaron las comunidades de colibríes en este espacio multidimensional, se encontró que las comunidades sobredispersas filogenéticamente tanto para el índice NRI como NTI (puntos rojos), estuvieron en general en sitios con mayores precipitaciones a lo largo del año y en los cuatrimestres más cálidos y fríos, y una mayor temperatura promedio anual (valores positivos en el eje *x*, Figura 9). Respecto a las comunidades con agrupamiento filogenético, se observó que tanto para NRI como para NTI (puntos azules) estas comunidades se ubicaron en sitios que presentaron valores altos de estacionalidad en la temperatura y en su rango de temperatura anual, pero tuvieron bajos valores de precipitación promedio anual (valores negativos en el eje *x*, Figura 9).

Las comunidades de colibríes con valores no significativos en la estructura filogenética, es decir, las comunidades con estructura filogenética al azar (puntos grises y verdes), mostraron un patrón aleatorio distribuyéndose en todas las áreas del espacio multidimensional (Figura 9).

Respecto al análisis de PCA para las variables de vegetación, las variables que más aportaron al primer componente fueron el porcentaje de vegetación arbórea, el porcentaje de radiación de la fracción fotosintéticamente activa, y el porcentaje del índice de área foliar. Por otro lado, las variables que más aportaron al segundo componente fueron el porcentaje de vegetación no arbórea y el porcentaje sin cobertura vegetal (Figura 10).

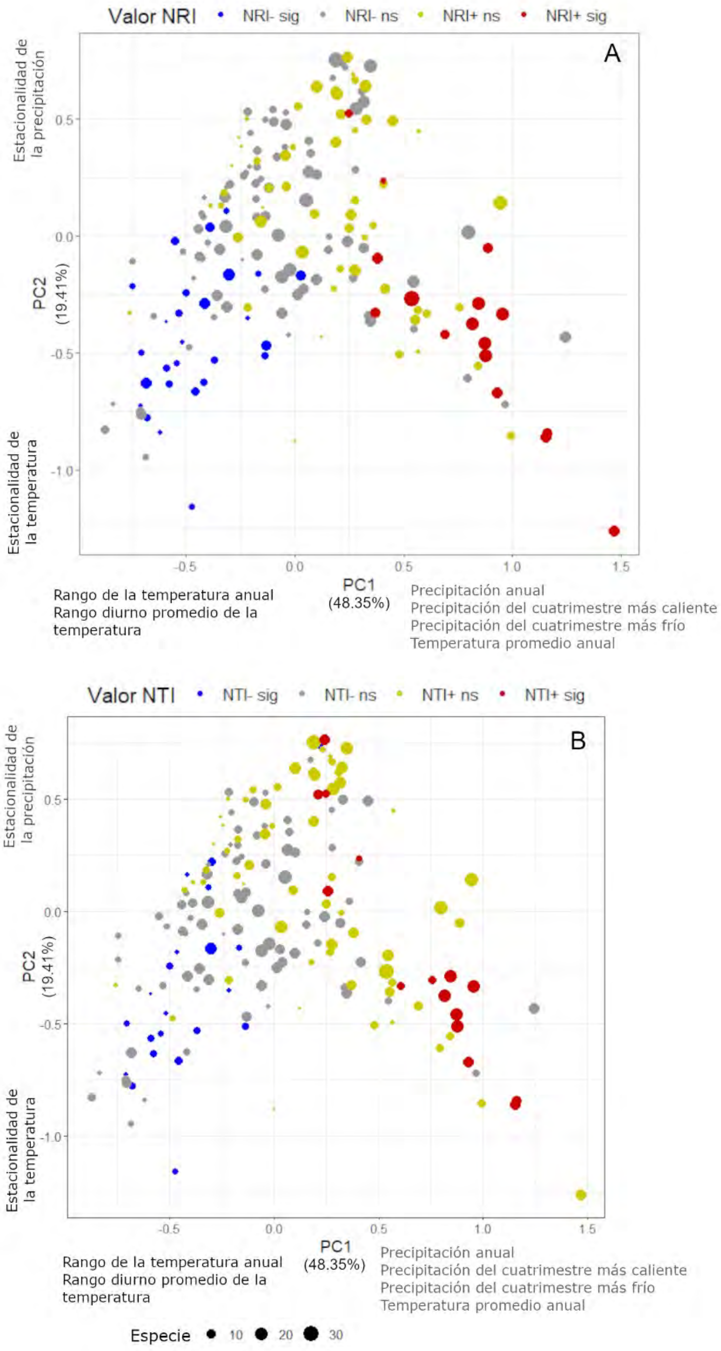


Figura 9: Gráfica de los dos primeros Componentes Principales para las variables climáticas. El color de los círculos corresponde al valor del índice NRI (A) y NTI (B), indicando si es positivo (+) o negativo (-), y a su significancia estadística respecto a los modelos nulos (sig: estadísticamente significativo, ns: no significativo estadísticamente). El tamaño de los círculos es proporcional al número de especies en cada comunidad. Se indican las variables que más aportan en cada uno de los ejes y su porcentaje de varianza explicada.

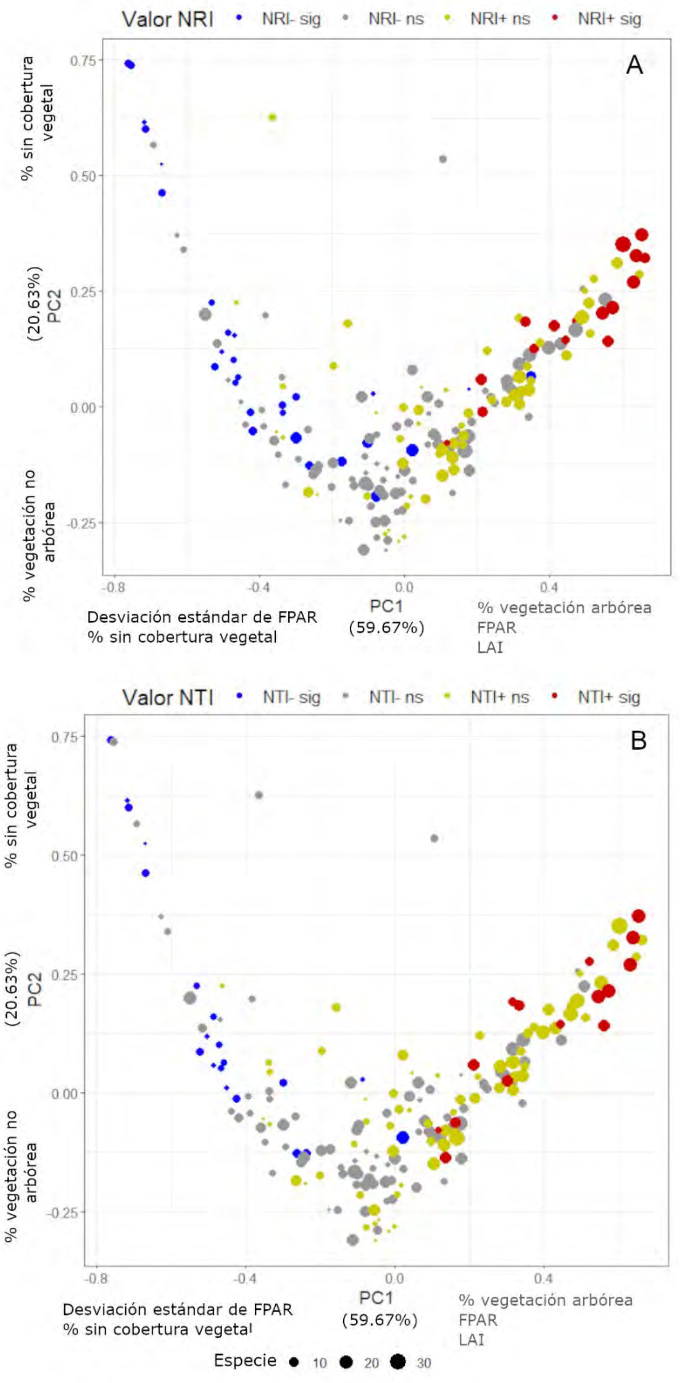


Figura 10: Gráfica de los dos primeros Componentes Principales para las variables de vegetación. El color de los círculos corresponde al valor del índice NRI (A) y NTI (B), indicando si es positivo (+) o negativo (-), y a su significancia estadística respecto a los modelos nulos (sig: estadísticamente significativo, ns: no significativo estadísticamente). El tamaño de los círculos es proporcional al número de especies en cada comunidad. Se indican las variables que más aportan en cada uno de los ejes y su porcentaje de varianza explicada.

Las comunidades de colibríes con sobredispersión filogenética significativa y no significativa respecto a los índices NRI y NTI (puntos rojos y amarillos, Figura 10) se ubicaron en sitios con valores altos de porcentaje de radiación de la fracción fotosintéticamente activa y de porcentaje del índice de área foliar, con coberturas arbóreas altas (valores positivos eje x), y coberturas no arbóreas intermedias (valores cercanos a 0.25 en el eje). Patrón opuesto a lo observado en las comunidades con atracción filogenética significativa (puntos azules, Figura 10) donde las comunidades se caracterizaron por presentarse en sitios con porcentajes bajos de cobertura arbórea y valores altos de superficie sin cobertura vegetal. Las comunidades con valores de NRI y NTI negativos no significativos (puntos grises, Figura 10) se ubicaron a lo largo del espacio multidimensional sin asociarse con alguna característica particular respecto a la cobertura vegetal.

El análisis LDA indicó que las variables estacionalidad de la precipitación, estacionalidad de la temperatura, precipitación del cuatrimestre más frío, porcentaje del índice de área foliar, porcentaje de no-cobertura arbórea, porcentaje de terreno sin cobertura, y porcentaje de cobertura arbórea predijeron en porcentajes variables el tipo de estructura filogénetica observada en las distintas comunidades de colibríes (Tabla 1).

Después de la exploración de la varianza y de la significancia de cada variable, el mejor modelo aditivo generalizado (GAM) para el índice NRI incluyó la estacionalidad de la precipitación, la estacionalidad de la temperatura, la precipitación del cuatrimestre más frío y el porcentaje del índice de área foliar, siendo esta última variable la que más varianza explicó (Tabla 2). Este modelo explicó el 57.3% de la devianza, y la sobredispersión filogenética se asoció a una alta estacionalidad de la precipitación, una mayor precipitación del cuatrimestre más frío, un mayor porcentaje de índices de área foliar, y una menor estacionalidad en la temperatura (Figura 11). En el caso del GAM para el índice NTI, el mejor modelo tuvo tres variables y explicó el 52.70% de la devianza (Tabla 3). Este modelo encontró que la sobredispersión filogenética se observó en comunidades con mayor precipitación en el cuatrimestre más frío, mayor índice de área foliar y menor estacionalidad de la temperatura (Figura 12).

Tabla 1: Porcentaje de observaciones correctamente clasificadas en las distintas categorías de estructura filogenética obtenido en el análisis discriminante lineal (LDA) para el índice de parentesco neto (NRI) y el índice de taxón más cercano (NTI).

Índice	Estructura filogenética	Porcentaje de predicción correcto
NRI	Agrupamiento filogenético significativo	62.96
NRI	Agrupamiento filogenético no significativo	74.72
NRI	Sobredispersión filogenética no significativa	32.2
NRI	Sobredispersión filogenética significativa	62.5
NTI	Agrupamiento filogenético significativo	57.14
NTI	Agrupamiento filogenético no significativo	65.52
NTI	Sobredispersión filogenética no significativa	48.57
NTI	Sobredispersión filogenética significativa	53.33

Tabla 2: Contribución de cada variable a la predicción del índice NRI, expresada como la estimación de la varianza explicada (R^2), la devianza explicada (Dev) y el valor de máxima verosimilitud realizada (REML) obtenidos al eliminar cada una de las variables del modelo completo. PS: Estacionalidad de la precipitación, TS: Estacionalidad de la temperatura, PCQ: Precipitación del cuatrimestre más frío, LAI: Porcentaje del índice de área foliar.

Modelo	Completo	-PS	-TS	-PCQ	-LAI
R^2	0.558	0.550	0.537	0.521	0.50
Dev	57.30	56.40	55.90	54.30	51.90
REML	245.58	247.09	254.42	256.28	257.44

Tabla 3: Contribución de cada variable a la predicción del índice NTI, expresada como la estimación de la varianza explicada (R^2), la devianza explicada (Dev) y el valor de máxima verosimilitud realizada (REML) obtenidos al eliminar cada una de las variables del modelo completo. TS: Estacionalidad de la temperatura, PCQ: Precipitación del cuatrimestre más frío, LAI: Porcentaje del índice de área foliar.

Modelo	Completo	-TS	-PCQ	-LAI
R2	0.508	0.482	0.485	0.43
Dev	52.70	50.40	50.30	44.60
REML	231.55	237.67	234.86	241.24

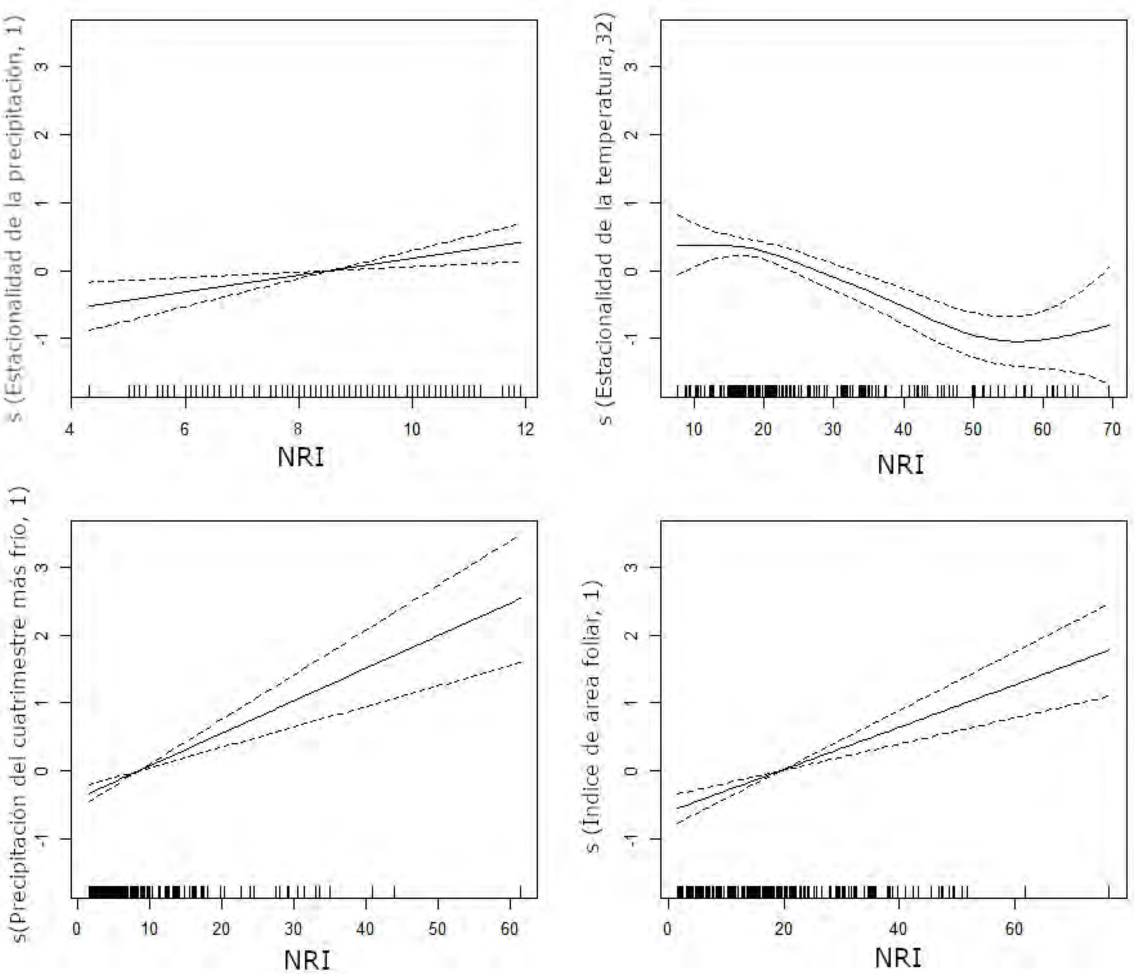


Figura 11: Curvas de suavizado estimadas para los modelos GAM entre el valor de NRI y cuatro variables ambientales. El eje x muestra los valores de NRI y el eje y muestra la contribución del suavizado a los valores ajustados. La línea sólida es el suavizado y las líneas discontinuas son los intervalos de confianza al 95%. Las líneas verticales pequeñas a lo largo del eje de x representan los valores de NRI observados.

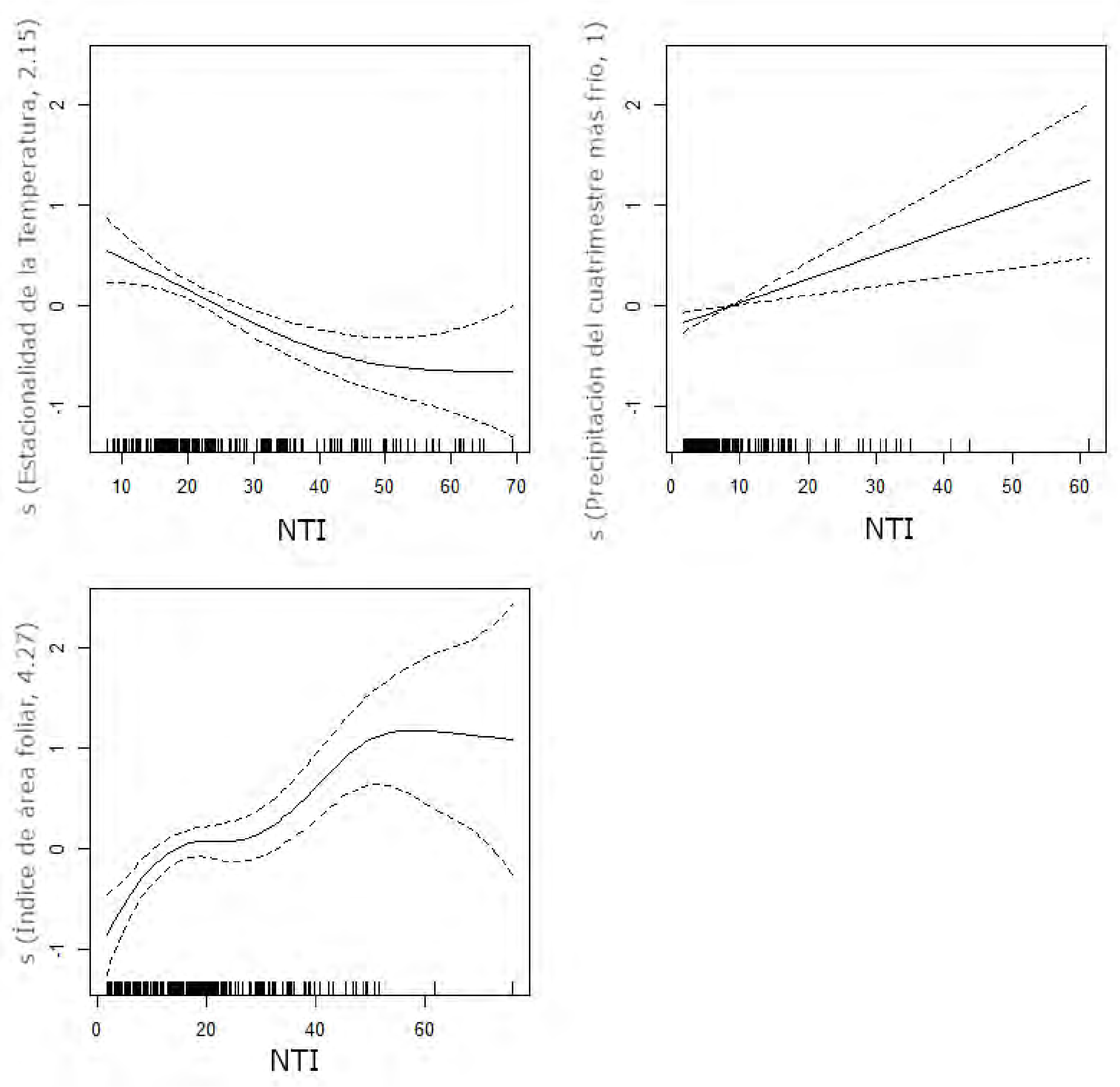


Figura 12: Curvas de suavizado estimadas para los modelos GAM entre el valor de NTI y tres variables ambientales. El eje x muestra los valores de NTI y el eje y muestra la contribución del suavizado a los valores ajustados. La línea sólida es el suavizado y las líneas discontinuas son los intervalos de confianza al 95%. Las líneas verticales pequeñas a lo largo del eje de x representan los valores de NTI observados.

DISCUSIÓN

Según lo esperado, los resultados obtenidos apoyan la hipótesis de que las comunidades de colibríes en México están estructuradas por la interacción de distintos factores ecológicos e históricos. Sin embargo, y contrario a lo esperado, el grado de estructuración filogenética no se explicó exclusivamente por la elevación y la precipitación, y sugiere el papel de otros mecanismos potenciales relacionados con factores climáticos (temperatura, precipitación y cobertura vegetal), geográficos (latitud) y evolutivos (procesos de diversificación a nivel de clado).

Índices de estructura filogenética y conjunto regional de especies

La estructura filogenética de las comunidades de colibríes en México fue independiente del índice calculado; comunidades con valores estadísticamente significativos para NRI lo fueron también para NTI (Anexo 10). Esto contrasta con lo encontrado por Velásquez-Puentes y Bacon (2016) en un estudio realizado con palmas (Arecaceae) en Bolivia. Ellos sugieren que las diferencias en la estructura filogenética observadas entre NRI y NTI se deben al efecto del levantamiento de los Andes, que promovió la diversificación in situ, la presencia de fuertes filtros ambientales y la limitación en el desplazamiento de las especies dispersoras, lo que favorecería el agrupamiento filogenético en la parte terminal del árbol. Para las comunidades de colibríes, el comportamiento similar de NRI y NTI sugiere que los mecanismos que dirigieron el patrón de diversificación de las especies que conformaron una comunidad se mantuvieron constantes a lo largo del tiempo.

En el presente trabajo se puso a prueba el efecto del conjunto regional de especies sobre los valores de estructura filogenética. Se observó que tanto para NRI como para NTI los resultados entre ambas escalas fueron prácticamente los mismos. La filogenia *Escala Continental* empleada en este trabajo representó el 31.94% de riqueza de especies de la familia Trochilidae, incluyó 8 de los 9 clados de colibríes (McGuire *et al.* 2014), y especies con distribuciones fuera de México que en algunos casos (como el clado de los Brillantes) son exclusivos de Sur América (Figuras 2 y 3). Es posible que la similitud en los resultados de ambas escalas se relacione con la historia evolutiva de los colibríes. Se ha propuesto que los análisis filogenéticos a escalas espaciales grandes (por ejemplo, continente) revelan el resultado de procesos biogeográficos e históricos (Webb *et al.* 2002), en los que el agrupamiento filogenético puede ser consecuencia de la interacción de los procesos de diversificación regional y del filtro ambiental (Webb *et al.* 2002, Cavender-Bares *et al.* 2009). El centro de origen de los colibríes actuales se ubica en las tierras bajas del Amazonas (Bleiweiss 1998), y el grupo se ha diversificado notablemente distribuyéndose en todo el continente desde Alaska, hasta Tierra del Fuego (Schuchmann 1999, McGuire *et al.* 2007, McGuire *et al.* 2014). En México, las especies de colibríes que conforman las comunidades no pertenecieron a un grupo de linajes restringido dentro de la filogenia; al contrario, las 58 especies registradas pertenecieron a 7 de los 9 clados descritos para toda la familia, por lo que no se observó el agrupamiento filogenético esperado para la *Escala Continental* respecto a la *Escala México* (Figuras 2 y 3).

Estructura filogenética y biogeografía de México

La historia biogeográfica de México, ha llevado a una gran complejidad fisiográfica, morfotectónica, climatológica y vegetacional; lo que hace de éste un país con una gran diversidad específica y ecosistémica (Morrone 2019). Cuando se correlacionó el patrón descrito en las variables ambientales más significativas con la regionalización biogeográfica de México, se observaron dos patrones principales: 1) un gradiente latitudinal en la estructura filogenética, y 2) una correspondencia entre la estructura filogenética de las comunidades y las provincias biogeográficas de México, definidas como áreas con identidad fisiográfica y ecológica (Morrone 2019).

El patrón latitudinal de las comunidades de colibríes con estructura filogenética significativa para NRI y para NTI corrobora que la historia geológica y biogeográfica de México ha sido importante para modelar la distribución de su fauna (Suárez-Atilano *et al.* 2014, Morrone 2019). Este mismo patrón se observó en las comunidades de serpientes neotropicales en Brasil (Cavalheri *et al.* 2015), en donde se encontró que las especies más cercanamente relacionadas se ubicaron a altas latitudes, mientras que las comunidades con sobredispersión filogenética se distribuyeron principalmente a latitudes bajas, atribuyéndose dicho patrón a la distribución limitada de las especies como resultado de la distribución restringida de los linajes más importantes de serpientes (Cavalheri *et al.* 2015). En México, el patrón latitudinal en la estructura filogenética coincidió con una marcada regionalización biogeográfica, donde la parte septentrional del país correspondiente a la región Neártica albergó a las comunidades agregadas filogenéticamente; mientras que en la parte austral, que pertenece a la región Neotropical, se localizaron las comunidades sobredispersas filogenéticamente (Morrone 2019) (Figuras 4 y 5).

La región Neártica en el territorio mexicano estuvo fuertemente modelada por los periodos glaciares e interglaciares del Pleistoceno (Metcalfe 2006). Los tipos de vegetación más abundantes actualmente son los matorrales xerófilos, los bosques secos, los bosques de cactáceas y las dunas (Morrone 2019). Estas comunidades vegetales se caracterizan por la presencia de arbustos o árboles no muy altos (algunos caducifolios); por presentar amplias superficies de suelo descubiertas, y por condiciones de poca precipitación con baja variación anual; con inviernos fríos y secos, y con grandes variaciones en la temperatura anual (Villaseñor 2014). Es importante resaltar que estas son las mismas características ambientales encontradas en los análisis de ordenamiento y modelamiento estadístico como determinantes de la estructura filogenética agregada (Figuras 9 y 10). Adicionalmente, 11 de las comunidades compuestas por especies de colibríes altamente emparentadas habitaron bosques de pino-encino, los cuales presentan una distribución insular en las cadenas montañosas del norte de las Sierras Madres Occidental y Oriental, y estando parcialmente inmersos en las provincias más áridas de la región Neártica (Morrone 2019). En Ecuador, las comunidades de colibríes con agrupamiento filogenético se asociaron con las zonas bajas (0-1000 msnm) y altas en los Andes (2500-4200 msnm) (Graham *et al.* 2009), mientras que en México éstas se asociaron con una gran variación en la elevación con comunidades localizadas desde el nivel del mar hasta los 2600 msnm (promedio 1249.83 msnm) (Figura 6). En las zonas tropicales, el estrés ambiental está asociado principalmente al gradiente altitudinal: en las zonas más bajas están los bosques tropicales estacionalmente secos (0–1000 msnm), los cuales se caracterizan por una baja humedad en el aire por efecto de la sombra de lluvia y por una marcada estación seca, en donde la precipitación es menor a 100mm. En las zonas más altas se encuentran los ecosistemas alpinos de alta montaña (c. 3000–4800 msnm), caracterizados por la baja presión atmosférica, las grandes fluctuaciones diarias en la temperatura, la radiación ultravioleta intensa y el efecto desecante del viento (Linares-Palomino 2006, Buytaert *et al.* 2011). En las zonas templadas de México las condiciones climáticas más extremas ocurren en los desiertos de Sonora, Baja California y Chihuahua, las cuales se ven favorecidas por la presencia de un gradiente latitudinal y altitudinal de la precipitación, sumado al incremento de la aridez desde hace 9000 años, a la predominancia de la zona de alta presión subtropical, y a la distancia a las fuentes de humedad (Metcalfe 2006). Este conjunto de características climáticas y de vegetación coinciden con un escenario en donde independientemente de la zona (tropical o templada), el filtro ambiental actúa como mecanismo potencial de la estructura filogenética de estas comunidades, ya que las condiciones ambientales imponen retos fisiológicos a los colibríes, promoviendo la coexistencia de especies ecológicamente similares y relacionadas filogenéticamente (Webb *et al.* 2002).

Respecto a las comunidades con sobredispersión filogenética, éstas se localizaron geográficamente al sur del país en la región Neotropical. Esta se caracteriza por su alta diversidad de plantas y animales, y por su clima predominantemente caliente y húmedo (Morrone 2019). Distintos estudios biogeográficos han descrito la conexión entre la región Neotropical Mesoamericana y la región Neotropical Suramericana; producto del intercambio biótico entre América del Norte y América del Sur entre el Jurásico Temprano y el Cretácico Temprano (Morrone 2019). La región Neotropical de México se compone por 9 provincias, y las comunidades de colibríes con sobredispersión filogenética se localizaron en cuatro de estas (Figuras 4 y 5). Distintos estudios biogeográficos han identificado importantes afinidades bióticas entre estas cuatro provincias, las cuales se caracterizan por un patrón topográfico muy complejo (con elevaciones que alcanzan los 4000 msnm), y por su gran diversidad climática con sitios que superan los 1000 mm de precipitación anual, acompañados de altas temperaturas (Morrone *et al.* 2017, Morrone 2019). La comunidad vegetal más abundante en esta región es el bosque tropical húmedo, el cual se caracteriza por la presencia abundante de árboles perennifolios y caducifolios, lianas y epífitas (Villaseñor 2014). Los análisis de las variables ambientales indicaron que las comunidades de colibríes con sobredispersión filogenética se ubicaron en localidades caracterizadas por precipitaciones anuales altas, por una alta estacionalidad en las lluvias, por presentar inviernos lluviosos, por una baja variación en la temperatura anual, y una mayor cobertura vegetal (principalmente arbórea) (Figuras 9 y 10); condiciones ambientales que favorecen el desarrollo de bosques tropicales húmedos (Villaseñor 2014). Este conjunto de características coinciden con un escenario de estabilidad climática, en donde la fuerza ecológica dominante potencial es la exclusión competitiva; aquella en donde las especies con requerimientos ecológicos similares se seleccionan negativamente (Webb *et al.* 2002), favoreciendo la sobredispersión filogenética y la colonización de linajes filogenéticos diferentes (Dagallier *et al.* 2020). La región Neotropical de México estaría actuando tanto como museo, permitiendo la permanencia de linajes y especies antiguas de colibríes de origen suramericano, y como cuna, donde la diversificación de especies de grupos como las Esmeraldas y las Gemas de Montaña es muy alta (Moreau & Bell 2013, Ornelas *et al.* 2015, Zamudio-Beltrán & Hernández-Baños 2018).

Las comunidades de colibríes con estructura filogenética aleatoria se distribuyeron ampliamente en el territorio mexicano, con registros en 12 de las 14 provincias biogeográficas (Anexo 11). Los análisis de ordenamiento y modelado mostraron que estas comunidades no se asociaron a un conjunto particular de condiciones ambientales (Figuras 9 y 10), y ocuparon una gran diversidad de tipos de vegetación (Anexo 11). Sin embargo, cabe recalcar que el 42.01% de estas comunidades se ubicaron en bosques templados (bosques de pino-encino) y bosques húmedos de montaña (bosque mesófilo); los cuales además de poseer la mayor riqueza de especies de plantas y endemismos (en el caso del bosque templado), son característicos de la Zona de Transición Mexicana (Morrone 2019). Como su nombre lo indica, esta zona se encuentra en medio de las regiones Neártica y Neotropical, principalmente en las Sierras Madre del Sur y en el Eje Volcánico Neotransversal (Metcalfe 2006, Villaseñor 2014, Morrone 2019). Se caracteriza por su gran complejidad geológica y biogeográfica, donde la contracción y expansión de los glaciares y de los hábitats de montaña durante el Último Glacial Máximo (UGM) (Caballero *et al.* 2010) sumada a la presencia de las cadenas montañosas, favorecieron la dispersión de elementos septentrionales hacia el sur y de elementos meridionales hacia el norte. Esta zona destaca por la mezcla de taxones de ambos orígenes y por la evolución de especies endémicas (cunas de diversidad, Morrone 2019, Dagallier *et al.* 2020). La diversidad biótica, junto a las amplias condiciones ambientales, favorecen la diversificación de especies y la existencia de numerosos nichos ecológicos, que pueden ser explotados por diferentes especies. En el caso de los colibríes, ésta sería la razón por la que las especies que componen estas comunidades estuvieron estructuradas al azar, ya que debido a la compleja historia geológica y biótica se da un balance entre los efectos de la diversificación, las interacciones inter-específicas y los filtros ambientales, resultando en una señal filogenética difusa (Cavender-Bares *et al.* 2009, Velásquez-Puentes & Bacon 2016)

Estructura y clados filogenéticos

Con excepción del clado monotípico Patagonia (*Patagona gigas*), las relaciones filogenéticas entre clados se encuentran bien definidas (McGuire *et al.* 2014), siendo las Abejas y las Gemas de Montaña los únicos clados de origen Norteamericano. A lo largo del tiempo han ocurrido distintos eventos de dispersión entre Centro y Sur América, que han favorecido la dispersión, colonización e intercambio de especies entre las dos regiones (McGuire *et al.* 2007, Ornelas *et al.* 2014). Clados como las Coquetas, los Ermitaños y los Topacios, junto con familias de plantas de origen suramericano que son importantes recursos de néctar (por ejemplo Bromeliaceae y Heliconiaceae), invadieron Centro América y se dispersaron hacia el norte a lo largo de la región Neotropical (McGuire *et al.* 2014, Morrone

2019, Rodríguez-Flores *et al.* 2019). Esto explicaría que las comunidades de colibríes con sobredispersión filogenética se localicen en esta región biogeográfica, ya que además de la favorabilidad del clima y diversidad biológica, allí se distribuye la mayor diversidad filogenética de colibríes, con la presencia de linajes de origen neártico y neotropical.

El desarrollo de barreras físicas como las cadenas montañosas, el cambio en las condiciones climáticas a lo largo del tiempo geológico, y el subsecuente cambio en la cobertura vegetal, modifican la distribución de las especies (Ramírez-Barahona & Eguiarte 2013, Ornelas *et al.* 2015). En México el Eje Neovolcánico Transversal, la Sierra Madre de Chiapas y el Itsmo de Tehuantepec son formaciones geológicas importantes en los procesos de diversificación, colonización y dispersión de distintos taxones (Ornelas *et al.* 2015, Morrone 2019). En el caso de los colibríes, estas barreras dividieron las comunidades con estructura filogenética agregada de las comunidades con estructura sobredispersa, y funcionaron como el límite septentrional para varias especies de colibríes de origen suramericano como *Florisuga mellivora* (Topacio), *Phaethornis striigularis* (Ermitaño), *Heliothryx barroti* (Mango) y *Lophornis helenae* (Coqueta), entre otras (Arizmendi & Berlanga 2014). Los procesos geológicos de México promovieron el aislamiento y diferenciación de poblaciones de clados como las Esmeraldas, las Gemas de Montaña y las Abejas, lo que sumado a la adaptabilidad ecológica de estos clados les permitió ocupar nuevos nichos ecológicos (Ornelas *et al.* 2013, Ramírez-Barahona & Eguiarte 2013, Ornelas *et al.* 2014, Zamudio-Beltrán & Hernández-Baños 2018, Hernández-Baños *et al.* 2020). Esto hace de las Sierras Madre Oriental, Occidental, del Sur y el Eje Neovolcánico Transversal reservorios de diversidad biológica, ya que ahí confluyen y coexisten especies de distintos clados de colibríes (Arizmendi & Berlanga 2014).

Analizar las características fenotípicas que están involucradas en la explotación del nicho ecológico es otra manera de investigar los mecanismos de ensamble de las comunidades ecológicas (Martins 2000, Revell *et al.* 2008, Velásquez-Puentes & Bacon 2016). En el caso de los colibríes, existe una cierta homogeneidad morfológica entre las especies a nivel de clado (McGuire *et al.* 2014, Rodríguez-Flores *et al.* 2019). Distintos estudios han demostrado que la morfología del pico, de las alas y el tamaño corporal son rasgos importantes que determinan el acceso y uso eficiente de los recursos de néctar (Stiles 1981, Dalsgaard *et al.* 2011, Maglianesi *et al.* 2014, Abrahamczyk & Kessler 2015). Los resultados sugieren una relación entre morfología y estructura filogenética en donde las comunidades con agrupamiento filogenético estuvieron compuestas principalmente por especies de Esmeraldas y Abejas, que al poseer una morfología generalista (tamaño pequeño a mediano y con picos cortos y rectos) (Rodríguez-Flores *et al.* 2019), pueden acceder al néctar producido por las plantas mayoritáriamente generalistas, propias de los ecosistemas estacionales, como los bosques secos y los matorrales xerófilos (Figuras 7 y 8) (Arizmendi & Ornelas 1990, Sanaphre-Villanueva *et al.* 2017, Bustamante-Castillo *et al.* 2020). En el caso de las comunidades con sobredispersión filogenética, la mayor diversidad y especialización morfológica (en términos de tamaño y morfología del pico) favorecerían una separación más fina de los nichos alimenticios de cada especie, permitiendo que una mayor cantidad de especies puedan coexistir y usar de manera eficiente la diversidad de recursos de néctar disponibles (Dalsgaard *et al.* 2011, Abrahamczyk & Kessler 2015).

Conclusiones y perspectivas

Los resultados sugieren que las comunidades de colibríes en México están estructuradas por una combinación de factores ecológicos, climáticos y evolutivos; donde las especies han respondido de manera diferente a los filtros ambientales impuestos por la estacionalidad en la precipitación y la temperatura, la cobertura vegetal, su origen biogeográfico, la historia geológica de México y su flexibilidad ecológica respecto al comportamiento migratorio y el uso de los recursos de néctar. Los resultados permiten crear nuevas hipótesis que puedan ser puestas a prueba para comunidades y especies de colibríes particulares. Las comunidades de colibríes más diversas de México, en términos ecológicos y evolutivos, se distribuyen en las distintas cadenas montañosas y tuvieron una estructura filogenética aleatoria (Des Granges 1979, Arizmendi 2001, Lara 2006b, López-Segoviano *et al.* 2019). Si las regiones montañosas actúan como cunas y museos de diversidad (Dagallier *et al.* 2020), y cada región posee procesos evolutivos que operaron independientemente, se esperaría que el recambio filogenético (diversidad filogenética beta) entre regiones sea menor (Velásquez-Puentes & Bacon 2016), y que procesos de diversificación recientes ocurran en conjunto con la persistencia de distintos linajes favoreciendo la acumulación de historia evolutiva (Sosa *et al.* 2018, Dagallier *et al.* 2020).

El clado de las Abejas es el único grupo dentro de la familia con especies que realizan migraciones latitudinales (Licona-Vera & Ornelas 2017), y se ha observado que la presencia temporal de estas especies modifica de manera inmediata las relaciones inter e intra específicas en las especies residentes (Rodríguez-Flores & Arizmendi 2016). Este hecho resalta la importancia de la escala temporal en las dinámicas ecológicas de las comunidades.

Dado que la presencia o ausencia de especies en una comunidad repercute en la estructura filogenética, se espera que el papel de las especies de Abejas migratorias sea incrementar los valores de NTI de las comunidades con estructura filogenética sobredispersa, y disminuir los valores de NRI de comunidades con agrupamiento filogenético. Para poner a prueba esta hipótesis sería interesante estimar los valores de estructura filogenética eliminando a estas especies de las comunidades.

Asimismo, sería interesante incluir en futuros estudios, información de rasgos ecológicos relevantes de las especies de colibríes como la morfología del pico (largo y curvatura) y el tamaño (peso corporal). Esta información permitiría analizar la distribución de los rasgos dentro de las comunidades, establecer si son compartidos por especies cercanas filogenéticamente, si están siendo segregados dentro de las especies (lo que sugeriría exclusión competitiva) o si son similares entre ellas (sugiriendo filtro ambiental). Igualmente, se recomendaría la estimación de análisis de diversidad beta y de diversidad filogenética beta, que brindarían información extra para poder diferenciar entre los procesos relacionados con la estructura del nicho ecológico y los procesos evolutivos y biogeográficos en la estructuración de las comunidades (Cavender-Bares *et al.* 2009, Graham *et al.* 2009). Finalmente, y como se sugirió anteriormente, es importante aprovechar el desarrollo de nuevas tecnologías como la secuenciación de nueva generación (NGS por sus siglas en inglés) y la incorporación de la bioinformática en el análisis de datos masivos (Big Data), para proponer una nueva hipótesis filogenética que permita poner a prueba las hipótesis generadas en este estudio. Respecto a las tecnologías de secuenciación de primera generación, las tecnologías NGS son capaces de generar cientos de miles o decenas de millones de secuencias cortas de DNA a un precio relativamente bajo (Thudi *et al.* 2012). Una opción sería el uso de la tecnología NGS de captura de secuencia (sequence capture), la cual se caracteriza por señalar exones o porciones conservadas del genoma. Esta tecnología ha sido utilizada tanto en la construcción de filogenias y como en estudios filogeográficos, y más recientemente se ha comprobado su utilidad en la comparación entre grupos de datos de múltiples escalas taxonómicas, estableciendo conclusiones generales sobre el impacto de procesos históricos a través de las biotas (Harvey *et al.* 2016).

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ANEXO 1.

Listado de comunidades de colibríes analizadas en el presente estudio. Para cada comunidad se indica el nombre del sitio, estado, coordenadas geográficas en grados decimales, elevación promedio, rango altitudinal y número de especies de colibríes reportadas. CLAVE: Es el código asignado a cada comunidad.

CLAVE	Sitio	Estado	Latitud	Longitud	Área (ha)	Elevación (msnm)	Elevación promedio (msnm)	Rango altitudinal (msnm)	Número de colibríes	Referencia
145	Área Natural Protegida Cuenca Alimentadora del Distrito Nacional de Riego 01 Pabellón	Aguascalientes	22.25975	-102.49923	97699	1700-3000	2350	1300	10	[1]
120	Área Natural Protegida Constitución de 1857	Baja California	32.07007	-115.89219	5009	1800	1800	0	5	[1]
121	Área Natural Protegida Sierra de San Pedro Mártir	Baja California	30.88818	-115.46752	72911	1000-2830	1915	1830	6	[1]
122	Área Natural Protegida Sierra Valle de los Cirios	Baja California	29.05230	-114.18375	2521776	0-1810	905	1810	6	[1]
184	Área de Importancia para la Conservación de las Aves Archipiélago Bahía de los Ángeles	Baja California Sur	28.99501	-113.50676	5404	0-200	100	200	6	[1]
183	Área de Importancia para la Conservación de las Aves Bahía Magdalena-Almejas	Baja California Sur	24.68471	-111.80230	10723	0-200	100	200	4	[1]
180	Área de Importancia para la Conservación de las Aves Oasis La Purísima y San Isidro	Baja California Sur	26.18187	-112.09208	866	0-200	100	200	3	[1]
181	Área de Importancia para la Conservación de las Aves Oasis San Pedro de la Presa	Baja California Sur	24.87148	-111.05279	84	200-500	350	300	3	[1]
182	Área de Importancia para la Conservación de las Aves Sierra La Giganta	Baja California Sur	25.82190	-111.45145	155046	200-1500	850	1300	4	[1]
125	Área Natural Protegida Cabo San Lucas	Baja California Sur	22.87408	-109.86731	3996	0-200	100	2020	4	[1]
123	Área Natural Protegida Complejo Lagunar Ojo de	Baja California Sur	27.81849	-114.13800	60166	0-20	10	20	3	[1]

	Liebre									
124	Área Natural Protegida El Vizcaíno	Baja California Sur	27.44370	-113.61719	2493091	0-1200	600	1200	6	[1]
1	Sierra de la Laguna	Baja California Sur	23.54750	-109.95667	20000	1800-2200	2000	400	1	[2]
173	Área Natural Protegida Bala'an Ka'ax	Campeche	19.38294	-89.07467	128390	10-350	180	340	8	[1]
172	Área Natural Protegida Calakmul	Campeche	18.36500	-89.65092	723185	0-300	150	300	12	[1]
174	Área Natural Protegida Los Petenes	Campeche	20.18234	-90.43046	282858	0-10	5	10	8	[1]
175	Área Natural Protegida Ría Celestún	Campeche	20.73640	-90.39053	81482	0-6	3	6	7	[1]
2	Penísula de Yucatán	Campeche	20.03778	-88.91583	30000000	0-400	200	400	15	[3]
166	Área Natural Protegida Cañón de Usumacinta	Chiapas	17.31583	-91.28785	46129	200-700	450	500	7	[1]
170	Área Natural Protegida Bonampak	Chiapas	16.70697	-91.07537	4357	200-1400	800	1200	20	[1]
165	Área Natural Protegida Cascada de Agua Azul	Chiapas	17.25750	-92.12472	2580	200-500	350	300	14	[1]
161	Área Natural Protegida Lagunas de Montebello	Chiapas	16.10773	-91.71415	6022	1380-1740	1560	360	16	[1]
167	Área Natural Protegida Metzabok	Chiapas	17.11621	-91.61843	3368	580-800	690	220	20	[1]
171	Área Natural Protegida Montes Azules	Chiapas	16.47159	-91.13877	331200	200-1500	850	1300	20	[1]
168	Área Natural Protegida Naha	Chiapas	16.97607	-91.58544	3847	840-1280	1060	440	20	[1]
164	Área Natural Protegida Palenque	Chiapas	17.48867	-92.05455	1772	200-800	500	600	12	[1]
160	Área Natural Protegida Volcán Tacaná	Chiapas	15.11518	-92.13390	6378	1200-4092	2646	2892	22	[1]
169	Área Natural Protegida Yaxchilan	Chiapas	16.86702	-90.98176	2621	250-750	500	500	20	[1]
8	Reserva Ecológica Huitepec	Chiapas	16.72200	-92.62486	136	2284-2528	2406	244	5	[4]
3	Reserva El Ocote	Chiapas	16.99917	-93.75000	101288	195-240	217.5	45	14	[5]
5	Reserva El Triunfo	Chiapas	15.79972	-93.06444	119117	1175-1680	1427.5	505	13	[5]
4	Reserva La Encrucijada	Chiapas	15.06028	-92.69333	144868	1-8	4	7	3	[5]
6	Reserva La Sepultura	Chiapas	16.10750	-93.59056	167310	400-1800	1100	1400	18	[5]

7	Reserva Laguna Bélgica	Chiapas	16.87889	-93.45611	47.5	850-1100	975	250	13	[5]
200	Área de Importancia para la Conservación de las Aves Maderas Chihuahua	Chihuahua	28.61713	-108.23106	19549	2000-3000	2500	1000	4	[1]
199	Área de Importancia para la Conservación de las Aves Sierra del Nido	Chihuahua	29.16862	-106.62075	401919	1500-3000	2250	1500	3	[1]
117	Área de Protección de Flora y Fauna Campo Verde	Chihuahua	29.83845	-108.50763	108069	1400-2600	2000	1200	7	[1]
131	Área Natural Protegida Cañón de Santa Elena	Chihuahua	29.10421	-103.82366	277210	725-2401	1563	1676	3	[1]
126	Área Natural Protegida Cascada de Bassaseachic	Chihuahua	28.14933	-108.22663	5803	1900-2100	2000	200	5	[1]
127	Área Natural Protegida Cerro Mohinora	Chihuahua	25.99046	-106.98809	9126	2100-3307	2703.5	1207	3	[1]
193	Corredor de Barrancas de la Sierra Madre Occidental	Chihuahua	26.72194	-107.71934	2469255	201-3201	1701	3000	16	[1]
114	Parque Nacional Cumbres de Majalca	Chihuahua	28.80533	-106.48233		1700	1700	0	5	[6]
116	Reserva de la Biosfera Janos	Chihuahua	30.82815	-108.53486	526482	1400-2600	2000	1200	8	[1]
15	Ajusco medio	Ciudad de México	19.23333	-99.25000	728	2400-2800	2600	400	11	[7]
11	Cuenca del Río Magdalena	Ciudad de México	19.24306	-99.25167	2992.8	2470-3850	3160	1380	8	[8]
14	Milpa Alta	Ciudad de México	19.21667	-99.10000	50	2505-2630	2567.5	125	14	[9]
12	Parque Urbano Bosque de San Juan de Aragón	Ciudad de México	19.45111	-99.08056	162	2240	2240	0	3	[10]
13	Reserva del Pedregal de San Ángel	Ciudad de México	19.30861	-99.17222	237.3	2270-2349	2309.5	79	8	[11]
129	Área Natural Protegida Cuatrociénagas	Coahuila de Zaragoza	26.89839	-102.08867	84347	700-2000	1350	1300	3	[1]
130	Área Natural Protegida Cuenca Alimentadora del Distrito Nacional de Riego 04 Don Martín	Coahuila de Zaragoza	27.77393	-101.91300	1519920	265-2203	1234	1938	8	[1]
133	Área Natural Protegida Maderas Del Carmen	Coahuila de Zaragoza	29.05201	-102.60470	208381	1000-2500	1750	1500	6	[1]
132	Área Natural Protegida Ocampo	Coahuila de Zaragoza	28.81176	-103.00886	344238	600-2100	1350	1500	4	[1]

112	Comarca Lagunera	Coahuila de Zaragoza	25.72248	-103.29232	4788800	1110	1110	0	5	[12]
153	Área Natural Protegida El Jabalí	Colima	19.46356	-103.67332	5179	1200-2300	1750	1100	8	[1]
154	Área Natural Protegida Las Huertas	Colima	19.31828	-103.75256	167	600-3860	2230	3260	16	[1]
10	Nevado de Colima	Colima	19.59675	-103.58779	9600	3283-3420	3351.5	137	13	[13]
9	Volcán de Colima	Colima	19.51139	-103.61806	9600	0-4270	2135	4270	21	[14]
198	Área de Importancia para la Conservación de las Aves Cuchillas de la Zarca	Durango	26.06042	-104.74429	629788	1000-2500	1750	1500	4	[1]
194	Área de Importancia para la Conservación de las Aves Parte Alta del Río Humaya	Durango	25.43492	-106.61523	435366	200-3000	1600	2800	13	[1]
196	Área de Importancia para la Conservación de las Aves Piélagos	Durango	24.33982	-105.62476	107546	500-3000	1750	2500	13	[1]
197	Área de Importancia para la Conservación de las Aves Santiaguillo	Durango	24.65216	-104.91004	380700	1500-3000	2250	1500	4	[1]
143	Área Natural Protegida La Michilía	Durango	23.45871	-104.30042	9325	2050-3150	2600	1100	10	[1]
128	Área Natural Protegida Mapimí	Durango	26.62747	-103.73327	342388	1150	1150	0	4	[1]
147	Área Natural Protegida Sierra Gorda de Guanajuato	Guanajuato	21.40770	-100.10920	236882	640-2530	1585	1890	19	[1]
20	Atoyac	Guerrero	17.05000	-100.08333	183800	750-2450	1600	1700	12	[15]
21	Cañón del Zopilote	Guerrero	17.78333	-99.56667	3100	1200-2000	1600	800	12	[15]
22	Chilpancingo	Guerrero	17.18333	-99.40000	233800	1200-2900	2050	1700	26	[15]
103	Cuenca del Río Papagayo	Guerrero	17.30000	-99.60000	1228700	0-1500	750	1500	5	[16]
23	Medio Huacapa	Guerrero	17.82278	-99.65880		1200-2400	1800	1200	14	[15]
24	Mezcala Grande	Guerrero	17.92966	-99.36804		750-2500	1625	1750	10	[15]
25	Omitlán Azul	Guerrero	17.12494	-99.53812		750-2600	1675	1850	15	[15]
26	Otatlán	Guerrero	17.67855	-100.21370		1000-2800	1900	1800	12	[15]
27	Papagayo	Guerrero	17.25226	-99.66919		750-2600	1675	1850	6	[15]
30	Sierra de Atoyac	Guerrero	17.33142	-100.16558		1036-1787	1411.5	751	18	[17]

28	Tixtla	Guerrero	17.56556	-99.40222	29000	1200-2800	2000	1600	4	[15]
149	Área Natural Protegida Los Mármoles	Hidalgo	20.87342	-99.22831	23150	1500-2820	2160	1320	15	[1]
31	Reserva de la Biosfera Barranca de Metztitlán	Hidalgo	20.97950	-98.94566	96042	1100-2600	1850	1500	12	[18]
110	Valle del Mezquital	Hidalgo	20.02683	-99.13244		2205- 2943	2574	738	11	[19]
144	Área Natural Protegida Cuenca Alimentadora del Distrito de Riego 043 Estado de Nayarit	Jalisco	22.17608	-104.28684	1553440	1100-2500	1800	1400	10	[1]
152	Área Natural Protegida La Primavera	Jalisco	20.64549	-103.56973	30500	1400-2200	1800	800	7	[1]
151	Área Natural Protegida Sierra de Quila	Jalisco	20.29798	-104.03722	15193	1350-2560	1955	1210	10	[1]
35	Estación Biológica Chamela	Jalisco	19.50000	-105.05000	1600	30-500	265	470	4	[20]
34	Laboratorio Natural Las Joyas	Jalisco	19.57056	-104.24694	1245	1952	1952	0	13	[21]
36	Zapata y Juan Gil	Jalisco	19.38417	-104.96500		20-90	55	70	5	[22]
37	Centro Ecológico de Formación Omeyocan	México	19.55833	-99.27500		2280	2280	0	6	[23]
42	Lago Nabor Carrillo	México	19.45139	-98.94806	1000	2236	2236	0	4	[24]
18	Parque de las Esculturas	México	19.65556	-99.37028	11.64	2703	2703	0	2	[25]
16	Parque Ecológico Espejo de los Lirios	México	19.65028	-99.21722	14.78	2200	2200	0	1	[26]
38	Parque Estatal Sierra de Nanchititla	México	19.07944	-100.26500	67410	420-2100	1260	1680	5	[27]
39	Parque Natural Sierra de Guadalupe	México	19.58778	-99.10500	8549.36	2350-3005	2677.5	655	4	[28]
41	Sur de la Cuenca de México	México	19.03333	-98.93333	960000	2500-3680	3090	1180	7	[29]
17	Vaso Regulador Carretas	México	19.50000	-99.16667	10	2250	2250	0	5	[30]
40	Vaso regulador El Cristo	México	19.50833	-99.22389		2261	22261	0	1	[31]
43	Ahuijillo Barreras	Michoacán de Ocampo	18.81799	-103.61682		1000-1200	1100	200	3	[15]
155	Área Natural Protegida Barranca del Cupatitzio	Michoacán de Ocampo	19.43120	-102.10428	362	1300-384	2570	2540	7	[1]
156	Área Natural Protegida Lago de Camécuaro	Michoacán de Ocampo	19.90281	-102.21009	10	1700	1700	0	3	[1]

157	Área Natural Protegida Pico de Tancítaro	Michoacán de Ocampo	19.43287	-102.31673	23154	2100-3860	2980	1760	16	[1]
158	Área Natural Protegida Zicuirán-Infiernillo	Michoacán de Ocampo	18.65834	-101.94339	265118	150-2650	1400	2500	6	[1]
44	Coalcomán	Michoacán de Ocampo	18.78333	-103.16667	288157	1400-2400	1900	1000	5	[15]
47	Chinameca	Morelos	18.55222	-98.95111		1050	1050	0	1	[32]
49	El Limón	Morelos	18.52083	-98.93556		1213	1213	0	1	[32]
45	El Paredón	Morelos	18.75000	-99.35000	19377.4	938-2265	1601.5	1327	5	[33]
53	El Tepehuaje	Morelos	18.58500	-98.97306		1300	1300	0	3	[32]
52	Ixtlilco El Chico	Morelos	18.55167	-98.87167		1070	1070	0	1	[32]
51	Ixtlilco El Grande	Morelos	18.52806	-98.84722		1060	1060	0	1	[32]
46	Los Sauces	Morelos	18.55222	-98.95111		1216	1216	0	3	[32]
48	Pitzotlán	Morelos	18.58250	-98.90278		1200	1200	0	1	[32]
50	Tepalcingo	Morelos	18.52083	-98.82444		1100	1100	0	2	[32]
54	Zona sujeta a conservación ecológica Sierra de Huautla	Morelos	18.33611	-98.85556	31314	1000-1670	1335	670	7	[34]
142	Área Natural Protegida Marismas Nacionales	Nayarit	22.11342	-105.51423	133855	0-200	100	200	8	[1]
55	Sierra de San Juan	Nayarit	21.33333	-104.88333	26231	1000-2040	1520	1040	17	[35]
105	Sierra de Vallejo	Nayarit	21.11167	-105.16278	70530	1420	1420	0	16	[36]
205	Área de Importancia para la Conservación de las Aves San Antonio Peña Nevada	Nuevo León	23.90668	-99.84781	77270	1000-3500	2250	1500	8	[1]
137	Área Natural Protegida Cerro de la Silla	Nuevo León	25.60357	-100.21826	6039	520-1821	1170.5	1301	3	[1]
135	Área Natural Protegida Cuenca alimentadora de los distritos nacionales de riego 026 Bajo Río San Juan	Nuevo León	25.21325	-100.36786	197157	1500-3400	2450	1900	11	[1]
136	Área Natural Protegida Cumbres de Monterrey	Nuevo León	25.41359	-100.32221	177396	1300-3550	2425	2250	6	[1]
115	Cerro El Potosí	Nuevo León	24.88044	-100.24722	1020000	2000-3200	2600	1200	6	[37]
58	Acatitlán	Oaxaca	18.07503	-97.57860		1200-2800	2000	1600	1	[15]
59	Alto Verde	Oaxaca	16.78753	-96.89060		1200-3200	2200	2000	5	[5]

210	Área de Importancia para la Conservación de las Aves Cerro de Oro	Oaxaca	18.12718	-96.30648	67547	0-500	250	500	11	[1]
211	Área de Importancia para la Conservación de las Aves Unión Zapoteco-Chinanteca	Oaxaca	17.52221	-96.39722	29239	0-2500	1250	2500	30	[1]
60	Bajo Verde	Oaxaca	16.36645	-97.72753		750-1800	1275	1050	14	[15]
79	Cerro San Felipe	Oaxaca	17.14074	-96.68932		2500-3000	2750	500	6	
62	Copalita	Oaxaca	15.97116	-96.28987		750-2800	1775	2050	16	[15]
63	Coyotepec	Oaxaca	17.06784	-96.44111		1200-2400	1800	1200	3	[15]
64	Huajuapan	Oaxaca	17.82594	-97.76409		1200-1400	1300	200	2	[15]
61	Medio Verde	Oaxaca	16.54141	-97.18176		750-2400	1575	1650	8	[15]
65	Mixtepec	Oaxaca	17.33489	-97.87870		1400-3200	2300	1800	3	[15]
56	Nizanda	Oaxaca	16.65833	-95.01111		90-700	395	610	3	
66	Oaxaca	Oaxaca	17.22105	-96.66377		1200-2600	1900	1400	2	[15]
67	Papaloapan	Oaxaca	17.95153	-96.46643		750-3400	2075	2650	14	[15]
73	Pluma Hidalgo	Oaxaca	15.86667	-96.35000	17990	1300	1300	0	11	
75	Región de la Cañada Valle de Tehuacán	Oaxaca	17.89861	-96.98167	1000000	2000	2000	0	3	
68	Río del Oro	Oaxaca	17.69634	-97.61274		1400-3200	2300	1800	7	[15]
69	San Antonio de la Virgen	Oaxaca	16.59369	-95.79219		1000-3600	2300	2600	7	[15]
70	San Francisco	Oaxaca	15.93390	-96.53905		750-2600	1675	1850	7	[15]
74	San Juan Coyula	Oaxaca	17.87939	-96.87555		1400-1750	1575	350	10	{42]
57	Santa María Tecomavaca	Oaxaca	17.86583	-97.03056		580-850	715	270	5	[43]
111	Sierra de Cuatro Venados	Oaxaca	16.97269	-96.87901	221000	1600 - 3000	2300	1400	14	[44]
71	Sordo Peñoles	Oaxaca	17.23993	-97.55876		800-3000	1900	2200	5	[15]
72	Tlacolula de Matamoros	Oaxaca	16.79489	-96.06824		1200-2800	2000	1600	12	[15]
209	Área de Importancia para la Conservación de las Aves Sierra de Zongolica y Tenango	Puebla	18.43756	-96.81060	272815	500-3000	1750	2500	23	[1]
150	Área Natural Protegida Cuenca Hidrográfica del	Puebla	20.16046	-98.06183	39557	560-2323	1441.5	1763	13	[1]

	Río Necaxa									
80	Campo experimental Las Margaritas	Puebla	19.97917	-97.28333	2523	200-800	500	600	8	{45]
81	Los Linderos	Puebla	18.28750	-98.63472		1200	1200	0	2	[32]
82	Puente Márquez	Puebla	18.38639	-98.30306		900-1000	950	100	1	[32]
85	San Isidro	Puebla	18.54583	-98.42500		1320	1320	0	1	[32]
84	Santa María Xuchapa	Puebla	18.53333	-98.46667		1300	1300	0	1	[32]
83	Tepexco	Puebla	18.64222	-98.67250		1200	1200	0	2	[32]
86	Valle de Tehuacán	Puebla	17.80000	-96.66667	1000000	600-2950	1775	2350	5	[46]
148	Área Natural Protegida Sierra Gorda	Querétaro	21.28880	-99.47829	383567	1300-3000	2150	1700	19	[1]
87	Reserva de la Biosfera Sierra Gorda	Querétaro	20.83333	-98.83333	383567	300-3100	1700	2800	11	[47]
178	Área Natural Protegida Sian Ka'an	Quintana Roo	19.78960	-87.79992	528148	0-20	10	20	8	[1]
179	Área Natural Protegida Uaymil	Quintana Roo	18.98686	-87.80743	89118	0-20	10	20	8	[1]
146	Área Natural Protegida Gogorrón	San Luis Potosí	21.80257	-100.91256	25000	1700-2880	2290	1180	10	[1]
139	Área Natural Protegida Sierra de Abra Tanchipa	San Luis Potosí	22.25992	-98.92994	21464	120-820	470	700	14	[1]
134	Área Natural Protegida Sierra La Mojonera	San Luis Potosí	24.14996	-101.05411	9201	1700-2470	2085	770	4	[1]
94	Gran Sierra Plegada	San Luis Potosí	22.49892	-99.47455		1000-2000	1500	1000	7	[48]
95	Karst Huasteco	San Luis Potosí	21.57434	-99.50030		200-1800	1000	1600	17	[48]
93	Llanuras y lomeríos	San Luis Potosí	22.14173	-98.68734		0-200	100	200	6	[48]
90	Llanuras y Sierras Potosino-Zacatecanas	San Luis Potosí	22.98492	-101.76647		2000	2000	0	6	[48]
88	Rioverde	San Luis Potosí	21.92806	-99.99694	324290	1400-2000	1700	600	2	[49]
96	Sierra Madre Oriental Potosina	San Luis Potosí	22.14556	-99.42813	481831	0-3180	1590	3180	18	[50]
91	Sierras y llanuras del norte de Guanajuato	San Luis Potosí	21.95632	-100.82545		2380-2960	2670	580	5	[48]
92	Sierras y Llanuras occidentales	San Luis Potosí	22.74918	-100.19751		1500-2000	1750	500	15	[48]

89	Sierras y lomeríos de Aldama y Río Grande	San Luis Potosí	23.25137	-100.84120		2000	2000	0	6	[48]
192	Área de Importancia para la Conservación de las Aves Bahía Santa María	Sinaloa	25.00240	-108.10759	108953	0-200	100	200	6	[1]
195	Área de Importancia para la Conservación de las Aves Las Bufas	Sinaloa	24.33681	-106.15907	10894	1000-3000	2000	2000	13	[1]
141	Área Natural Protegida Meseta de Cacaxtla	Sinaloa	23.63181	-106.65301	50862	0-360	180	360	7	[1]
140	Área Natural Protegida Playa Ceuta	Sinaloa	23.85859	-106.92648	77	0-30	15	30	6	[1]
104	El Palmito	Sinaloa	23.58889	-105.86667	14270000	1800-2500	2150	700	13	[51]
188	Área de Importancia para la Conservación de las Aves Álamos- Río Mayo	Sonora	27.56707	-108.81867	238125	0-2000	1000	2000	14	[1]
186	Área de Importancia para la Conservación de las Aves Baserac-Sierra Tabaco-Rio Bavispe	Sonora	30.03271	-108.75109	245494	500-3000	1750	2500	12	[1]
187	Área de Importancia para la Conservación de las Aves Cuenca del Río Yaqui	Sonora	28.36442	-109.44844	671651	0-2000	1000	2000	15	[1]
190	Área de Importancia para la Conservación de las Aves Estero del Soldado	Sonora	27.96263	-110.97572	774	0-200	100	200	5	[1]
189	Área de Importancia para la Conservación de las Aves Estero Santa Cruz	Sonora	28.80941	-111.87067	6135	0-4	2	4	2	[1]
191	Área de Importancia para la Conservación de las Aves Zonas Húmedas de Yávaros	Sonora	26.72611	-109.59191	29458	0-200	100	200	7	[1]
119	Área Natural Protegida El Pinacate	Sonora	31.90485	-113.76385	714557	200-1206	703	1006	6	[1]
118	Área Natural Protegida Sierra de Álamos	Sonora	27.00880	-108.76836	92890	2000-2500	2250	500	14	[1]
107	Madrean Sky Land Archipielago	Sonora	31.04216	-111.60438		800-1650	1225	850	3	[52]
185	Sistema de Sierras de la Sierra Madre Occidental	Sonora	30.71160	-110.19853	2289950	500-2500	1500	2000	15	[1]
163	Área Natural Protegida	Tabasco	18.60960	-91.99801	706148	0	0	0	10	[1]

	Laguna de Términos									
162	Área Natural Protegida Pantanos de Centla	Tabasco	18.29629	-92.45392	302707	0-7	3.5	7	7	[1]
97	Centla Marshes Biosphere Reserve	Tabasco	17.96250	-92.10833	13665	1-7	3.5	6	6	[53]
204	Área de Importancia para la Conservación de las Aves Cerro del Metate	Tamaulipas	22.75365	-97.98043	19733	0-200	100	200	6	[1]
206	Área de Importancia para la Conservación de las Aves Desembocadura del Río Soto La Marina	Tamaulipas	23.73275	-97.87785	31380	0-200	100	200	2	[1]
202	Área de Importancia para la Conservación de las Aves El Cielo	Tamaulipas	23.14793	-99.27346	184039	0-2500	1250	2500	20	[1]
203	Área de Importancia para la Conservación de las Aves Sierra de Tamaulipas	Tamaulipas	23.32680	-98.41327	259296	200-1500	850	1300	4	[1]
138	Área Natural Protegida Laguna Madre y delta del Río Bravo	Tamaulipas	24.93325	-97.62237	572807	0-150	75	150	2	[1]
106	Reserva de la Biosfera El Cielo	Tamaulipas	23.20273	-99.27792	144530.51	200-2320	1260	2120	18	[54]
98	Parque Nacional La Malinche	Tlaxcala	19.23042	-98.02213	45852	2900	2900	0	10	[55]
99	Tlaxcala	Tlaxcala	19.28333	-98.23333		2200	2200	0	6	[56]
208	Área de Importancia para la Conservación de las Aves Humedales de Alvarado	Veracruz de Ignacio de la Llave	18.62948	-95.87574	208816	0-200	100	200	5	[1]
207	Área de Importancia para la Conservación de las Aves Tecolutla	Veracruz de Ignacio de la Llave	20.46691	-97.01933	661	0-200	100	200	3	[1]
212	Área de Importancia para la Conservación de las Aves Uxpanapa	Veracruz de Ignacio de la Llave	17.26732	-94.39503	362191	0-1500	750	1500	14	[1]
159	Área Natural Protegida Los Tuxtlas	Veracruz de Ignacio de la Llave	18.46496	-94.98634	155122	650-1720	1185	1070	15	[1]
101	Chavarrillo	Veracruz de Ignacio de la Llave	19.42517	-96.79178	842	600-1160	880	560	10	[57]

100	Cofre de Perote	Veracruz de Ignacio de la Llave	19.49996	-97.13669	320000	2400-4200	3300	1800	11	[58]
201	Humedales del Sur de Tamaulipas y Norte de Veracruz	Veracruz de Ignacio de la Llave	22.18740	-98.15498	650000	0-60	30	60	11	[1]
102	Parque Ecológico Francisco Xavier Clavijero	Veracruz de Ignacio de la Llave	19.50000	-96.95000	217	1280	1280	0	11	[59]
108	Tuxpan	Veracruz de Ignacio de la Llave	21.01224	-97.41886	400	10	10	0	6	[60]
177	Área Natural Protegida Otoch Ma´Ax Yetel Kooh	Yucatán	20.67923	-87.65687	5367	0-34	17	34	7	[1]
176	Área Natural Protegida Yum Balam	Yucatán	21.50694	-87.27414	154052	100-1160	630	1060	7	[1]
109	Reserva de la Biosfera Río Lagartos	Yucatán	21.53971	-87.82508	60347.82	10	10	0	8	INE
113	Parque Nacional Sierra de Órganos	Zacatecas	23.74944	-103.76417	1125	2120-2560	2340	440	5	[61]

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ANEXO 2.

Especies de colibríes incluidas en las dos reconstrucciones filogenéticas. MEX: Especies de colibríes incluidas en la filogenia para las especies reportadas para México. Para cada gen se muestra el número de acceso en el GenBank [1] y el artículo donde ha sido citada la secuencia (REF). ORNELAS: Son secuencias proporcionadas por el laboratorio del Dr. Juan Francisco Ornelas (INECOL, A.C.)

Clado	Especie	MEX	ND2	REF.	ND5	REF.	12S	REF.	AK1	REF.
Esmeralda	*Amazilia amabilis*		ORNELAS		ORNELAS		KC858346	[2]	EU042436	[3]
Esmeralda	*Amazilia beryllina*	X	KM199045	[4]	KC858613	[2]	KC858370	[2]	KM389509	[5]
Esmeralda	*Amazilia candida*	X	KC858463	[2]	KC858585	[2]	KC858342	[2]	KJ601789	[6]
Esmeralda	*Amazilia cyanocephala*	X	KC858470	[2]	KC85860	[2]	KC858358	[2]	KJ601793	[6]
Esmeralda	*Amazilia cyanura*	X	KM199092	[4]	KC858614	[2]	KC858371	[2]	KJ601794	[6]
Esmeralda	*Amazilia decora*		KC858447	[2]	KC858569	[2]	KC858326	[2]	EU042437	[3]
Esmeralda	*Amazilia edward*		KC858494	[2]	KC858617	[2]	KC858374	[2]	KJ601795	[6]
Esmeralda	*Amazilia fimbriata*		EU042520	[3]	KC858587	[2]	KC85834	[2]	EU042438	[3]
Esmeralda	*Amazilia lactea*		KC858465	[2]	KC858588	[2]	KC858345	[2]	GU167149	[7]
Esmeralda	*Amazilia rutila*	X	KC858497	[2]	KC858620	[2]	KC858376	[2]	EU042440	[3]
Esmeralda	*Amazilia saucerrottei*		KC858492	[2]	KC858615	[2]	KC858372	[2]	EU042441	[3]
Esmeralda	*Amazilia tzacatl*	X	KC858510	[2]	KC858634	[2]	KC858391	[2]	EU042442	[3]
Esmeralda	*Amazilia versicolor*		KC858464	[2]	KC858586	[2]	KC858343	[2]	EU042443	[3]
Esmeralda	*Amazilia violiceps*	X	KC858514	[2]	KC858637	[2]	KC858395	[2]	KJ601802	[6]
Esmeralda	*Amazilia viridicauda*		GU167206	[7]	KC858576	[2]	KC858333	[2]	GU167152	[3]
Esmeralda	*Amazilia viridifrons*	X	KC858518	[2]	KC858641	[2]	KC858399	[2]	KJ601804	[6]
Esmeralda	*Amazilia viridigaster*		EU042526	[2]	KC858616	[2]	KC858373	[2]	EU042444	[3]
Esmeralda	*Amazilia yucatanensis*	X	KC858506	[2]	KC858626	[2]	KC858384	[2]	KJ601806	[6]
Mango	*Androdon aequatorialis*		EU983393	[8]					AY830539	[9]
Mango	*Anthracothorax nigricollis*		EU042527	[3]	KC858542	[2]	KC858299	[2]	EU042445	[3]
Mango	*Anthracothorax prevostii*	X	KC858418	[2]	KC858541	[2]	KC858298	[2]	GU167155	[3]
Esmeralda	*Aphantochroa cirrochloris*		EU042528	[3]					EU042446	[3]

Abeja	*Archilochus alexandri*	X	EU042529	[3]					EU042447	[3]
Abeja	*Archilochus colubris*	X	KC858533	[2]	KC858655	[2]	KC858412	[2]	AY830541	[9]
Abeja	*Atthis heloisa*	X	KC858534	[2]	AY275887	[2]	AY281072	[2]	KX855468	[10]
Brillante	*Boissonneaua flavescens*		EU042530	[3]					EU042448	[3]
Brillante	*Boissonneaua matthewsii*		AY830466	[9]					AY830542	[9]
Abeja	*Calliphlox bryantae*		EU042531	[3]					EU042449	[3]
Abeja	*Calliphlox mitchellii*		AY830516	[9]					AY830591	[9]
Abeja	*Calothorax lucifer*	X	KX855351	[10]	KC858654	[2]	KC858411	[2]	KX855475	[10]
Abeja	*Calothorax pulcher*	X	KC858531	[2]	AY275889	[2]	AY281074	[2]	KX855473	[10]
Abeja	*Calypte anna*	X	EU042532	[3]					EU042450	[3]
Abeja	*Calypte costae*	X	EU042533	[3]					EU042451	[3]
Esmeralda	*Campylopterus curvipennis*	X	KC858426	[2]	KC858549	[2]	KC858306	[2]		
Esmeralda	*Campylopterus excellens*	X	KC858428	[2]	KC858550	[2]	KC858307	[2]		
Esmeralda	*Campylopterus hemileucurus*	X	KC858430	[2]	KC858552	[2]	KC858309	[2]	EU042452	[3]
Esmeralda	*Campylopterus largipennis*		AY830467	[9]	KC858553	[2]	KC858310	[2]	AY830543	[9]
Esmeralda	*Campylopterus rufus*	X	KC858429	[2]	KC858551	[2]	KC858308	[2]	KJ601826	[6]
Esmeralda	*Campylopterus villaviscensio*		AY830468	[9]	KC858554	[2]	KC858311	[2]	AY830544	[9]
Esmeralda	*Chalybura buffonii*		EU042537	[3]					EU042455	[3]
Esmeralda	*Chlorestes notata*		EU042539	[3]					EU042457	[3]
Esmeralda	*Chlorostilbon canivetii*	X	KC858433	[2]	KC858555	[2]	KC858312	[2]	KJ601834	[6]
Esmeralda	*Chlorostilbon melanorhynchus*		AY830470	[9]					AY830546	[9]
Esmeralda	*Chlorostilbon mellisugus*		AY830471	[9]					AY830547	[9]
Brillante	*Coeligena bonapartei*		GU167216	[7]	KC858543	[2]	KC858300	[2]	GU167162	[3]
Brillante	*Coeligena coeligena*		EU042541	[3]					FJ903649	[3]
Brillante	*Coeligena torquata*		KC858420	[2]	AY275890	[2]	AY281075	[2]	AY830549	[9]
Mango	*Colibri thalassinus*	X	KC858417	[2]	KC858540	[2]	KC858297	[2]	EU042462	[3]
Esmeralda	*Cynanthus latirostris*	X	KC858435	[2]	KC858557	[2]	KC858314	[2]	KJ601856	[6]
Esmeralda	*Cynanthus sordidus*	X	KC858434	[2]	KC858556	[2]	KC858313	[2]	KJ601858	[6]
Esmeralda	*Damophila julie*		EU042545	[3]					EU042463	[3]

Abeja	*Doricha eliza*	X	KC858530	[2]	KC858653	[2]	KC858410	[2]	KX855485	[10]
Mango	*Doryfera johannae*		KC858416	[2]	KC858539	[2]	KC858296	[2]	EU042465	[3]
Brillante	*Ensifera ensifera*		FJ903534	[11]					AY830554	[9]
Brillante	*Eriocnemis luciani*		AY830480	[9]					AY830555	[9]
Gema de Montaña	*Eugenes fulgens*	X	ORNELAS		KC858651	[2]	KC858408	[2]	AY830556	[9]
Mango	*Eulampis holosericeus*		EU983432	[8]					AY830605	[9]
Esmeralda	*Eupherusa cyanophrys*	X	KC858523	[2]	KC858647	[2]	KC858404	[2]	KJ601867	[6]
Esmeralda	*Eupherusa eximia*	X	ORNELAS		KC858646	[2]	KC858403	[2]	EU042468	[3]
Esmeralda	*Eupherusa nigriventris*		EU042553	[3]					EU042469	[3]
Esmeralda	*Eupherusa poliocerca*	X	KC858522	[2]	KC858645	[2]	KC858402	[2]	KJ601868	[6]
Ermitaño	*Eutoxeres aquila*		AY830483	[9]					AY830558	[9]
Topacio	*Florisuga mellivora*	X	ORNELAS		KC858536	[2]	KC858293	[2]	AY830560	[9]
Ermitaño	*Glaucis aeneus*		EU042554	[3]					EU042470	[3]
Brillante	*Haplophaedia aureliae*		AY830487	[9]					AY830562	[9]
Coqueta	*Heliangelus amethysticollis*		AY830489	[9]					AY830564	[9]
Coqueta	*Heliangelus micraster*		GU167230	[7]					GU167176	[3]
Coqueta	*Heliangelus spencei*	X	KC858422	[2]	KC858544	[2]	KC858301	[2]		
Brillante	*Heliodoxa jacula*		AY830491	[9]					AY830566	[9]
Gema de Montaña	*Heliomaster constantii*	X	KC858529	[2]	AY275886	[2]	AY281071	[2]	KJ601873	[6]
Gema de Montaña	*Heliomaster longirostris*	X	KC858528	[2]	KC858652	[2]	KC858409	[2]	AY830568	[9]
Mango	*Heliothryx barroti*	X	AY830494	[9]					AY830569	[9]
Esmeralda	*Hylocharis cyanus*		EU042561	[3]					EU042477	[3]
Esmeralda	*Hylocharis eliciae*	X	KC858436	[2]	KC858558	[2]	KC858315	[2]	EU042478	[3]
Esmeralda	*Hylocharis grayi*		EU042563	[3]						
Esmeralda	*Hylocharis leucotis*	X	KC858440	[2]	KC858562	[2]	KC858319	[2]	DQ223035	[12]
Esmeralda	*Hylocharis xantusii*	X	EU543353	[13]	DQ196590	[12]			DQ223034	[12]
Gema de Montaña	*Lampornis amethystinus*	X	KC858526	[2]	KC858649	[2]	KC858406	[2]	DQ223024	[12]
Gema de Montaña	*Lampornis calolaemus*		EU042565	[3]	ABA42067	[12]			EU042480	[3]
Gema de Montaña	*Lampornis castaneoventris*		EU042566	[3]	DQ196582	[12]			EU042481	[3]

Gema de Montaña	*Lampornis clemenciae*	X	KC858525	[2]	KC858648	[2]	KC858405	[2]	DQ223023	[2]
Gema de Montaña	*Lampornis hemileucus*		EU042567	[3]	DQ196585	[12]			EU042482	[3]
Gema de Montaña	*Lampornis viridipallens*	X	KC858524	[2]	AY275885	[2]	AY281070	[2]	DQ223026	[12]
Gema de Montaña	*Lamprolaima rhami*	X	KC858527	[2]	KC858650	[2]	KC858407	[2]	DQ223033	[12]
Esmeralda	*Lepidopyga coeruleogularis*		AY830497	[9]					AY830572	[9]
Esmeralda	*Leucippus baeri*		KC858442	[2]	KC858564	[2]	KC858321	[2]	GU167183	[3]
Esmeralda	*Leucippus taczanowskii*		KC858441	[2]	KC858563	[2]	KC858320	[2]		
Coqueta	*Lophornis delattrei*		AY830500	[9]					AY830575	[9]
Coqueta	*Lophornis pavoninus*		EU042568	[3]					EU042483	[3]
Coqueta	*Metallura phoebe*		EU042569	[3]					EU042484	[3]
Coqueta	*Metallura tyrianthina*		AY830502	[9]					AY830577	[9]
Coqueta	*Oreotrochilus chimborazo*		AY830506	[9]					AY830581	[9]
Gema de Montaña	*Panterpe insignis*		AY830509	[9]					AY830584	[9]
Esmeralda	*Phaeochroa cuvierii*	X	GU167244	[7]					GU167190	[3]
Ermitaño	*Phaethornis augusti*		EU042576	[3]					EU042491	[3]
Ermitaño	*Phaethornis longirostris*	X	ORNELAS		ORNELAS		ORNELAS		EU042497	[3]
Ermitaño	*Phaethornis striigularis*	X	ORNELAS		ORNELAS		ORNELAS		KJ601914	[6]
Abeja	*Selasphorus platycercus*	X	KX855382	[10]	AY275888	[2]	AY281073	[2]	AY830597	[9]
Abeja	*Selasphorus rufus*	X	KX855388	[10]	KC858656	[2]	KC858413	[2]	EU042505	[3]
Coqueta	*Sephanoides fernandensis*		EU042591	[3]					EU042506	[3]
Abeja	*Selasphorus calliope*	X	KF792866	[14]					EU042508	[3]
Esmeralda	*Taphrospilus hypostictus*		AY830523	[9]					AY830598	[9]
Esmeralda	*Thalurania colombica*		AY830524	[9]					AY830599	[9]
Esmeralda	*Thalurania furcata*		AY830525	[9]					AY830600	[9]
Ermitaño	*Threnetes leucurus*		AY830526	[9]					AY830601	[9]
Abeja	*Tilmatura dupontii*	X	KC858535	[2]	KC858657	[2]	KC858414	[2]	KJ601963	[6]
Topacio	*Topaza pella*		AY830528	[9]					AY830603	[9]

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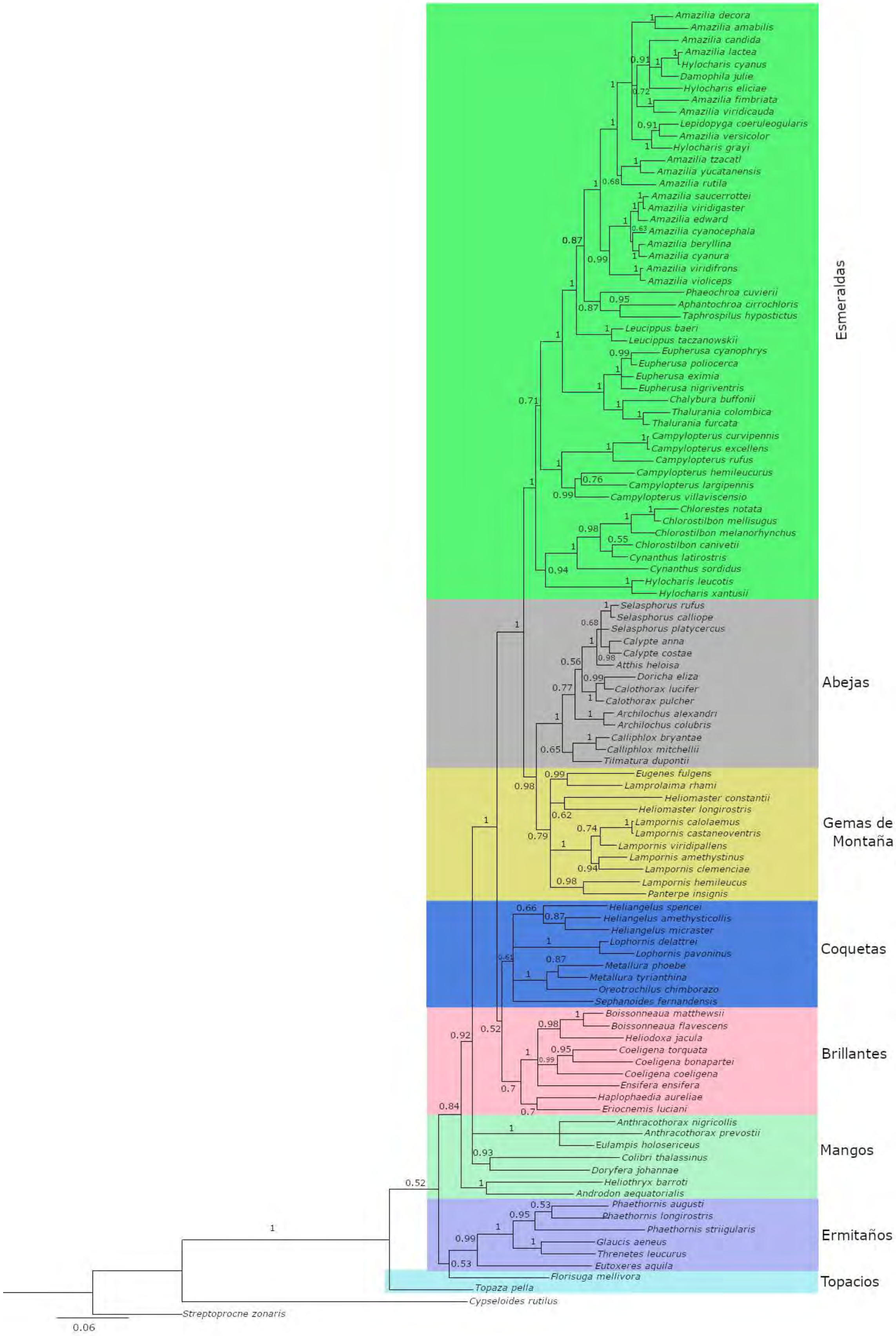
ANEXO 3.

Hipótesis filogenética de todas las especies de colibríes (*Escala continental*) generada a partir del método de Inferencia Bayesiana con los datos combinados del intrón 5 del Adenilato Kinasa, la subunidad 2 y 5 de la NADH deshidrogenasa, y el gen 12S ribosomal. La discriminación de los codones de los genes mitocondriales ND2 y ND5 mejoraron considerablemente el soporte del modelo filogenético (Anexo 5). Los números en las ramas indican la probabilidad Bayesiana posterior. Los colores agrupan las especies de colibríes por clados filogenéticos siguiendo a McGuire y colaboradores (2014).

REFERENCIAS ANEXO 3

McGuire, J.A., *et al.*, Molecular Phylogenetics and the Diversification of Hummingbirds. Current Biology, 2014. 24(8): p. 910-916.


Amazilia decora
Amazilia amabilis
Amazilia candida
Amazilia lactea
Hylocharis cyanus
Damophila julie
Hylocharis eliciae
Amazilia fimbriata
Amazilia viridicauda
Lepidopyga coeruleogularis
Amazilia versicolor
Hylocharis grayi
Amazilia tzacatl
Amazilia yucatanensis
Amazilia rutila
Amazilia saucerrottei
Amazilia viridigaster
Amazilia edward
Amazilia cyanocephala
Amazilia beryllina
Amazilia cyanura
Amazilia viridifrons
Amazilia violiceps
Phaeochroa cuvierii
Aphantochroa cirrochloris
Taphrospilus hypostictus
Leucippus baeri
Leucippus taczanowskii
Eupherusa cyanophrys
Eupherusa poliocerca
Eupherusa eximia
Eupherusa nigriventris
Chalybura buffonii
Thalurania colombica
Thalurania furcata
Campylopterus curvipennis
Campylopterus excellens
Campylopterus rufus
Campylopterus hemileucurus
Campylopterus largipennis
Campylopterus villaviscensio
Chlorestes notata
Chlorostilbon mellisugus
Chlorostilbon melanorhynchus
Chlorostilbon canivetii
Cynanthus latirostris
Cynanthus sordidus
Hylocharis leucotis
Hylocharis xantusii
Selasphorus rufus
Selasphorus calliope
Selasphorus platycercus
Calypte anna
Calypte costae
Atthis heloisa
Doricha eliza
Calothorax lucifer
Calothorax pulcher
Archilochus alexandri
Archilochus colubris
Calliphlox bryantae
Calliphlox mitchellii
Tilmatura dupontii
Eugenes fulgens
Lamprolaima rhami
Heliomaster constantii
Heliomaster longirostris
Lampornis calolaemus
Lampornis castaneoventris
Lampornis viridipallens
Lampornis amethystinus
Lampornis clemenciae
Lampornis hemileucus
Panterpe insignis
Heliangelus spencei
Heliangelus amethysticollis
Heliangelus micraster
Lophornis delattrei
Lophornis pavoninus
Metallura phoebe
Metallura tyrianthina
Oreotrochilus chimborazo
Sephanoides fernandensis
Boissonneaua matthewsii
Boissonneaua flavescens
Heliodoxa jacula
Coeligena torquata
Coeligena bonapartei
Coeligena coeligena
Ensifera ensifera
Haplophaedia aureliae
Eriocnemis luciani
Anthracothorax nigricollis
Anthracothorax prevostii
Eulampis holosericeus
Colibri thalassinus
Doryfera johannae
Heliothryx barroti
Androdon aequatorialis
Phaethornis augusti
Phaethornis longirostris
Phaethornis striigularis
Glaucis aeneus
Threnetes leucurus
Eutoxeres aquila
Florisuga mellivora
Topaza pella
Cypseloides rutilus
Streptoprocne zonaris
Esmeraldas
Abejas
Gemas de Montaña
Coquetas
Brillantes
Mangos
Ermitaños
Topacios
0.06

ANEXO 4.

Hipótesis filogenética de las especies de colibríes en México (*Escala México*) generada a partir del método de Inferencia Bayesiana con los datos combinados del intrón 5 del Adenilato Kinasa, la subunidad 2 y 5 de la NADH deshidrogenasa, y el gen 12S ribosomal. La discriminación de los codones de los genes mitocondriales ND2 y ND5 mejoraron considerablemente el soporte del modelo filogenético (Anexo 6). Los números en las ramas indican la probabilidad Bayesiana posterior. Los colores agrupan las especies de colibríes por clados filogenéticos siguiendo a McGuire y colaboradores (2014). Las especies *Lophornis pavoninus* y *Thalurania furcata* (en color rojo) se incluyeron como nodos substitutos a las especies mexicanas *Lophornis brachylopha* y *Thalurania ridgwayi* de las cuales no hay secuencias disponibles.

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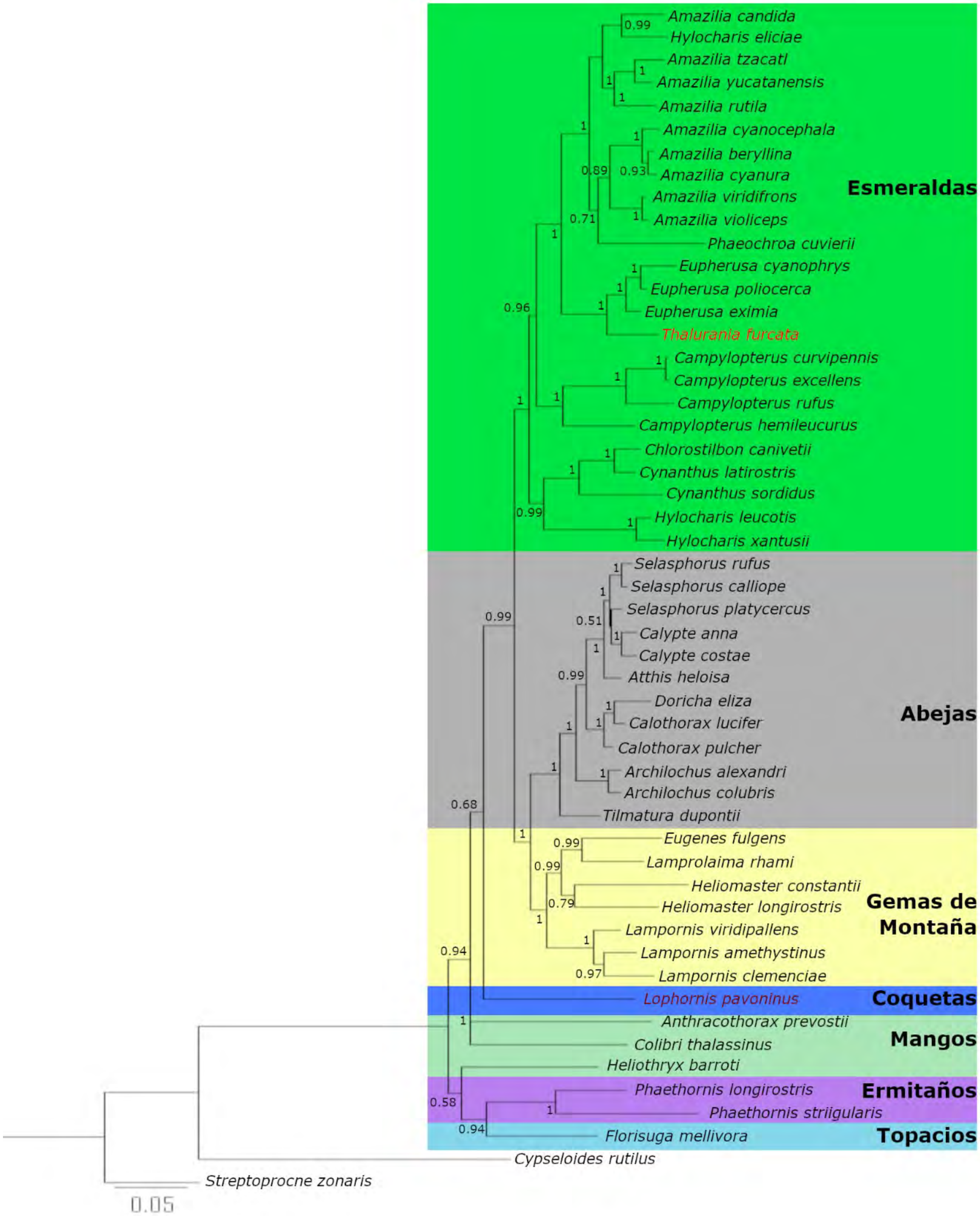
McGuire, J.A., *et al.*, Molecular Phylogenetics and the Diversification of Hummingbirds. Current Biology, 2014. 24(8): p. 910-916


Amazilia candida
Hylocharis eliciae
Amazilia tzacatl
Amazilia yucatanensis
Amazilia rutila
Amazilia cyanocephala
Amazilia beryllina
Amazilia cyanura
Amazilia viridifrons
Amazilia violiceps
Phaeochroa cuvierii
Eupherusa cyanophrys
Eupherusa poliocerca
Eupherusa eximia
Thalurania furcata
Campylopterus curvipennis
Campylopterus excellens
Campylopterus rufus
Campylopterus hemileucurus
Chlorostilbon canivetii
Cynanthus latirostris
Cynanthus sordidus
Hylocharis leucotis
Hylocharis xantusii
Esmeraldas
Selasphorus rufus
Selasphorus calliope
Selasphorus platycercus
Calypte anna
Calypte costae
Atthis heloisa
Doricha eliza
Calothorax lucifer
Calothorax pulcher
Archilochus alexandri
Archilochus colubris
Tilmatura dupontii
Abejas
Eugenes fulgens
Lamprolaima rhami
Heliomaster constantii
Heliomaster longirostris
Lampornis viridipallens
Lampornis amethystinus
Lampornis clemenciae
Gemas de Montaña
Lophornis pavoninus
Coquetas
Anthracothorax prevostii
Colibri thalassinus
Heliothryx barroti
Mangos
Phaethornis longirostris
Phaethornis striigularis
Ermitaños
Florisuga mellivora
Topacios
Cypseloides rutilus
Streptoprocne zonaris
0.05
0.99
1
1
1
1
1
0.89
0.93
1
0.71
1
1
1
0.96
1
1
1
1
1
1
1
0.99
1
1
1
0.99
0.51
1
1
0.99
1
1
1
1
1
0.68
1
0.99
0.99
0.79
1
1
0.97
0.94
1
0.58
1
0.94

ANEXO 5.

Resultados de los Factores de Bayes para las seis particiones probadas para la hipótesis filogenética que incluyó todas las especies de colibríes (*Escala continental*). La media armónica más alta fue obtenida en el modelo ECON6a.nex (en negrilla).

Partición	**Modelo**	**Media armónica**
1. Todos los genes simultáneamente sin partición: (ND2 - ND5 - 12S rRNA - AK1).	ECON1a.nex	-23753.05
2. Igual a la partición 1 pero dejando que MrBayes calcule los parámetros.	ECON1b.nex	-23762.67
3. Genes mitocondriales vs. nuclear: (ND2 - ND5 - 12S rRNA) (AK1)	ECON2a.nex	-23599.88
4. Discriminando cada uno de los genes (ND2) (ND5) (12S rRNA) (AK1).	ECON3a.nex	-23341.94
5. Discriminando los codones de los genes mitocondriales ND2 y ND5, con la posición 1 y 2 respecto a la posición 3: (ND2-pos1 y 2) (ND2-pos3) (ND5-pos1 y 2) (ND5-pos3) (12S rRNA) (AK1).	ECON4a.nex	-23110.55
6. Discriminando los codones de los genes mitocondriales ND2 y ND5, con la posición 1 y2 respecto a la posición 3: (ND2-pos1 y 2) (ND2-pos3) (ND5-pos1 y 2) (ND5-pos3) (12S rRNA) (AK1). Pero a diferencia del modelo 4 en donde se incorporaron los modelos de evolución obtenidos por el programa jModelTest, en esta partición se emplearon los modelos de evolución propuestos por Shapiro *et al.* (2006): HKY+G para la posición 1 y 2, y el modelo GTR+G para la posición 3.	ECON5a.nex	-23246.73
7. Discriminando los codones de los genes mitocondriales ND2 y ND5: (ND2-pos1) (ND2-pos2) (ND2-pos3) (ND5-pos1) (ND5-pos2) (ND5-pos3) (12S rRNA) (AK1).	ECON6a.nex	**-22880.44**

ANEXO 6.

Comparaciones de las medias armónicas entre el mejor modelo (ECON6a.nex) y las demás particiones para la hipótesis filogenética que incluye todas las especies de colibríes (*Escala continental*). Debido a que la comparación con los otros modelos da valores mayores a 10, es apropiado decir que el modelo 6a provee una mejor explicación de los datos comparados con los otros modelos.

M1	**M2**	**log*e B*10**	**2log*e B*10**
ECON6a.nex	ECON1a.nex	872.61	1745.22
ECON6a.nex	ECON1b.nex	882.23	1764.46
ECON6a.nex	ECON2a.nex	719.44	1438.88
ECON6a.nex	ECON3a.nex	461.5	923
ECON6a.nex	ECON4a.nex	230.11	460.22
ECON6a.nex	ECON5a.nex	366.29	732.58

ANEXO 7.

Resultados de los Factores de Bayes para las seis particiones probadas para la hipótesis filogenética que incluyó las especies de colibríes reportadas en México (*Escala México*). La media armónica más alta fue obtenida en el modelo EMEX6a.nex (en negrilla).

Partición	Modelo	Media armónica
1. Todos los genes simultáneamente sin partición: (ND2 - ND5 - 12S rRNA - AK1).	EMEX1a.nex	-15792.33
2. Igual a la partición 1 pero dejando que MrBayes calcule los parámetros.	EMEX1b.nex	-15793.41
3. Genes mitocondriales vs. nuclear: (ND2 - ND5 - 12S rRNA) (AK1)	EMEX2a.nex	-15669.23
4. Discriminando cada uno de los genes (ND2) (ND5) (12S rRNA) (AK1).	EMEX3a.nex	-15468.64
5. Discriminando los codones de los genes mitocondriales ND2 y ND5, con la posición 1 y 2 respecto a la posición 3: (ND2-pos1 y 2) (ND2-pos3) (ND5-pos1 y 2) (ND5-pos3) (12S rRNA) (AK1).	EMEX4a.nex	-15274.02
6. Discriminando los codones de los genes mitocondriales ND2 y ND5, con la posición 1 y2 respecto a la posición 3: (ND2-pos1 y 2) (ND2-pos3) (ND5-pos1 y 2) (ND5-pos3) (12S rRNA) (AK1). Pero a diferencia del modelo 4 en donde se incorporaron los modelos de evolución obtenidos por el programa jModelTest, en esta partición se emplearon los modelos de evolución propuestos por Shapiro *et al.* (2006): HKY+G para la posición 1 y 2, y el modelo GTR+G para la posición 3.	EMEX5a.nex	-15326.19
7. Discriminando los codones de los genes mitocondriales ND2 y ND5: (ND2-pos1) (ND2-pos2) (ND2-pos3) (ND5-pos1) (ND5-pos2) (ND5-pos3) (12S rRNA) (AK1).	EMEX6a.nex	**-15093.96**

ANEXO 8.

Comparaciones de las medias armónicas entre el mejor modelo (EMEX6a.nex) y las demás particiones para la hipótesis filogenética que incluye las especies de colibríes reportadas en México (*Escala México*). Debido a que la comparación con los otros modelos da valores mayores a 10, es apropiado decir que el modelo 6a provee una mejor explicación de los datos comparados con los otros modelos.

M1	**M2**	**log*e* *B*10**	**2log*e* *B*10**
EMEX6a.nex	EMEX1a.nex	698.37	1396.74
EMEX6a.nex	EMEX1b.nex	699.45	1398.9
EMEX6a.nex	EMEX2a.nex	575.27	1150.54
EMEX6a.nex	EMEX3a.nex	374.68	749.36
EMEX6a.nex	EMEX4a.nex	180.06	360.12
EMEX6a.nex	EMEX5a.nex	232.23	464.46

ANEXO 9.

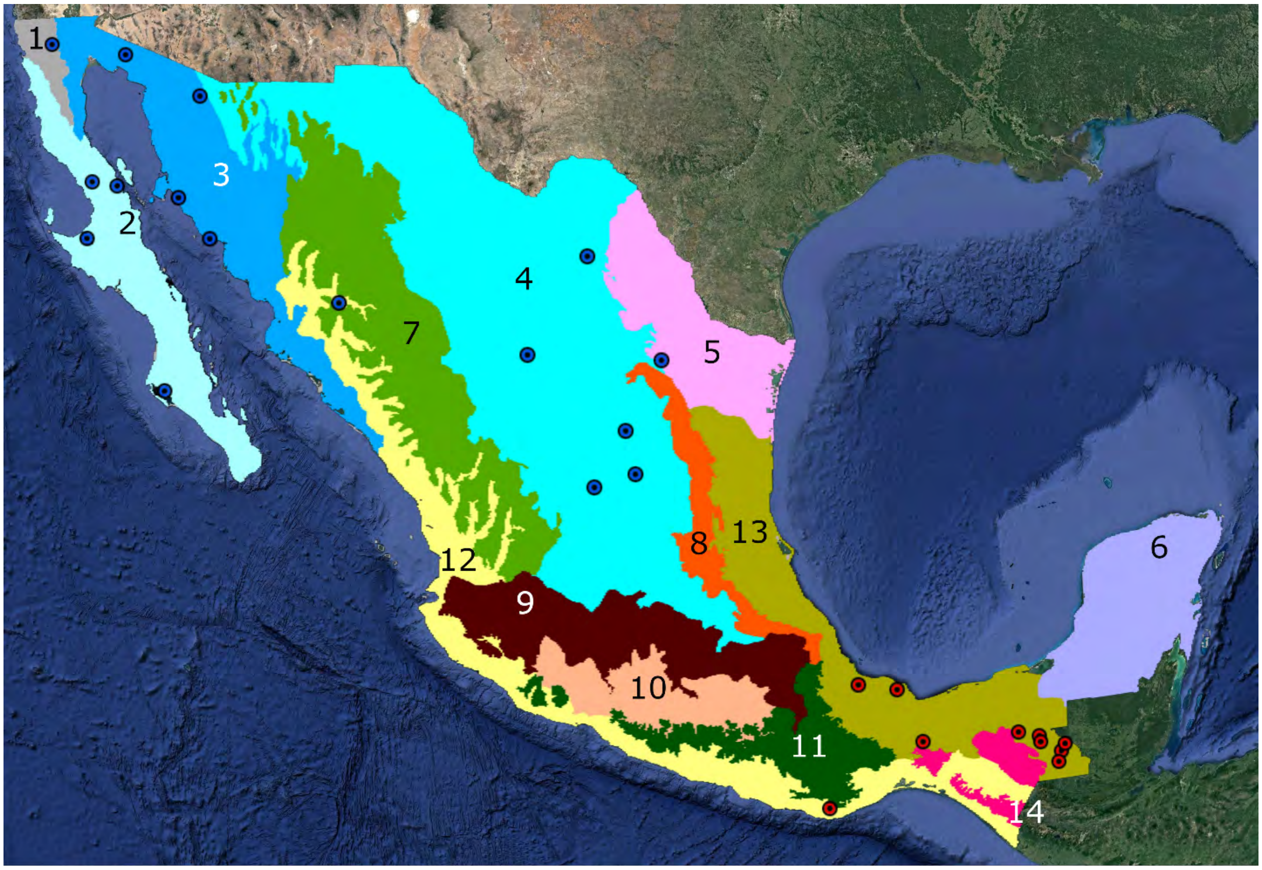
Comunidades de colibríes (COM) con valores de índice de parentesco neto (NRI) e índice de taxón más cercano (NTI) estadísticamente significativo para las filogenias de escala continental (ECON) y escala México (EMEX). Se indica el Estado de la República en donde se ubica la comunidad, el número de especies de colibríes (SPP), el número de especies migratorias latitudinales (MIG) y el número de clados filogenéticos presentes en la comunidad (CLAD), siguiendo la clasificación de McGuire *et al.* (2007). Información detallada para cada comunidad (COM) se encuentra en el Anexo 1.

COM	SPP	MIG	CLAD	ESTADO	NRIECON	NRIEMEX	NTIECON	NTIEMEX
C112	5	5	1	Coahuila	-3.7103	-3.6397	-2.7183	-2.6414
C123	3	3	1	Baja California Sur	-3.6897	-3.4196	-2.5272	-2.5397
C120	5	5	1	Baja California	-3.5196	-3.4221	-2.4432	-2.3503
C107	3	3	1	Sonora	-3.4241	-3.3926	-2.7553	-2.7125
C130	8	6	2	Coahuila	-3.3024	-3.1593	-2.1527	-2.0980
C134	4	4	1	San Luis Potosí	-3.1056	-2.8594	-2.0159	-2.0439
C189	2	2	1	Sonora	-3.0049	-2.6042	-2.7975	-2.7734
C89	6	5	2	San Luis Potosí	-2.8480	-2.6124	-2.0373	-1.9916
C137	3	3	1	Nuevo León	-2.6655	-2.6126	-2.0180	-1.9741
C119	6	5	2	Sonora	-2.5945	-2.2931	-1.8363	-1.8071
C193	16	8	3	Chihuahua	-2.4852	-2.4189	-1.7384	-1.6201
C190	5	4	2	Sonora	-2.4593	-2.4685	-1.7842	-1.7424
C122	6	5	2	Baja California	-2.4439	-2.2964	-1.7829	-1.7605
C184	6	5	2	Baja California Sur	-2.4011	-2.3976	-1.7500	-1.7695
C90	6	5	2	San Luis Potosí	-2.3761	-2.3431	-1.7986	-1.6546
C183	4	3	2	Baja California Sur	-2.1557	-2.0682	-1.8547	-1.8091
C70	7	0	5	Oaxaca	1.7933	1.7950	2.2218	2.0806
C208	5	1	4	Veracruz	1.8991	1.8251	1.9231	1.9670
C169	20	1	7	Chiapas	2.2612	2.1772	2.0025	1.8420
C159	15	1	7	Veracruz	2.2803	2.0141	1.6404	1.8420
C170	20	1	7	Chiapas	2.2836	2.1556	1.9955	1.8420

C167	20	1	7	Chiapas	2.3268	2.0752	1.9525	1.8420
C171	20	1	7	Chiapas	2.3730	2.0383	2.0189	1.8420
C168	20	1	7	Chiapas	2.4052	1.9243	1.9308	1.8420
C165	14	1	6	Chiapas	2.5171	2.3860	2.5412	1.8420

ANEXO 10.

Mapa de México indicando las comunidades de colibríes donde tanto el índice de parentesco neto (NRI) como el índice de taxón más cercano (NTI) fueron estadísticamente significativos. Los puntos azules indican las comunidades con agrupamiento filogenético ($p > 0.90$) y los puntos rojos son las comunidades con sobredispersión filogenética ($p < 0.05$). Los colores en el mapa representan las Provincias biogeográficas de México (Morrone 2019) 1) Californiana; 2) Baja California; 3) Sonora; 4) Desierto Chihuahuense; 5) Tamaulipas; 6) Península de Yucatán; 7) Sierra Madre Occidental; 8) Sierra Madre Oriental; 9) Faja Volcánica Transmexicana; 10) Cuenca del Balsas; 11) Sierra Madre del Sur; 12) Tierras bajas del Pacífico; 13) Veracruzana; 14) Tierras Altas de Chiapas. Fuente: Google Earth (2018).



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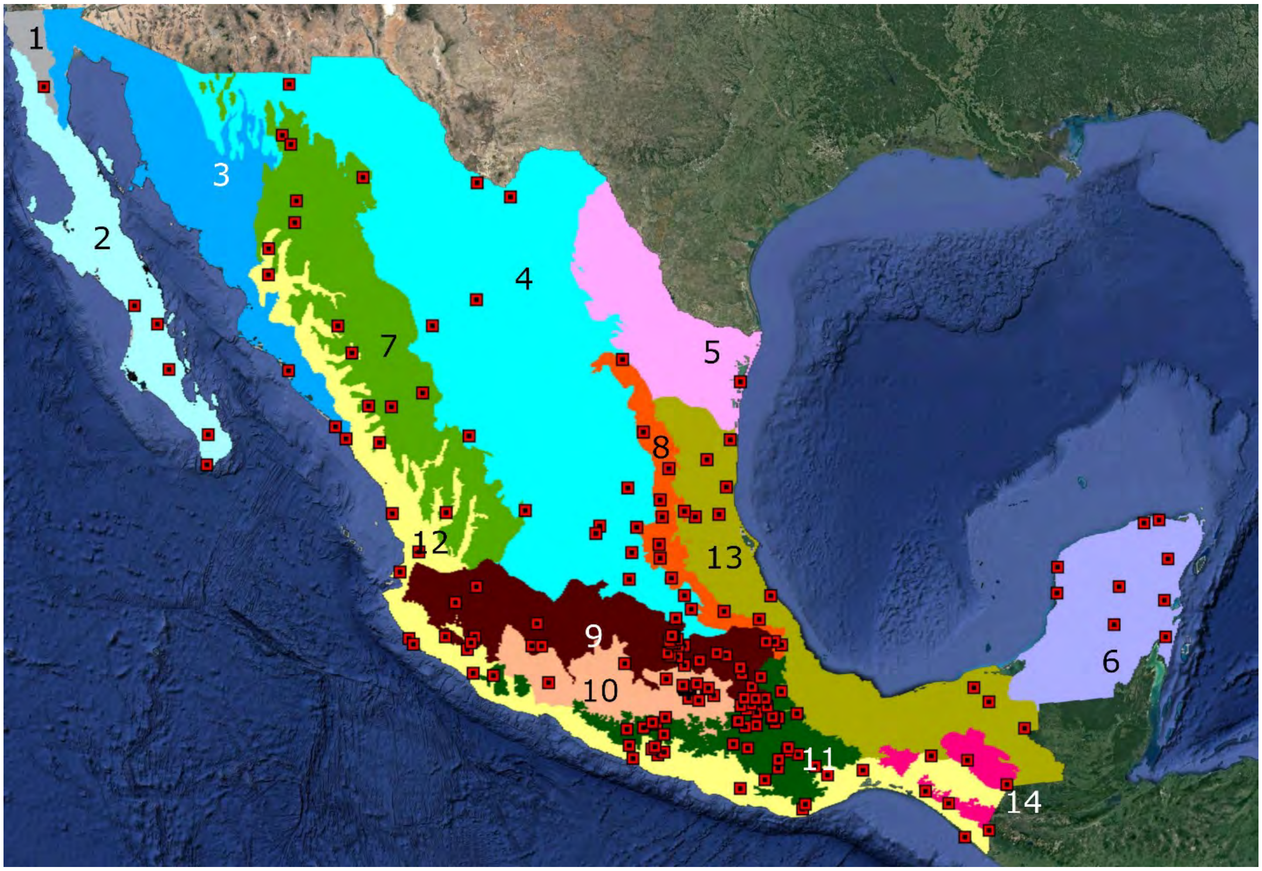
ANEXO 11.

Mapa de México indicando las comunidades de colibríes donde el índice de taxón más cercano (NTI) no fue estadísticamente significativo (puntos rojos). Los colores en el mapa representan las Provincias biogeográficas de México (Morrone 2019) 1) Californiana; 2) Baja California; 3) Sonora; 4) Desierto Chihuahuense; 5) Tamaulipas; 6) Península de Yucatán; 7) Sierra Madre Occidental; 8) Sierra Madre Oriental; 9) Faja Volcánica Transmexicana; 10) Cuenca del Balsas; 11) Sierra Madre del Sur; 12) Tierras bajas del Pacífico; 13) Veracruzana; 14) Tierras Altas de Chiapas. Fuente: Google Earth (2018).



REFERENCIAS ANEXO 11

Morrone, J. J. 2019. Regionalización biogeográfica y evolución biótica de México: encrucijada de la biodiversidad del Nuevo Mundo. Revista Mexicana de Biodiversidad 90: e902980.

ANEXO 12.

Listado de las 8 variables ambientales y de las 7 variables de características de vegetación para las 121 comunidades de colibríes en México. AMT: Temperatura promedio anual, MDTR: rango diurno promedio, TS: estacionalidad de la temperatura, TAR: rango de la temperatura anual, AP: precipitación anual, PS: estacionalidad de la precipitación, PWQ: precipitación del cuatrimestre más caliente, PCQ: precipitación del cuatrimestre más frío, FPAR: porcentaje de Radiación de la Fracción Fotosintéticamente Activa, FPARSD: desviación estándar de la Radiación de la Fracción Fotosintéticamente Activa, LAI: porcentaje del índice de área foliar, LAISD: desviación estándar del índice de área foliar, NT: porcentaje de no-cobertura arbórea, NV: porcentaje de terreno sin cobertura, TC: porcentaje de cobertura arbórea.

Comunidad	AMT	MDTR	TS	TAR	AP	PS	PWQ	PCQ	FPAR	FPARSD	LAI	LAISD	NT	NV	TC
	°C	°C	%	°C	mm	%	mm	mm	%	%	%	%	%	%	%
1	18.20	13.80	36.98	23.30	49.70	11.70	35.40	6.50	46.9330	5.1153	12.8759	2.1590	69.6241	17.9199	12.4560
2	25.90	13.40	18.87	19.50	114.20	6.30	30.90	11.20	42.2182	3.0674	76.2011	4.4291	38.0228	5.4159	56.5613
3	23.60	11.50	17.46	17.10	115.30	7.20	28.90	14.20	69.7683	2.5974	38.2768	4.1193	39.5964	3.5724	56.8312
4	27.60	13.80	7.63	17.50	270.20	9.10	35.10	9.10	68.6988	2.9064	27.9266	2.6821	50.0700	6.2348	43.6951
5	22.10	13.80	11.01	18.80	212.60	9.40	63.20	2.70	72.9147	2.9711	38.7042	3.9741	36.6279	4.1395	59.2325
6	22.10	13.00	12.27	18.30	150.30	9.90	45.90	1.90	69.6313	3.1881	33.8920	3.6846	43.7731	6.2413	49.9856
7	23.30	12.00	17.22	17.50	103.70	7.70	27.80	8.00	64.1289	3.2995	30.1930	3.2631	51.5761	6.8624	43.3940
8	13.80	12.70	11.53	17.20	120.10	7.20	54.90	7.70	55.7860	3.8190	22.0846	2.7211	55.4785	8.0716	36.4499
9	14.00	13.20	18.24	20.70	102.80	9.30	43.00	5.70	59.8061	3.7754	23.5755	3.0742	57.4211	8.2610	34.3179
10	14.00	13.20	18.24	20.70	102.80	9.30	43.00	5.70	54.3804	4.3164	22.7035	2.9785	59.5866	9.1446	31.2688
11	11.90	15.20	15.72	21.70	113.10	9.40	32.10	3.70	86.6453	5.1476	61.7774	3.0116	48.8526	20.2533	30.9579
12	15.80	17.30	20.52	24.80	62.60	8.80	18.90	2.20	25.7422	5.4584	6.1347	1.3651	40.2075	54.0021	5.7904
13	11.90	15.20	15.72	21.70	113.10	9.40	32.10	3.70	43.7204	5.1390	14.2919	2.5224	40.0383	33.3300	18.6316
14	14.90	17.00	19.86	24.50	82.90	9.20	24.60	2.70	42.8700	5.0564	13.9016	2.4243	52.2484	25.7717	21.9798
15	11.90	15.20	15.72	21.70	113.10	9.40	32.10	3.70	48.4679	5.2271	17.3655	3.0400	47.3620	19.7550	32.9401
16	15.40	16.60	20.59	24.30	76.10	9.30	22.50	2.10	33.6663	5.3398	8.6665	1.6162	55.1204	36.5994	8.2801
17	15.40	16.60	20.59	24.30	76.10	9.30	22.50	2.10	32.7674	5.3434	8.9146	1.7063	42.1437	50.1461	7.7101
18	12.90	15.40	17.39	22.30	103.20	9.00	29.50	4.50	45.4152	5.2070	15.5167	2.5391	54.7504	22.6926	22.5570

19	27.90	14.80	9.57	18.70	150.20	11.00	35.10	1.40	63.5032	4.1910	24.6375	3.6164	59.4170	6.9070	33.6759
20	27.50	11.90	7.51	15.20	122.70	11.10	52.50	2.10	63.8785	4.3128	27.5178	3.8135	55.0740	5.2510	39.6750
21	23.80	14.20	14.91	20.30	74.60	9.90	19.30	3.40	43.6664	4.9664	14.5489	2.1546	71.3257	11.4742	17.5859
22	24.70	14.00	10.57	18.80	146.70	11.10	34.50	2.00	58.7056	4.0904	21.4589	2.6432	59.0393	6.3383	34.6224
23	23.80	14.20	14.91	20.30	74.60	9.90	19.30	3.40	44.9819	4.9073	15.4494	2.2442	70.8857	10.5889	18.5254
24	25.00	15.00	17.11	22.30	78.90	10.10	22.60	2.50	41.8248	5.2084	13.5703	2.1164	75.5715	10.9259	13.5026
25	27.40	13.80	8.66	17.90	133.20	11.00	30.30	4.80	57.1877	4.2805	21.0802	2.7505	62.2672	6.4104	31.3224
26	21.20	12.30	12.85	18.10	132.60	10.50	30.70	5.00	55.4109	4.3943	22.8799	3.1238	57.0914	6.8770	36.0316
27	24.20	13.20	10.32	17.90	153.10	10.90	34.50	5.20	58.1400	4.1406	21.5674	2.6956	58.2335	6.9503	34.8162
28	21.90	14.40	13.65	20.60	92.50	10.20	23.60	2.00	47.5853	4.6476	17.6004	2.1922	69.9178	10.6402	19.7506
30	25.10	12.50	9.26	16.80	159.60	10.80	36.40	3.30	74.6922	2.5448	42.3374	4.2987	36.4382	2.9528	60.6090
31	17.20	14.20	24.48	22.40	126.50	7.80	31.90	9.40	67.3867	3.6368	32.3491	3.7785	48.4522	6.0080	45.5403
32	13.00	15.80	17.11	22.20	69.80	7.40	24.50	4.00	41.1485	5.1583	13.3364	2.2333	55.5179	22.0473	22.4348
33	19.10	13.60	15.01	20.30	127.20	10.30	50.40	6.60	63.3166	4.0160	28.0875	3.6839	53.1380	5.1423	41.7197
34	19.10	13.60	15.01	20.30	127.20	10.30	50.40	6.60	65.5395	4.0333	29.6723	4.0220	50.1889	4.8632	44.9480
35	26.10	13.20	16.64	18.10	83.30	10.90	43.00	2.90	61.0384	5.5317	25.2636	4.9172	67.4448	8.8343	23.7209
36	25.90	12.70	15.85	17.50	88.50	11.20	46.30	3.20	59.2527	5.5156	23.0962	4.2212	49.5407	7.4598	42.9997
37	15.40	16.60	20.59	24.30	76.10	9.30	22.50	2.10	42.7498	5.2574	13.6137	2.3231	48.7454	35.8588	15.3957
38	19.60	14.40	15.96	21.40	114.80	9.90	29.40	3.60	49.1821	4.4448	17.2693	2.3468	68.4412	9.1596	22.3991
39	15.30	17.30	20.65	24.90	64.90	8.80	29.90	2.10	37.5337	4.8886	9.2833	1.5038	52.6925	41.9986	5.3089
40	15.40	16.60	20.59	24.30	76.10	9.30	22.50	2.10	44.8027	4.9905	13.8500	2.1961	46.5050	42.0800	11.4151
41	13.80	16.00	16.13	22.70	100.80	9.30	30.50	2.90	51.0164	4.4749	16.9082	2.4008	66.5888	12.3660	21.0452
42	15.20	17.80	20.22	25.50	59.70	8.60	19.20	2.10	32.5573	5.3807	8.7041	1.7001	50.7906	40.2327	8.9767
43	25.40	12.80	14.91	17.60	93.70	10.70	52.10	2.80	55.7526	4.2812	20.5366	2.7258	63.6876	7.2520	29.0604
44	21.60	12.50	15.32	19.20	129.50	10.10	51.60	4.70	58.2015	4.2362	23.3524	3.0680	59.3891	5.4962	35.1146
45	23.50	16.10	18.12	23.40	95.70	10.50	28.30	2.80	46.4326	4.6607	15.1910	2.1506	73.8210	11.4729	14.7061
46	23.80	16.90	18.01	24.20	83.20	10.40	24.70	2.20	48.9148	4.4333	16.4660	2.1552	73.4638	11.5726	14.9636
47	23.80	16.90	18.01	24.20	83.20	10.40	24.70	2.20	48.1991	4.4524	16.5091	2.2002	74.6576	11.1350	14.2074
48	23.80	16.90	18.01	24.20	83.20	10.40	24.70	2.20	55.0712	3.9521	17.8561	2.0562	74.5055	11.7142	13.7803
49	23.80	16.90	18.01	24.20	83.20	10.40	24.70	2.20	48.3360	4.4846	16.8758	2.2582	74.6170	11.0253	14.3576

50	24.00	17.40	19.30	25.00	80.40	10.00	24.20	2.60	55.2924	4.0040	18.2019	2.1172	74.8156	11.5039	13.6804
51	23.80	16.90	18.01	24.20	83.20	10.40	24.70	2.20	47.7997	4.5540	15.5493	2.0902	74.7178	11.5348	13.7474
52	23.80	16.90	18.01	24.20	83.20	10.40	24.70	2.20	47.7178	4.5175	15.4112	2.0606	75.5774	11.3005	13.1221
53	23.80	16.90	18.01	24.20	83.20	10.40	24.70	2.20	56.3489	3.8822	18.8711	2.1408	74.1207	11.3746	14.5047
54	23.60	16.60	18.27	23.90	81.60	10.60	25.20	1.60	48.9878	4.5643	17.2913	2.2980	74.5799	10.8594	14.5606
55	22.10	14.20	22.21	21.20	113.80	11.70	74.00	3.80	56.9480	3.9914	22.0408	2.7201	60.8422	8.2224	30.9353
56	26.70	9.90	16.49	15.50	87.40	10.90	25.00	1.70	50.0989	4.0364	16.6888	2.0753	66.7601	8.9833	24.2565
57	21.40	14.60	20.79	22.10	64.20	9.20	18.90	3.60	36.3157	4.7492	11.0435	1.8059	64.2660	15.6621	20.0719
58	15.80	16.50	17.43	23.60	61.10	9.50	24.80	2.30	27.2846	5.0776	6.4546	1.2997	60.9559	26.6479	12.3962
59	17.80	15.10	12.18	20.90	90.50	9.40	33.30	2.80	51.4026	4.8638	20.1072	3.0771	59.0183	11.8852	29.0965
60	24.30	15.70	12.67	21.00	174.20	10.60	45.70	3.60	66.9812	3.8433	29.1318	3.6520	52.1640	4.6436	43.1924
61	20.50	16.20	13.85	22.30	143.80	9.70	46.80	4.20	62.1063	4.1930	25.6994	3.4909	51.9164	6.7903	41.2934
62	24.30	14.00	9.24	17.80	148.30	9.70	46.00	4.20	68.8813	3.4282	34.6126	3.8110	42.6879	3.2741	54.0380
63	13.40	12.80	10.36	17.60	117.90	8.30	15.40	7.50	52.2767	4.8082	21.9398	3.4340	50.4589	13.4739	36.0672
64	19.10	17.40	18.47	24.60	74.20	9.50	27.10	2.50	33.3293	5.0625	8.5047	1.4973	67.2509	20.5520	12.1971
65	17.70	17.60	14.23	23.90	97.50	9.20	31.30	3.40	46.7450	4.6685	15.1245	2.1658	62.7323	15.1896	22.0781
66	15.00	13.70	12.49	19.30	99.70	8.60	30.70	6.20	56.9544	4.8279	24.0665	3.8130	50.1702	11.1839	38.6459
67	22.90	10.30	21.34	17.30	383.30	7.80	84.10	31.50	41.6645	5.2099	13.7675	2.1616	75.7000	10.8280	13.4720
68	16.10	17.10	17.05	24.20	69.90	9.10	26.90	2.60	33.3797	5.0264	8.6520	1.5091	62.7336	22.9876	14.2788
69	18.10	11.70	11.56	16.40	121.60	9.00	32.70	6.90	48.8178	4.7489	17.9205	2.6160	64.3277	10.1039	25.5684
70	23.10	14.40	9.36	18.40	144.00	9.60	41.00	4.60	70.0854	3.2184	35.6307	3.6660	42.3842	3.4766	54.1392
71	16.30	17.60	13.83	23.80	88.90	9.10	32.40	3.30	43.6418	4.8046	13.2630	1.9918	61.2236	19.4866	19.2898
72	18.60	12.90	13.90	18.60	96.20	8.90	28.60	5.10	43.7962	4.7553	14.4165	2.1580	66.0700	13.2650	20.6450
73	23.20	14.20	9.39	18.20	161.70	9.50	47.00	5.60	73.0000	3.3617	35.9261	3.6484	44.9917	3.5236	51.4847
74	20.30	13.60	19.48	20.80	113.70	8.80	28.50	9.00	55.6092	3.9961	24.1781	3.0217	53.7731	8.7482	37.4786
75	20.30	13.60	19.48	20.80	113.70	8.80	28.50	9.00	41.4632	4.5072	13.9906	2.0685	61.8569	14.9337	23.2094
76	21.40	14.60	20.79	22.10	64.20	9.20	18.90	3.60	39.9712	4.5745	12.8245	1.9520	63.4244	15.5855	20.9901
77	21.40	14.60	20.79	22.10	64.20	9.20	18.90	3.60	43.7654	4.5505	14.1210	2.0998	64.2824	13.0121	22.7055
78	21.40	14.60	20.79	22.10	64.20	9.20	18.90	3.60	38.1576	4.7439	11.7513	1.8809	63.5903	16.4107	19.9990
79	19.10	15.60	16.33	22.50	71.50	9.30	26.40	2.00	47.5392	4.9189	17.5900	2.7790	58.3470	16.4571	25.1959

80	20.10	10.70	26.61	18.60	266.20	5.60	81.30	33.00	67.6319	2.9409	32.5848	3.4168	49.1504	5.9884	44.8612
81	24.40	17.00	21.48	25.40	83.50	10.00	25.50	2.60	49.1863	4.5848	17.2362	2.2930	73.0543	11.5768	15.3689
82	23.80	17.20	21.23	24.90	81.90	9.70	27.70	2.90	50.3276	4.4026	15.5458	1.9765	75.0358	14.6906	10.2736
83	24.00	17.40	19.30	25.00	80.40	10.00	24.20	2.60	53.4293	4.1535	16.3109	1.9749	76.1942	12.0792	11.7266
84	22.80	17.40	18.87	24.20	81.60	10.30	27.30	2.60	55.9183	4.0261	18.1578	2.1219	74.1228	12.6078	13.2693
85	22.80	17.40	18.87	24.20	81.60	10.30	27.30	2.60	54.8322	4.0894	17.4506	2.0689	74.8846	12.8651	12.2502
86	16.70	13.60	15.96	20.10	132.00	8.50	32.40	12.30	70.5621	3.1668	38.8615	4.3882	34.6974	5.6234	59.6791
87	16.00	13.80	23.27	21.90	117.10	7.70	29.60	11.50	62.8252	3.8801	28.0270	3.4727	49.4548	6.5379	44.0073
88	21.60	14.20	33.71	24.40	51.20	8.20	20.10	4.20	39.0798	4.8722	10.4818	1.7444	71.0269	16.1996	12.7734
89	17.20	16.60	31.08	26.00	39.90	5.30	16.80	5.70	23.6987	6.3974	4.3532	1.2770	55.8063	38.3953	5.7984
90	16.90	17.80	26.21	26.10	26.80	6.60	10.70	3.10	18.1956	6.8000	3.2112	1.1612	49.7053	48.3404	1.9543
91	17.70	16.90	24.98	25.60	39.70	7.50	13.20	2.80	25.2056	5.9342	5.0882	1.2683	55.2186	36.7390	8.0425
92	20.10	16.10	32.37	26.00	50.90	6.80	22.50	5.00	33.2492	5.1289	7.8169	1.4361	63.2558	22.9762	13.7680
93	25.00	11.10	36.07	21.20	102.70	8.10	42.60	7.80	41.9957	3.4710	10.9045	1.1956	12.5287	72.4391	15.0322
94	20.80	13.30	33.75	23.50	136.50	8.90	59.60	7.30	60.1188	3.7104	26.4664	2.9284	51.2116	7.5852	41.2032
95	21.80	14.10	32.69	24.00	78.50	9.30	28.50	4.20	52.2977	4.5967	18.9665	2.7786	58.8620	7.5101	33.6279
96	21.30	13.10	33.55	23.00	100.90	8.60	42.60	6.00	65.3552	3.5313	31.2441	3.5057	48.4763	7.5641	43.9596
97	26.80	10.40	19.42	16.70	212.20	5.30	54.60	35.00	59.8639	3.7842	21.3631	2.6407	56.4264	11.0256	32.5479
98	12.20	15.70	15.92	21.70	96.40	8.40	32.60	4.00	37.5258	5.2910	11.1235	1.9400	62.7041	22.8926	14.4033
99	15.60	15.30	18.45	22.10	81.60	8.70	26.20	2.20	38.7340	5.1356	10.6945	16.1794	66.3025	21.7458	11.9516
100	14.90	12.00	18.00	18.10	172.10	7.60	46.00	16.00	49.5514	4.2336	20.6460	2.6001	54.2392	16.7486	29.0121
101	21.70	10.90	22.49	18.00	107.40	8.20	29.30	7.90	56.7955	3.8214	21.8054	2.5336	60.4418	8.5445	31.0136
102	18.10	9.80	20.94	16.50	162.10	6.60	44.00	16.50	66.0095	3.3488	29.4314	3.2616	52.5489	7.8186	39.6326
103	26.00	13.90	10.23	18.60	141.50	11.10	33.10	4.40	58.9256	4.0478	21.9912	2.6917	57.5869	6.9514	35.4616
104	20.30	11.90	27.82	20.20	117.70	9.50	43.30	14.00	60.9736	5.0267	24.3609	3.9560	62.8508	5.9202	31.2290
105	24.00	13.20	23.01	19.50	125.50	11.70	76.70	4.00	68.6225	4.5203	30.4024	4.7882	50.0826	4.9522	44.9652
106	18.70	13.80	31.51	23.10	85.10	7.80	36.80	5.80	64.4501	3.8672	30.0742	3.7672	46.1335	7.6386	46.2278
107	18.10	17.30	63.16	33.60	41.40	8.50	19.90	9.80	21.0110	6.8322	3.4329	1.1357	47.2968	49.4477	3.2525
108	24.30	8.80	32.29	17.40	126.60	6.40	49.80	13.80	109.4973	3.3459	15.1830	1.5893	52.3480	14.9790	32.6730
109	25.30	11.20	21.13	16.80	74.10	5.10	25.70	12.20	56.4698	3.6744	20.9408	2.4972	52.8088	15.7387	31.4525

110	15.30	16.00	18.98	23.30	62.90	7.80	21.40	3.70	34.9790	4.8433	8.2542	1.3552	67.2831	23.8506	8.8666
111	16.10	14.80	11.52	20.40	89.50	9.30	32.30	3.10	48.9771	4.8316	17.4341	2.6449	62.0281	14.1364	23.8355
112	21.10	17.40	51.33	31.50	21.00	7.30	9.60	2.30	25.4660	5.9606	4.9125	1.1644	52.1626	46.2078	1.6296
113	14.90	17.10	34.55	27.90	56.10	9.60	21.70	4.50	26.4907	6.0834	5.3450	1.3166	57.8588	35.4185	6.7227
114	14.00	17.00	56.18	32.80	49.60	11.10	29.30	2.60	28.2293	5.9108	5.3486	1.2449	54.9332	32.8062	12.2605
115	13.20	14.60	22.75	21.80	59.90	5.10	20.80	7.90	32.4516	5.2624	7.5840	1.4059	52.7585	34.2654	12.9760
116	16.10	18.50	64.93	36.40	38.80	7.90	19.00	6.50	20.9569	6.2349	3.7434	1.1132	46.3579	51.5839	2.0586
117	14.70	17.40	60.56	34.40	51.80	8.40	27.70	8.80	43.7975	4.3084	11.7163	1.6439	54.6908	13.1333	32.1759
118	21.80	17.30	43.46	30.00	75.80	10.70	45.10	10.10	46.8900	4.7377	17.1217	2.4722	66.8078	12.1478	21.0443
119	21.90	15.00	61.98	31.40	9.30	6.50	3.70	2.90	10.5879	3.7438	1.6769	0.5796	6.0056	93.8334	0.1609
120	12.20	13.50	57.33	28.90	38.90	5.80	9.70	14.20	22.1785	5.1484	3.6848	0.9253	44.3452	50.2520	5.4027
121	9.60	12.60	45.09	25.10	64.00	7.80	12.90	33.60	24.3281	4.9663	4.1747	0.9526	53.3267	38.9824	7.6908
122	18.70	16.70	43.04	28.20	14.20	6.60	2.50	6.70	12.9547	5.6380	2.0268	0.8357	24.7198	74.6908	0.5894
123	20.80	16.50	37.55	26.60	9.70	6.00	2.30	4.00	10.3902	2.8015	1.8650	0.5144	14.4624	84.2759	1.2617
124	20.80	16.90	37.32	26.90	12.30	7.00	5.70	4.30	11.7759	4.4711	1.8054	0.6636	6.2821	93.6551	0.0627
125	23.10	11.90	34.44	20.80	25.10	11.80	16.90	2.20	32.5367	5.6466	6.9950	1.4559	66.7124	28.4850	4.8025
126	14.50	17.90	45.35	30.80	92.00	10.00	54.10	13.20	45.4407	4.4753	13.0278	1.9382	55.1431	14.3899	30.4670
127	13.90	15.80	34.39	25.90	107.70	8.60	57.90	17.60	50.8915	4.7958	16.6590	2.7101	53.1692	12.2969	34.5339
128	19.30	16.50	49.94	30.30	28.10	8.60	13.90	2.80	13.8731	6.0388	2.2138	0.9282	17.8604	81.7437	0.3959
129	21.20	15.40	58.32	30.90	22.40	5.60	7.90	2.90	23.1053	6.0071	4.2831	1.1524	44.6561	49.0359	6.3080
130	19.30	14.10	53.46	28.30	40.40	6.60	15.50	3.90	33.3896	4.8071	7.2495	1.2838	62.7620	24.6640	12.5740
131	20.50	16.50	69.44	35.60	28.40	8.10	14.30	1.90	14.4128	5.5435	2.3404	0.8758	30.7260	67.7487	1.4896
132	20.60	15.30	64.29	32.90	22.50	5.70	10.00	2.70	16.1791	6.9369	2.5374	1.0632	32.8846	65.7014	1.4140
133	16.80	13.10	52.42	27.80	43.50	7.20	18.50	4.00	28.9782	5.6062	5.9224	1.2582	53.9528	34.3220	11.7252
134	17.40	18.50	33.99	27.80	31.10	5.30	12.40	4.30	23.4742	5.7566	4.1872	1.1320	48.5379	47.2881	4.1740
135	12.00	13.70	24.12	21.30	59.50	5.60	21.20	7.00	40.8773	4.5541	10.5735	1.6545	58.0743	17.2524	24.6734
136	17.50	13.50	34.01	23.00	70.50	7.80	29.20	5.40	51.4526	4.1727	18.6795	53.8623	2.4039	11.9894	34.1482
137	20.10	12.60	45.86	25.60	66.80	8.10	26.80	4.80	48.6472	4.3668	17.2561	2.2772	52.6259	27.8234	19.5507
138	23.40	11.00	47.17	24.50	72.10	5.00	18.70	12.70	29.8918	4.3541	6.5444	1.1358	58.6663	34.0486	7.2851
139	23.40	11.40	36.45	21.80	127.40	8.30	57.40	8.10	57.3844	3.3859	21.2602	2.2822	58.3204	8.9404	32.7392

140	25.50	13.90	35.38	23.40	52.40	11.00	26.30	5.20	42.5817	4.5523	12.0215	1.8057	71.2799	16.6723	12.0478
141	24.80	12.20	32.01	20.50	75.30	11.20	39.10	7.00	49.7499	5.2601	17.2801	2.8419	69.4008	10.2114	20.3877
142	24.70	11.10	27.20	18.10	108.20	11.90	62.50	3.20	51.1854	4.0871	18.7990	2.5797	56.1623	17.9571	25.8807
143	14.30	14.90	33.72	24.90	54.30	10.20	20.90	4.10	37.1101	4.6590	8.9545	1.4157	61.3745	19.5312	19.0943
144	17.80	14.90	28.60	24.20	79.20	10.10	31.30	8.50	46.8181	4.6019	14.7466	2.0656	66.9290	13.5698	19.5012
145	16.30	17.20	27.48	26.50	51.40	9.20	21.50	4.10	33.4014	5.2347	7.8956	1.4255	64.1118	23.3251	12.5631
146	18.00	17.50	26.47	26.60	44.40	7.70	19.40	2.60	28.7020	5.6026	5.9173	1.2833	59.7941	32.9840	7.2220
147	19.60	16.10	27.08	24.90	61.70	8.70	18.60	3.60	40.3317	4.5363	11.4231	1.7394	64.5388	14.4869	20.9744
148	22.00	14.80	31.79	24.70	99.20	9.00	38.70	6.30	56.5716	4.3931	21.3578	2.9958	57.6128	6.9700	35.4173
149	17.90	15.20	24.12	23.10	77.40	7.90	21.70	6.20	52.7159	4.6861	19.0135	2.8625	58.1855	9.3906	32.4239
150	14.40	13.90	19.00	20.80	131.90	7.80	30.40	12.60	63.2164	3.8325	28.9291	3.4308	50.0061	6.1526	43.8413
151	18.90	14.90	21.15	23.20	93.70	9.60	43.30	5.60	53.6880	4.5112	19.6599	2.6685	67.4245	8.4515	24.1241
152	18.40	15.80	23.37	25.00	90.00	10.90	44.30	3.60	42.9036	4.7992	12.9926	1.9458	66.0964	19.0566	14.8470
153	22.50	14.30	15.36	21.00	89.00	10.80	34.90	4.00	53.9829	4.0472	19.4675	2.4780	59.8800	8.8569	31.2631
154	25.20	14.10	14.85	19.80	95.40	11.00	35.90	4.60	57.2896	3.7657	20.3537	2.3980	63.6190	8.2059	28.1751
155	17.10	15.30	18.07	22.90	137.50	10.40	29.20	4.60	58.8062	3.9517	23.0209	2.8791	54.8802	7.8177	37.3022
156	17.70	16.70	23.74	25.80	95.90	10.00	23.00	3.90	48.5925	4.5996	17.1036	2.4040	64.2866	13.7519	21.9615
157	13.30	14.00	17.67	21.30	124.00	10.00	53.70	4.30	19.1712	6.6170	3.2901	1.1980	42.1962	56.0531	1.7506
158	28.20	14.90	15.52	21.80	64.00	10.10	12.40	3.50	43.4721	4.8466	15.7767	2.2701	69.2078	14.9129	15.8793
159	22.20	8.90	19.17	15.10	289.80	6.20	47.90	43.80	61.2756	3.2474	15.6338	2.9375	45.8714	6.7057	47.4229
160	18.30	12.30	8.85	16.00	299.50	7.50	99.70	9.10	70.4143	2.5002	39.6753	3.6365	39.2347	3.8018	56.9636
161	19.60	13.50	10.48	18.00	196.10	7.00	46.80	20.30	59.7626	3.4141	28.9147	3.3854	48.6656	6.0606	45.2738
162	26.40	10.10	18.83	15.70	185.00	5.50	32.10	30.60	55.9128	4.2094	21.3622	2.7524	58.0602	13.1255	28.8143
163	26.50	9.60	18.99	15.40	135.40	5.30	39.60	20.30	68.2951	3.7964	35.2366	4.1775	44.8974	9.9665	45.1361
164	25.50	11.20	18.44	17.40	269.60	5.20	75.60	40.90	71.3513	2.4499	32.0202	2.5446	40.4413	14.2857	45.2731
165	25.50	11.60	17.88	17.60	245.80	5.50	54.80	33.60	80.4203	1.6018	48.6672	3.7492	45.0301	4.7303	50.2396
166	25.50	11.10	18.78	17.10	220.10	5.80	50.10	29.20	74.5181	2.2430	4.8278	3.2806	39.0724	8.3376	52.5957
167	23.70	11.70	16.86	17.20	247.00	6.10	56.70	29.10	78.5665	1.9008	47.2904	4.1269	40.7866	7.8509	52.9635
168	22.40	12.10	15.46	17.10	256.80	6.30	59.20	28.10	78.1291	1.9946	47.3964	4.4594	39.1254	4.9032	55.9714
169	25.70	10.60	17.69	16.30	208.60	6.30	49.10	24.50	79.7011	1.9093	49.1606	4.4270	34.8618	3.5276	61.6106

170	24.70	11.10	16.56	16.60	237.70	6.90	55.00	24.00	77.7295	2.0030	47.4157	4.3848	30.2194	3.7237	67.1563
171	24.60	11.40	15.13	16.50	270.70	6.90	61.20	27.50	76.2608	2.0160	46.8689	4.2941	26.3611	2.6562	70.9827
172	24.70	11.50	22.12	18.50	115.40	5.80	31.50	13.60	82.0876	1.8050	51.6787	4.6188	31.5151	5.2108	63.2741
173	25.50	12.40	20.65	19.10	107.40	6.20	27.10	10.40	80.4066	2.3512	49.4301	4.9211	35.1600	3.2461	61.5939
174	26.80	10.60	20.82	17.00	92.00	8.00	21.60	6.50	70.4372	4.0109	35.4327	4.8578	48.1476	11.1117	40.7407
175	26.50	9.10	19.79	14.80	82.70	8.40	29.50	7.30	65.5958	4.2576	29.5701	4.1716	52.9597	11.5441	35.4962
176	25.30	10.60	20.25	16.10	90.50	4.30	30.20	16.40	69.7478	3.3592	37.8370	3.9782	44.5576	10.9619	44.4805
177	25.30	11.50	18.25	16.60	126.50	5.20	48.50	14.80	82.0113	2.2656	50.7028	4.6236	34.0543	4.7449	61.4323
178	26.00	11.10	16.89	15.90	125.60	5.20	44.50	17.10	76.3048	2.5084	45.4826	4.3691	34.8687	10.1592	54.9721
179	26.20	9.10	15.12	13.20	125.00	5.10	44.30	17.40	64.6036	3.4487	35.1105	3.8964	40.6652	14.5411	44.7936
180	21.60	15.10	41.84	25.80	14.70	8.60	8.10	4.60	21.0940	5.6787	3.5831	0.9933	51.4746	45.3172	3.2082
181	21.20	14.50	39.63	24.50	22.00	10.70	14.90	2.80	22.7405	5.8393	4.3192	1.0897	54.5361	41.1978	4.2660
182	20.70	14.70	42.61	25.60	28.40	10.20	18.20	6.20	27.5293	5.0678	5.2727	1.1141	61.5190	29.6088	8.8722
183	21.40	11.00	31.32	19.90	7.20	7.00	3.00	2.00	21.1971	6.4030	3.8358	1.1672	40.4076	56.8740	2.7184
184	19.30	16.50	44.84	28.40	13.90	6.10	4.40	6.00	11.5576	4.2186	1.8010	0.6282	15.4948	83.9816	0.5260
185	16.80	17.20	61.45	34.20	51.10	9.30	27.80	9.60	29.7671	5.2943	5.9604	1.2051	58.5241	28.2366	13.2393
186	15.20	17.30	61.22	34.40	50.90	8.30	26.80	8.80	41.1437	4.6197	10.3215	1.5506	57.1713	17.1695	25.6591
187	22.30	17.40	50.17	31.50	69.90	9.90	40.60	11.20	42.7165	4.6512	14.8786	2.2203	67.1465	13.5713	19.2822
188	20.70	17.30	46.45	30.90	79.50	9.90	45.60	11.20	48.6379	4.7807	17.2599	2.5802	62.9535	12.6660	24.3805
189	23.80	15.40	54.40	29.10	13.80	8.40	7.90	3.50	15.4846	6.0279	2.4316	0.9246	20.5867	78.7719	0.6415
190	24.70	11.50	49.80	24.10	20.10	11.20	14.30	3.10	22.3081	6.0539	3.9949	1.1254	50.7619	43.8812	5.3569
191	24.00	16.50	51.59	28.80	30.20	10.70	20.40	4.50	25.8156	5.1799	5.4159	1.1993	59.0358	37.5301	3.4341
192	24.80	15.80	41.57	26.00	61.20	11.60	44.60	6.20	35.1752	4.4000	9.6308	1.5580	58.0059	30.6631	11.3310
193	21.40	17.40	42.18	29.80	80.10	9.90	47.40	11.30	50.0428	4.7590	17.5697	2.4591	59.8393	13.3454	26.8153
194	19.10	14.90	34.09	25.10	97.70	8.60	34.30	16.30	53.6724	4.8819	19.1452	2.6167	56.8851	11.9792	31.1357
195	14.00	12.00	29.01	20.40	122.80	8.50	65.90	19.90	68.1258	4.6196	30.5008	4.2441	51.6713	7.0783	41.2504
196	12.30	13.90	31.84	23.10	97.70	9.10	54.00	13.50	48.3905	4.3210	16.8225	2.1094	50.5285	13.1827	36.2888
197	14.80	16.50	35.13	26.70	59.20	10.60	34.80	4.40	31.3753	5.4409	6.8134	1.3569	62.0400	26.7313	11.2287
198	18.20	19.00	45.47	32.10	38.40	9.90	22.00	1.90	22.8149	6.2091	4.3207	1.2052	57.8542	38.0205	4.2025
199	12.60	17.40	57.15	33.50	54.10	10.60	33.30	3.30	28.4395	5.4005	5.7185	1.2205	58.8720	30.7500	10.3781

200	12.90	17.60	47.70	31.10	75.90	9.30	42.60	11.40	41.4755	4.5298	10.6334	1.5741	56.5030	15.7159	27.7811
201	24.30	9.30	33.71	18.60	95.10	8.50	42.80	8.10	44.5805	3.3329	10.5240	1.1358	64.8457	14.7143	20.4400
202	18.30	13.70	31.20	23.00	94.30	8.10	40.80	6.20	66.2208	3.7110	31.6786	3.9142	44.9248	7.5767	47.5564
203	20.30	11.60	33.63	21.00	101.00	7.70	47.30	8.20	74.9900	2.6162	40.9183	3.9522	35.8322	8.4154	55.7524
204	23.70	8.70	34.82	18.40	97.70	9.20	52.70	6.40	43.0486	3.4038	10.5194	1.1692	66.3419	13.7340	19.9241
205	15.20	15.50	25.27	23.30	63.10	6.50	23.70	6.00	47.1117	4.9058	16.9340	2.3543	53.2492	17.6235	29.1272
206	23.80	11.60	40.76	23.10	95.60	7.20	37.40	11.20	57.1027	3.5154	19.1351	2.1178	50.6559	21.0804	28.2634
207	24.20	9.60	30.49	17.80	139.00	5.80	49.80	16.10	52.9456	3.6306	17.2819	1.9246	55.4244	15.2816	29.2940
208	26.30	9.30	21.69	16.30	131.40	9.10	26.20	7.90	55.0552	3.8322	18.4328	2.2597	57.6803	7.8766	34.4431
209	24.90	11.60	21.74	18.90	286.50	8.70	70.40	15.60	71.5753	2.9935	38.0743	3.7778	41.2212	3.8600	54.9187
210	25.00	9.70	23.85	17.30	289.30	8.80	63.90	18.10	59.9390	3.4808	23.0481	2.4507	52.9544	6.3960	40.6496
211	16.70	12.50	14.96	18.40	202.40	7.80	47.30	22.70	73.4439	3.1680	43.1280	4.7049	27.4011	3.1903	69.4086
212	25.00	10.40	19.47	17.10	367.40	5.50	64.00	61.30	64.3058	2.5486	34.8481	3.3482	40.1020	4.5421	55.3559

CONCLUSIONES FINALES

Los colibríes son un sistema adecuado para estudiar mecanismos de estructuración de comunidades, ya que la taxonomía de los linajes principales está bien descrita (McGuire *et al.* 2007, Graham *et al.* 2009), existen estudios filogeográficos recientes para distintos grupos de especies (Jiménez & Ornelas 2015, Ornelas *et al.* 2015, Hernández-Baños *et al.* 2020), habitan una gran diversidad de condiciones ambientales (Schuchmann 1999), pueden coexistir desde dos hasta más de 22 especies (Des Granges 1979, Arizmendi 2001), tienen una estrecha relación con los recursos de néctar a distintas escalas temporales y espaciales (Stiles 1981, Dalsgaard *et al.* 2011, Malpica & Ornelas 2014), y la variación de rasgos morfológicos del pico y de las alas son determinantes en su capacidad de vuelo y alimentación (Stiles 1981, 1985, Stiles *et al.* 2005). Los resultados obtenidos en esta tesis demuestran la importancia de la escala geográfica a la que se realiza un estudio para interpretar la importancia de los mecanismos implicados, ya que la naturaleza biológica de la atracción y repulsión filogenética dependen directamente de ésta (Webb *et al.* 2002).

A la escala local la dominancia, la territorialidad y la disponibilidad de recursos de néctar son factores determinantes en la estructuración de las comunidades de colibríes. El acceso al néctar de las plantas visitadas por los colibríes está mediado no solo por la cantidad de flores disponibles, sino por la jerarquía y la estrategia de forrajeo de los colibríes a escalas intra e interespecíficas (Feinsinger & Colwell 1978, Carpenter *et al.* 1993). La capacidad de los colibríes para evaluar y responder a los cambios en el ambiente es crucial, ya que estos factores no son estáticos ni en el tiempo ni en el espacio, y están sujetos a dinámicas locales de migración (latitudinal y/o altitudinal), densidad de individuos, y fenología de floración (Lyon 1976, Bennett *et al.* 2014). La competencia por el uso de los recursos de néctar ejerce una fuerza importante sobre el comportamiento de los colibríes, determinando las estrategias de forrajeo y los patrones de explotación del néctar, favoreciendo o afectando negativamente la coexistencia de los colibríes (Feinsinger 1976). Estas interacciones repercuten directamente en la permanencia y/o exclusión local de una especie dentro de la comunidad, lo que a su vez afecta a largo plazo la composición de las comunidades de colibríes.

El agrupamiento filogenético en la composición de especies de colibríes en México, donde el 86.21% de las especies que se distribuyen en el país pertenecen a las Abejas, a las Esmeraldas y a las Gemas de Montaña, es el resultado de procesos biogeográficos e históricos que operan a escalas temporales y espaciales grandes (Webb *et al.* 2002). Posterior a su origen en las tierras bajas de Sur América (Bleiweiss 1998), los colibríes actuales se diversificaron en dirección Norte y Sur colonizando las zonas templadas de ambos hemisferios (McGuire *et al.* 2014, Ornelas *et al.* 2014). A lo largo del proceso de diversificación, los colibríes muestran un gradiente de generalización tanto en la morfología, como en los patrones de interacción entre los clados y las plantas que visitan como recursos de néctar. Es así como las Esmeraldas y las Abejas, los clados más recientes que se han diversificado y/o originado en Norte América (McGuire *et al.* 2014, Ornelas *et al.* 2014, Licona-Vera & Ornelas 2017), y gracias a sus picos rectos cortos a intermedios, a sus alas cortas y a su tamaño corporal pequeño, se han adaptado a distintos ecosistemas, visitan una gran diversidad de recursos de néctar (Abrahamczyk & Kessler 2014), y presentan bajo conservadurismo de nicho. El patrón opuesto ocurre en los clados más antiguos de origen suramericano, como los Ermitaños, los Topacios y los Mangos, donde la morfología más especializada y un mayor conservadurismo de nicho, ha limitado su dispersión colonizando principalmente los ecosistemas más tropicales a lo largo del continente.

Los procesos locales y continentales descritos anteriormente contribuyeron en la estructuración de las comunidades de colibríes en México, donde los mecanismos principales fueron la competencia, el filtro ambiental y la historia biogeográfica. La estructura filogenética de las comunidades de colibríes en este país estuvo fuertemente relacionada con la estacionalidad climática en la precipitación y la temperatura, y con la cobertura vegetal. Según lo esperado, este patrón ambiental tomó mayor relevancia en el caso de las comunidades con agrupamiento filogenético, donde el filtro ambiental es extremo y grupos como las Abejas y las Esmeraldas pueden coexistir gracias a su tolerancia a climas áridos, y a sus morfologías y comportamientos generalistas (Graham *et al.* 2009, Rodríguez-Flores *et al.* 2019). En el caso de las comunidades con sobredispersión filogenética significativa, estas se ubicaron en ecosistemas tropicales y la coexistencia de especies pertenecientes a clados poco abundantes en México, con origen y morfologías variadas se debe al efecto de la competencia, donde las especies más cercanas en términos ecológicos son excluidas (Webb *et al.* 2002). En las comunidades con agrupamiento filogenético aleatorio, es evidente el papel de los procesos locales, donde la competencia intra e interespecífica por los recursos de néctar y los cambios en la composición originados por la migración latitudinal y altitudinal, toman mayor relevancia que la distancia filogenética entre las especies.

En el caso de los colibríes la morfología del pico, de las alas y el tamaño corporal son rasgos relevantes que limitan aspectos fundamentales en su ecología, como el acceso a las flores, las técnicas de forrajeo y la dominancia (Abrahamczyk & Kessler 2014, Maglianesi *et* *al.* 2014). En futuras aproximaciones, además de la inclusión de la información morfológica, se recomienda estimar los índices de diversidad filogenética, los cuales permiten establecer la dinámica de los patrones filogenéticos de las comunidades a lo largo de gradientes ambientales y espaciales (Webb *et al.* 2002, Graham *et al.* 2009). Combinar información filogenética con datos ecológicos obtenidos a nivel local es una estrategia para explorar la manera en la que los procesos históricos se acoplan con las dinámicas anuales a menor escala.

Con una aproximación diferente, los estudios filogeográficos y de genética de poblaciones son útiles para elucidar (1) los patrones contemporáneos que explican la subdivisión dentro de las especies o complejos de especies, y (2) explorar preguntas biogeográficas a nivel temporal y espacial que provean información sobre ensamble y diversificación biótica (Arbogast & Kenagy 2001, Ornelas *et al.* 2013). Al combinar información de estructura y diversidad filogenética, con información filogeográfica y morfológica a nivel comunitario será factible proponer preguntas de investigación más detalladas que profundicen el patrón encontrado en este trabajo. Por ejemplo, si el patrón de evolución y dispersión de los colibríes está conectado con la biogeografía de sus recursos de néctar (Licona-Vera & Ornelas 2017), sería interesante estimar la estructura y diversidad filogenética no solo de los colibríes sino de los recursos de néctar que usan, buscando patrones concordantes en los procesos de diferenciación morfológica, evolución y dispersión a lo largo del tiempo.

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