



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE CIENCIAS

**Estructuración y evolución morfológica de ensambles de colibríes y su
relación con la oportunidad ecológica en Norteamérica**

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:

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M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Comité de Posgrado en Ciencias Biológicas, celebrada el día **15 de agosto de 2022** se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la estudiante **PUGA CABALLERO AURA LIBERTAD** con número de cuenta **303090658** con la tesis titulada: **"Estructuración y evolución morfológica de ensamblajes de colibríes y su relación con la oportunidad ecológica en Norteamérica"**, realizada bajo la dirección del **DR. LUIS ANTONIO SÁNCHEZ GONZÁLEZ**:

Presidente: **DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA**
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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 22 de noviembre de 2022

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA



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Resumen en español

La evolución de las especies depende tanto de la generación de variación, dinámicas poblacionales así como de la influencia ambiental. Los factores ambientales son muy variados y abarcan desde condiciones climáticas, eventos catastróficos hasta cambios en la distribución de los recursos. Igualmente, las especies comparten con otras en tiempo y espacio entablando diferentes tipos de interacciones las cuales ejercen su propia influencia sobre la morfología de las especies. Todos estos factores promueven patrones filogenéticos y fenotípicos distintivos en los linajes que pueden ser analizados e interpretados dependiendo de su contexto geográfico. En el Capítulo 1 de la presente tesis, se buscó analizar dichos patrones en los ensambles de colibríes de Norteamérica para determinar qué factores y procesos han sido los más relevantes para este grupo en esta zona geográfica. Para esto, se utilizó una filogenia recortada de la familia Trochilidae, una matriz de 11 atributos morfológicos de estas aves y una matriz de presencias de las especies en las ecorregiones presentes en Norteamérica. Con estos datos se calcularon los valores de estructuración filogenética y fenotípica de los ensambles por ecorregión. Este análisis geográfico mostró que en las regiones de mayor latitud (región Neártica) la estructura filogenética es agrupada (es decir conformada por especies cercanamente emparentadas) mientras que la estructura fenotípica no es diferente al azar. En tanto que las regiones Transicional y Neotropical mayormente no muestran estructura filogenética ni fenotípica, exceptuando en dos ecorregiones neotropicales. Estos valores de estructuración están asociados con la riqueza de especies y la diversidad filogenética; lo que sugiere que el proceso de ensamblaje de las comunidades de colibríes de Norteamérica ha sido influenciado por filtrado de hábitat, competencia interespecífica y por interacciones mutualistas. Posteriormente, en el Capítulo 2 se analizó la influencia de tres condiciones de oportunidad ecológica (acceso a un nuevo espacio geográfico, ausencia de competidores e innovación evolutiva) en la evolución morfológica de los colibríes norteamericanos. Para esto, se calculó la disparidad de atributos a través del tiempo lo que mostró patrones de disparidad coincidentes con el acceso a un nuevo espacio geográfico. Por otra parte, el efecto de los competidores potenciales fue evaluado estimando los contrastes

independientes (disparidad fenotípica) y la diversidad de linajes a través del tiempo. Los resultados mostraron que el tamaño corporal es un atributo fundamental en los primeros procesos de reparto de nicho; mientras que la variación en la forma del pico y el ala son parte de un reparto secundario. Igualmente, se mostró que la presencia de competidores puede generar efectos de prioridad que limita tanto la diversificación fenotípica como taxonómica de linajes de más reciente arribo. Los colibríes norteamericanos presentan varios pulsos de radiación relacionados con diferentes condiciones de oportunidad ecológica. La evolución de los colibríes en el continente americano es una secuencia constante de pulsos de radiación, relacionados con el levantamiento de las cadenas montañosas, la llegada a América del Norte y la expansión a las regiones más frías a través de la facilitación y evolución del comportamiento migratorio.

Abstract

The evolution of species depends both on the generation of variation, population dynamics as well as environmental influence. Environmental factors are very varied and range from climatic conditions, catastrophic events to changes in the distribution of resources. Likewise, species share time and space with others, engaging in different types of interactions which exert their own influence on the morphology of the species. All these factors leave distinctive phylogenetic and phenotypic patterns in the lineages that can be analyzed and interpreted according to their geographical context. This study sought to analyze these patterns in North American hummingbird assemblages to determine which factors and processes have been the most relevant in the assembly of this group. For this, a trimmed phylogeny of the Trochilidae family, a matrix of 11 morphological attributes and a matrix of presences of the species in the ecoregions present in North America. With these data, the phylogenetic and phenotypic structuring values of the assemblages by ecoregion were calculated. This geographic analysis showed that in the higher latitude regions (Nearctic region) the phylogenetic structure is clustered while the phenotypic structure is not different from random. While in the Transitional and Neotropical regions there is mostly no phylogenetic or phenotypic structure, except in two neotropical ecoregions. These structuring values are associated with species richness and phylogenetic diversity; suggesting that the assembly process of North American hummingbird communities has been influenced by habitat filtering, interspecific competition, and mutualistic interactions. The influence of three ecological opportunity conditions (access to a new geographic space, subsequent absence of a promoter, and evolutionary innovation) on the morphological evolution of North American hummingbirds was analyzed. For this, the disparity of attributes over time was calculated, which showed patterns of disparity that coincided with access to a new geographic space. On the other hand, the effect of potential competitors was evaluated by estimating independent contrasts (phenotypic disparity) and lineage diversity over time. The results showed that body size is a fundamental attribute in the first processes of niche partitioning; while the variation in the shape of the bill and the wing are part of a secondary partitioning. Likewise, it is shown that the presence of

competitors can generate priority effects that limit both the phenotypic and taxonomic diversification of more recent arrival lineages. North American hummingbirds exhibit various radiation pulses related to different ecological opportunity conditions. The evolution of hummingbirds in the Americas is a constant sequence of radiation pulses, related to the uplift of mountain ranges, arrival in North America, and expansion to colder regions through behavioral facilitation and the evolution of migratory behavior.

Introducción General

Una comunidad natural consiste en un grupo de especies que habitan en mismo espacio y tiempo (Begon et al., 2006). La estructura de una comunidad está determinada por la riqueza de especies y por la abundancia de individuos que aportan cada una de estas. Al proceso en el que se establecen las especies que formaran parte de la comunidad se le conoce como ensamblaje. Este proceso puede ser muy complejo y está influenciado por varios factores que operan a diferentes escalas espaciales y temporales (Emerson & Gillespie, 2008; Cavender-Bares et al., 2009). Primero, la historia biogeográfica y las condiciones climáticas operan para determinar la comunidad regional, a partir del cual se ensamblarán los conjuntos de especies que cohabitarán en un determinado espacio geográfico (Diamond, 1975; Leibold, 1998; Webb eta al., 2002). Posteriormente, la interacción de diferentes fuerzas, como la abundancia y diversidad de recursos y las distintas interacciones interespecificas, pueden producir diferentes combinaciones de especies a partir de la composición regional (Wehier et al., 1998; Kiers et al., 2010; Pontarp & Petchey, 2016). Con el paso del tiempo, estas fuerzas pueden influenciar la evolución fenotípica de cada una de las especies (Agrawal, 2007), además de generar cohesión dentro la comunidad, lo que le permite responder a diferentes eventos que potencialmente pueden modificar su estructura, como pueden ser la invasión por nuevas especies, disturbios o extinción (Diamond, 1975; Elmqvist, 2003; Losos & Mahler, 2010).

Composición regional

Las condiciones climáticas del espacio geográfico (ecológico) y la historia biogeográfica (evolución) de los linajes (Gaston, 2000; Olson et al., 2001) son de los principales factores que impactan la composición de las comunidades a escala regional. Estudios de biodiversidad a escala global sugieren que los patrones de riqueza y recambio de especies pueden ser explicados mayormente por variables climáticas como precipitación, temperatura (Kreft & Jetz, 2007). Otro de los patrones más reconocidos es el gradiente latitudinal de biodiversidad (LDG; por sus siglas en inglés). Este patrón ha motivado un gran número de estudios usando diferentes grupos taxonómicos, y de los que

han surgido diferentes hipótesis que buscan explicar este patrón. Estas hipótesis pueden agruparse en tres principales grupos: (1) hipótesis ecológica, (2) hipótesis histórica y (3) hipótesis evolutiva. Sin embargo, estos tres grupos de hipótesis coinciden en que las condiciones climáticas, específicamente las altas temperaturas y la estabilidad climática de la región tropical han influido en los picos de biodiversidad de estas regiones (Mittelbach & McGill, 2019).

Además de los factores climáticos, la historia biogeográfica de los linajes es un factor determinante de la composición de especies a nivel regional, la cual está disponible para el ensamblaje de las comunidades naturales (Diamond, 1975; Mazel et al., 2017a). Los mamíferos son un excelente ejemplo, puesto que en distintos estudios se ha observado que el ensamblaje de mamíferos marsupiales de Australia es muy similar fenotípica y ecológicamente (e.g. forma de cráneo en linajes carnívoros) a los ensamblajes de mamíferos placentarios de otros continentes (Goswami et al., 2011; Mazel et al., 2017b). La distancia filogenética de los marsupiales australianos con respecto a los mamíferos placentarios de otros continentes es explicada en parte, por los movimientos tectónicos de Australia con respecto al resto de los continentes (Mazel et al., 2017a). De manera similar, Jønsson et al. (2015) describieron que las aves paseriformes en cuatro regiones biogeográficas presentaban, durante sus eventos de dispersión, un patrón biogeográfico en el que el primer linaje en arribar a una región se diversificó aceleradamente, construyendo la diversificación morfológica y taxonómica de los linajes subsecuentes, por lo que la composición regional cambiará drásticamente entre regiones.

Factores como el filtro de hábitat y las interacciones interespecíficas actúan sobre el proceso de estructuración de las comunidades a diferentes escalas. Estos factores pueden producir patrones fenotípicos y filogenéticos contrastantes en las comunidades, ya sea a través de estructuras agrupadas o sobredispersas (Webb et al., 2002; Cadotte y Tucker, 2017).

Filtro de hábitat

El filtro de hábitat hace referencia a la restricción que las condiciones ambientales ejercen sobre las especies, generando que solo algunas especies sean capaces de subsistir en dichas condiciones ecológicas (Webb et al., 2002). Como consecuencia de dicha restricción las especies que forman parte de la comunidad presentan adaptaciones a las condiciones ambientales. Las especies cercanamente emparentadas pueden presentar mismas o adaptaciones similares generando atracción fenotípica (Webb et al., 2002; Emerson & Gillespie, 2008). Esta tendencia fenotípica puede tener una repercusión en la misma diversidad genética de la comunidad entera, dependiendo si la evolución de los caracteres relacionadas ha sido conservada o convergente (Emerson & Gillespie, 2008). En el caso de que los caracteres con relevancia ecológica hayan tenido una evolución conservada (conservadurismo de nicho), el filtro de hábitat selecciona conjuntamente un fenotipo y un genotipo (Webb et al., 2002; Emerson & Gillespie, 2008; Cadotte & Tucker, 2017); en el caso de que los caracteres ecológicos sean convergentes, el filtrado de hábitat solo reducirá la diversidad fenotípica pero no la genética (Emerson & Gillespie, 2008; Cadotte & Tucker, 2017). Entonces el resultado del filtrado de hábitat es la coexistencia de especies muy similares tanto fenotípica como ecológicamente. Esto puede dar lugar a un reparto de nicho ecológico (niche filling) mediante la variación de atributos “secundarios” ecológicamente relevantes, a través del proceso de desplazamiento de carácter, el cual les permite diversificarse (ver Price et al., 2014).

Las comunidades que se forman en los gradientes altitudinales son un ejemplo de filtrado de hábitat. La constricción de condiciones ambientales como la disminución de la temperatura y disponibilidad de oxígeno a lo largo del gradiente implican retos fisiológicos para las especies que explotan estos hábitats, generando fuerte filtro biológico. Los colibríes (Apodiformes: Trochilidae) son un grupo de aves con vuelo de un alto requerimiento energético, sin embargo, son muy diversos en altas elevaciones en todo el continente. Un estudio realizado por Altshuler et al. (2004) sobre los cambios morfológicos y de vuelo en 49 especies de colibríes andinos a lo largo del gradiente altitudinal encontró que modificaciones en la amplitud del área total del ala, son parte de los

mecanismos que presentan los colibríes para mejorar su desempeño aerodinámico a altas elevaciones evitando aumentar los requerimientos energéticos y de oxigenación. Estudios filogenéticos, morfológicos y ecológicos de la familia Trochilidae han descrito que los ensamblajes de colibríes andinos son más similares morfológicamente entre sí que con respecto a la composición regional (Weinstein et al., 2014). Igualmente, dichos ensamblajes están compuestos por especies cercanamente relacionadas, pertenecientes a los clados de los Brillantes y las Coquetas (Altshuler, 2006; McGuire et al., 2014), cuyos tiempos de diversificación están relacionados con la formación de la cordillera de los Andes (McGuire et al., 2014). Complementariamente, Weinstein et al. (2017) observaron que las comunidades de colibríes en los Andes están formadas por especies con relaciones filogenéticas intermedias, en la que la tolerancia es un atributo conservado, pero que la competencia interespecífica limita la coexistencia de especies estrechamente relacionadas.

Interacciones interspecíficas

Además del filtrado de hábitat, las interacciones interespecíficas son factores determinantes para la prevalencia de una especie dentro de una comunidad (Diamond, 1975; Webb et al., 2002; Kiers et al., 2010). Una especie puede establecer distintos tipos de relaciones con otras especies, en los que se vea afectada o beneficiada en diferente proporción (Pontarp & Petchey, 2016). El tipo y la intensidad de las interacciones son a la vez determinados por el fenotipo y contribuyen a moldearlo (Ricklefs & Travis, 1980).

La competencia interespecífica se presenta cuando dos especies comparten el uso de un recurso limitado y la población de una de estas resulta disminuida como consecuencia de esta interacción (Mittelbach & McGill, 2019). Especies hermanas o cercanas filogenéticamente tienden a tener requerimientos muy similares, en especial si sus tiempos de divergencia son recientes por lo que la interacción puede considerarse intensa (Webb et al., 2002). Este tipo de interacciones pueden presentar un patrón de repulsión fenotípica, resultando en exclusión competitiva en la que una de las especies competidoras es expulsada del espacio geográfico (Webb et al., 2002; Cavender-Bares et

al., 2009). En el noroeste de México López-Segoviano et al., (2018) encontraron que las especies de colibríes de una misma comunidad competían entre sí por los parches de flores con mayor cantidad de néctar. El resultado de dicha interacción es determinado por el tamaño corporal, favoreciendo a las especies con los tamaños corporales más grandes. A escala local, la exclusión competitiva puede generar un patrón de “tablero de damas” (checkerboard) en la presencia de especies y de sobredispersión fenotípica, puesto que solo una especie con determinado fenotipo ocupa un determinado espacio (Diamond 1975; Webb et al., 2002). La sobredispersión fenotípica puede ocurrir a través de dos mecanismos: (1) repulsión fenotípica, y (2) desplazamiento de carácter. La repulsión fenotípica se presenta cuando especies coexistentes poseen el mismo fenotipo para aprovechar los mismos recursos por los cuales competirán, el cual da como resultado la exclusión de una de las especies de la comunidad (Webb et al., 2002; Cavender-Bares et al., 2009). El desplazamiento de carácter se presenta cuando una o ambas especies competidoras usan extremos diferentes de la varianza de un carácter para liberarse del estrés competitivo por un recurso (Brown & Wilson, 1956; ver Losos & Mahler, 2010).

Por otro lado, las interacciones competitivas no se limitan a ocurrir entre especies estrechamente relacionadas ni con una alta similitud morfológica; especies con relaciones filogenéticas muy distantes que coinciden en al menos un atributo funcional pueden competir intensamente. Igualmente, la competencia entre especies no relacionadas tiene la capacidad de moldear la morfología de las especies involucradas (Wilcox et al., 2018), ya que igualmente el desplazamiento de carácter permitirá liberar a las especies de un estrés competitivo. Otro mecanismo entre especies competidoras para favorecer su coexistencia consiste en la reducción de su abundancia poblacional, mudando el estrés competitivo al plano intraespecífico (Diamond, 1975; Chesson, 2000).

Respuesta fenotípica

Como se mencionó anteriormente, las interacciones interespecíficas y las condiciones abióticas tienen la capacidad de influir en la morfología de las especies, especialmente si las especies coexisten por un largo periodo (Agrawal, 2007). Si la coexistencia es prolongada, las relaciones entre especies pueden reforzarse e intensificarse, acompañadas de evolución fenotípica y diversificación de los linajes (Agrawal, 2007; Cavender-Bares, 2009). Dichos procesos a su vez dependen de la capacidad genotípica de las especies para responder fenotípicamente a las presiones externas. Primero, la mutación genética es la fuerza evolutiva que puede producir la variedad de fenotipos que responderán a las presiones externas. Sin embargo, la naturaleza azarosa de la mutación puede complicar que la especie presente un fenotipo adecuado a eventuales cambios en el ambiente (Futuyma, 2005). Un mecanismo que permite a las especies responder a los cambios ambientales casi inmediatamente es la plasticidad fenotípica e incluye la plasticidad del desarrollo y la flexibilidad fenotípica (West- Eberhard, 2005; Moczek et al., 2011). La plasticidad de desarrollo es la capacidad de un genotipo para alterar sus procesos de desarrollo y resultados fenotípicos en respuesta a diferentes condiciones ambientales, mientras que la flexibilidad fenotípica son los cambios reversibles en un mismo individuo (West- Eberhard, 2005). El impacto evolutivo de la respuesta plástica depende de si genera novedades evolutivas que puedan fijarse en la población (West- Eberhard, 2005; Moczek et al., 2011).

Otros procesos pueden tener repercusión en la evolución fenotípica de los linajes, como la deriva génica, la cual consiste en la modificación de la proporción de alelos (y posiblemente fenotípica) dentro de una población que es generada por azar. Procesos de deriva génica, como el “efecto de cuello de botella” o “efecto fundador” pueden reducir la diversidad genética y fenotípica y así eliminar respuestas adaptativas a condiciones ambientales; también pueden fijar rápidamente cualquier adaptación que llegue a presentarse en los individuos de la población (Sax et al., 2007). Por otra parte, las especies también pueden presentar mecanismos demográficos que disminuyen el estrés de algunas interacciones interespecíficas, como la depredación y la competencia (Diamond 1975; Chesson, 2000). Estos mecanismos consisten en disminuir la diferencia de adecuación con

otras especies (ecualización) competidoras y aumentar la intensidad de competencia intraespecífica (estabilización) a través de fluctuaciones en la densidad poblacional (Chesson, 2000). La producción de variación fenotípica (mutación y plasticidad) y las respuestas demográficas pueden tener implicaciones a largo plazo en las especies puesto que pueden generar divergencia poblacional y, eventualmente, a la diferenciación de linajes (Chesson, 2000; Agrawal, 2001; Ghalambor et al., 2007).

Es claro que las condiciones abióticas y bióticas por las que se encuentra rodeada una especie son la manifestación de la selección natural, la cual genera cambios en la distribución fenotípica de la especie y a su vez las interacciones de la especie con su ambiente se verán afectadas (Agrawal, 2007). La selección natural puede tanto moldear la evolución fenotípica de un linaje como aumentar el número de linajes a través del proceso de especiación (Futuyma, 2005). El tipo de especiación que resulta más relevante para el proceso de estructuración de comunidades es la especiación simpátrida, puesto que ocurre dentro del mismo espacio (Stroud & Losos, 2016). El grado de heterogeneidad en la distribución de los recursos y la existencia de zonas de intensificación de las interacciones interespecíficas generan que los individuos de una población no se encuentren bajo las mismas presiones ecológicas, lo que puede resultar en selección disruptiva, generando divergencia entre las poblaciones (Oyama, 2009; Losos & Mahler, 2010). En el proceso de especiación simpátrida, la selección sexual desempeña un papel importante, puesto que refuerza y amplía la diferenciación de las poblaciones (Schluter, 2000). Durante el aislamiento precigótico, la heterogeneidad de recursos y de interacciones genera diferentes probabilidades de cópula entre la población reforzando la divergencia ecológica; igualmente, la divergencia se acentúa si los atributos bajo selección natural están relacionados con las preferencias de pareja. En el caso del aislamiento post-cigótico, se amplía la divergencia al no favorecer al híbrido o fenotipo intermedio (Schluter, 2000). El proceso de especiación simpátrida puede dar lugar a la diversificación ecológica (especiación ecológica) dentro de un mismo linaje, generando una mayor riqueza fenotípica y de especies dentro de una misma comunidad. Esta diversificación ecológica puede dar lugar a patrones de especiación excepcionales, como la radiación adaptativa (Stroud & Losos, 2016).

Las radiaciones adaptativas son diversificaciones relativamente rápidas a partir de un ancestro común que resultan en varias especies que presentan una amplia divergencia ecológica (Glor, 2010; Losos & Mahler, 2010; Welborn & Langerhans, 2015). Jønsson et al. (2012) describieron la radiación adaptativa de Vangidae, una familia de aves de Madagascar. Esta familia monofilética, presenta dos incrementos en la tasa de diversificación morfológica y de especies en dos eventos separados por ~15 millones de años de diferencia: (1) durante la colonización en el Oligoceno Tardío, y (2) durante el Mioceno Tardío. El primer incremento de diversificación generó diversidad en el tamaño corporal entre linajes ecomorfológicamente similares que se distribuyeron en diferentes hábitats a lo largo de Madagascar. Durante el segundo evento, el incremento en la variación de la forma del pico y de estrategias de forrajeo ampliaron la diversidad ecomorfológica. La radiación de los vangas permite ejemplificar varios aspectos del concepto de oportunidad ecológica. Varios autores han propuesto que un linaje puede encontrar oportunidad ecológica bajo diferentes circunstancias, como: (1) acceso a un nuevo espacio geográfico, (2) ausencia de especies antagonistas, (3) innovación evolutiva para el acceso a nuevos recursos (Schluter, 2000). En el caso de los vangas, los dos eventos de aumento en la tasa de diversificación empatan con estos tres criterios de oportunidad ecológica. Durante la colonización de Madagascar, Vangidae se encontró con un nuevo espacio geográfico con probable ausencia de competidores; el segundo incremento fue posible a través de la innovación evolutiva que consistió en procesos de desplazamiento de carácter en cuanto a la forma de pico y así se llevaron a cabo nuevas estrategias de forrajeo que liberaron el estrés de competencia con otras poblaciones. Aunque durante la radiación de los vangas, más de una circunstancia se dio para generar oportunidad ecológica, es el acceso a un nuevo espacio geográfico, (e.g. colonización de islas) el que brinda un aumento abrupto de oportunidad ecológica. Sin embargo, es importante destacar que por sí misma la oportunidad ecológica no es capaz de generar acelerados procesos de diversificación en un linaje, es igual de relevante la capacidad de los linajes de generar respuestas adaptativas y diversificar ecológicamente en los nuevos espacios geográficos (ver Dugo-Cota et al., 2019). Los ejemplos clásicos de radiación adaptativa se han

descrito en ambientes restringidos como islas grandes, archipiélagos y lagos, aunque eso no implica que no tengan lugar en sistemas continentales. Las radiaciones adaptativas de grupos de aves que se han descrito en sistemas continentales están ligadas directa e indirectamente a la formación de cadenas montañosas (Claramunt, 2010; McGuire et al., 2014; Price et al., 2014). Particularmente, en la familia Trochilidae, una parte importante de su diversidad (~140 especies) en Sudamérica está ligada a la formación de la cordillera de los Andes, lo que dio acceso a nuevos espacios geográficos. Aunque en Norte América la riqueza de especies de colibríes es notablemente menor, la tasa de especiación es acelerada, lo que sugiere que puede ser un caso de radiación adaptativa (McGuire et al., 2014).

Resistencia conjunta

Conforme se ensambla una comunidad y sus elementos bióticos evolucionan y diversifican, las poblaciones se vuelven más estables, y la comunidad se vuelve “resistente” a la incorporación de nuevos elementos (Glor, 2010; Rowsey et al, 2018). El orden de incorporación de las especies a la comunidad facilitará o complicará la llegada y establecimiento de nuevas especies, lo que se le conoce como efecto de incumbencia o prioridad (Fukami, 2015). Este efecto puede ocurrir a diferentes escalas. En comunidades de aves de bosques templados de Norte América, la estructura de la comunidad de especies residentes y el orden de llegada de las especies migratorias influye en la estructura filogenética de la comunidad invernal, lo cual genera que aun en condiciones similares se puedan formar comunidades distintas Klingbeil y Willing (2016). Una posible consecuencia del efecto de prioridad consiste que los nuevos linajes en la comunidad tienen menores probabilidades de diversificar aun después de establecerse (Rowsey et al., 2018; Jønsson et al. 2015).

Familia Trochilidae

La familia Trochilidae (colibríes) es una familia muy diversa con presencia en la mayoría de los tipos de hábitats y climas a lo largo del continente (Bleiweiss, 1998; Altshuler & Dudley, 2002; Stiles, 2008;

Abrahamczyk & Kessler, 2015). Debido a su alta especialización en la alimentación nectarívora, los colibríes contribuyen significativamente en el proceso de polinización de aproximadamente 1,200 especies de plantas, así como en los procesos evolutivos que han moldeado la morfología y sistemas reproductivos de sus flores (Rodríguez-Flores et al., 2019). A su vez, esta variedad de morfologías permite que las especies de colibríes puedan coexistir, repartiéndose el espacio ecológico de una localidad y formar ensamblajes complejos (Rodríguez-Flores y Arizmendi, 2016).

Como se ha mencionado anteriormente, los ensamblajes de colibríes son influenciados por diferentes factores, como el filtrado de hábitat, mutualismo y la competencia interespecífica (Martin & Ghalambor, 2014; Rodríguez-Flores & Arizmendi, 2016, Bribiesca et al. 2019). Norte América está habitada por pocos clados de colibríes, Abejas y Gemas de Montaña, cuya llegada es relativamente reciente. Estos clados presentan tasas de diversificación aceleradas. La amplia diversidad morfológica y la amplia distribución ecológica sugieren que estos taxones pueden considerarse como una radiación adaptativa (McGuire et al., 2014; Rodríguez-Flores et al., 2019).

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Objetivo general

Analizar como las diferentes fuentes de oportunidad ecológica (llegada a un nuevo espacio geográfico, ausencia de competidores y el desarrollo de innovaciones evolutivas) han influido en la evolución morfológica y formación de los ensamblajes de colibríes en Norteamérica.

Para poder cumplir con el objetivo general, se le subdividirá en dos partes:

Objetivos particulares

Estructuración morfológica de ensamblajes de colibríes en Norteamérica

1. Describir el reparto del espacio morfológico-ecológico de los ensamblajes de colibríes en distintas ecorregiones.
2. Determinar la estructuración morfológica y filogenética de los ensamblajes de colibríes para las temporadas de verano e invierno.
3. Contrastar los patrones de estructuración morfológica y filogenética entre las temporadas de verano y de invierno.

Evolución morfológica y oportunidad ecológica de colibríes en Norteamérica

4. Analizar el espacio morfológico ocupado por cada clado principal presente en la región.
5. Analizar la evolución del espacio morfológico de colibríes a través del tiempo midiendo la disparidad fenotípica de los clados Abejas y Gemas de Montaña.
6. Comparar la variación morfológica (disparidad y contrastes independientes) con posibles momentos de oportunidad ecológica.
7. Describir el proceso de formación de ensamblajes de colibríes integrando la información filogenética, fenotípica y la oportunidad ecológica.

Hipótesis

El proceso de estructuración de los ensamblajes de colibríes norteamericanos ha sido influenciado por eventos de oportunidad ecológica que han permitido incrementos de diversidad taxonómica y morfológica. Igualmente, el filtrado de hábitat y la competencia interespecífica entre miembros de la misma familia, han dado lugar al reparto del espacio ecológico a través de la divergencia morfológica.

Por lo que se espera que:

- 1) La estructuración filogenética y fenotípica de los ensamblajes de colibríes tenderán a presentar patrones de agrupamiento hacia la región Neártica, mientras que hacia la región Neotropical los ensamblajes presentarán patrones de sobredispersión.
- 2) Los movimientos migratorios no modificarán los patrones de estructuración en las regiones Neotropical y Transicional, puesto que las especies migratorias tienden a evitar especies cercanamente relacionadas.
- 3) Los principales clados de colibríes presentes en Norteamérica (Abejas, Gemas de Montaña y Esmeraldas) posean espacios morfológicos poco sobrelapados entre sí.
- 4) La estructuración fenotípica y filogenética de los ensambles presenten un patrón de sobredispersión en ambas temporadas.
- 5) El clado formado por Abejas y Gemas de Montaña presentarán una amplia divergencia morfológica inicial que se irá reduciendo con la acumulación de especies en la región.

Para cumplir los siete objetivos particulares planteados y responder a la pregunta de investigación, el trabajo se dividió en dos capítulos. En el Capítulo 1 se abordaron los objetivos de 1 a 3. Se buscó determinar si los ensambles de colibríes presentan patrones filogenéticos y fenotípicos a escala biogeográfica (Neártica, Transicional y Neotropical) y de 105 ecorregiones a lo largo de Norteamérica. Para esto se consideraron un árbol filogenético molecular de colibríes y 11 atributos morfológicos que se utilizaron para calcular los valores de estructuración filogenética, distancia media entre parejas (MPD, por sus siglas en inglés) y distancia media entre parientes más cercanos (MNTD); así como

los valores de estructuración fenotípica (pMPD y pMNTD). Dado que algunas especies son migratorias, también se consideraron por separado los ensamblajes en temporada reproductiva (breeding) y temporada invernal (wintering) y realizó una prueba *t-pareada* para determinar si existen diferencias entre estaciones. Posteriormente, se realizaron modelos lineales (LM) para determinar la relación de los patrones de estructura filogenética y fenotípica con la riqueza de especies, la diversidad filogenética y la proporción de especies en clados con alta tasa de diversificación. Los resultados mostraron un patrón de gradiente geográfico latitudinal en la estructura filogenética y fenotípica, las cuales variaron desde una estructura agrupada en el Neártico y algunas ecorregiones Transicionales, ensamblajes aleatorios en la región Transicional y en la mayoría de las ecorregiones neotropicales, hasta patrones de sobredispersión en dos ecorregiones neotropicales. Los ensamblajes invernales mostraron cambios significativos en la estructura filogenética con respecto a los ensamblajes de la época reproductiva en las regiones Transición y Neotropical, pero mostró un cambio significativo en la estructura fenotípica en las ecorregiones Neárticas. Por su parte los LM mostraron que la riqueza de especies y la diversidad filogenética tienen asociaciones negativas y positivas con las medidas de estructura filogenética y fenotípica en ambas temporadas. Esto sugiere que el proceso de ensamblaje de las comunidades de colibríes de Norteamérica ha sido influenciado por filtrado de hábitat, competencia interespecífica y por interacciones mutualistas. Esto se encuentra publicado en el artículo "From clustering to overdispersion: a north to south gradient in the patterns of phylogenetic structure in North American hummingbird assemblages", en la revista indizada *Organisms Diversity & Evolution*.

Los objetivos particulares 4 a 7 se abordaron en el Capítulo 2, donde se analizó la influencia que tres condiciones para la oportunidad ecológica (acceso a un nuevo espacio geográfico, ausencia de competidores e innovación evolutiva) pudieron haber tenido en la evolución morfológica de los colibríes norteamericanos. Para esto se utilizaron un árbol filogenético molecular de colibríes y 11 rasgos morfológicos con los que se realizó un análisis filogenético de componentes principales (PPCA; por sus siglas en inglés). Con los cuatro ejes principales (PC1-PC4) se construyeron gráficos

de disparidad a través del tiempo (DTT; por sus siglas en el inglés) para inspeccionar la evolución de los rasgos morfológicos. Para evaluar el efecto de los competidores potenciales, se estimó la diversidad de linajes a través del tiempo y los contrastes independientes estandarizados (IC) y ese evaluó su relación con la tasa de evolución morfológica a través de modelos de regresión. Los resultados de este estudio mostraron que el clado Abejas y el clado de Gemas de Montaña ocupan espacios morfológicos relativamente bien diferenciados en cuanto a tamaño corporal, pero las especies pertenecientes a los clados Esmeraldas y Ermitaños ocuparon una amplia gama de tamaños corporales. En cuanto a los rasgos del pico se mostró que todos los clados superpusieron en el rango entre tamaño corporal intermedio y pequeño, y de picos más rectos. Sin embargo, el clado de Ermitaños ocupa, en su mayoría el espacio de los picos curvos y más largos. Mientras que los resultados de la forma del ala indican que las especies migratorias tienden a tener una forma más ancha. Los gráficos de disparidad sugieren que el tamaño del cuerpo es un rasgo conservado en el clado Abejas +Gemas de Montaña, y que la forma del pico y las alas son rasgos altamente lábiles. Por otro lado, los cambios en la disparidad de los rasgos del pico y la forma del ala cambiaron en coincidencia con varias invasiones de Esmeralda. Los modelos de regresión indican que la diversidad de linajes está relacionada con el aumento del tamaño corporal, las características del pico, la longitud de los tarsos y la variación de la forma del ala. Esto forma parte del manuscrito "Ecological opportunity as a promoter of morphological evolution in a likely North American hummingbird species radiation in North America", mismo que ha sido enviado a la revista indizada Journal of Evolutionary Biology.

Capítulo 1:(Artículo requisito) From clustering to overdispersion: a north to south gradient in the patterns of phylogenetic structure in North American hummingbird assemblages



From clustering to overdispersion: a north to south gradient in the patterns of phylogenetic structure in North American hummingbird assemblages

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Abstract

Hummingbirds are a highly specialized bird group whose species assemblages may show differential patterns of phylogenetic and phenotypic diversification, largely driven by ecological and geographical factors, as well as by mutualistic interactions with plants. Here, based on a molecular phylogenetic tree of hummingbirds and 11 morphological traits, we estimated phylogenetic and phenotypic structure at the scale of biogeographic (Nearctic, Transitional, and Neotropical) and 105 ecoregions across North America. Since some species are migratory, we discriminated between breeding and winter species assemblages and performed a paired t test to determine if there are significant differences in the assemblages' structure between regions and seasons. We also performed linear models (LM) to determine the relationship of phylogenetic and phenotypic structure patterns with species richness, phylogenetic diversity, and proportion of species in clades with high diversification rates. Phylogenetic and phenotypic structure results ranged from clustered in Nearctic and some Transition ecoregions, to random in Transition and most Neotropical ecoregions, to overdispersion in two Neotropical ecoregions. Winter assemblages showed significant shifts in phylogenetic or phenotypic structure from resident assemblages in Transition and Neotropical ecoregions but showed a significant shift in phenotypic structure in Nearctic ecoregions. LMs showed that species richness and phylogenetic diversity presented negative and positive relationships with phylogenetic and phenotypic structure measures in both seasons. Our results suggest that the assembly process of North American hummingbird communities has been influenced by filtering, competition, and mutualism processes largely determined by the species pool available at different biogeographic regions.

Keywords Assembly process · Habitat filtering · Interspecific competition · Migratory behavior · Nectarivores · Trochilidae

Introduction

The phylogenetic structure of species assemblages is the result of a highly complex process influenced by factors including lineage history, geographic and climatic conditions, biotic interactions, and historical contingency (Emerson & Gillespie, 2008; Cavender-Bares et al., 2009; Fukami, 2015; Segar et al., 2020). These factors may act individually, additively, or interactively over different spatial and temporal scales. For an example, interspecific interactions like competition operate at local scales and over relatively short periods, while climatic conditions may operate at regional scales over long time periods. Each of these factors (or combinations of factors) can lead to overdispersed, clustered, or random patterns in the phylogenetic and phenotypic structure of natural communities (Cavender-Bares et al., 2009; Pontarp & Petchey, 2016;

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Cadotte & Tucker, 2017); put another way, the same or highly similar assembly patterns can be the product of different factors. It is therefore necessary to evaluate phylogenetic and phenotypic data together to better discriminate between the significance of the factors involved in the evolution of natural communities (Cavender-Bares et al., 2009; Emerson & Gillespie, 2008; Webb et al., 2002).

Clustering patterns refer to the coexistence of species that are phylogenetically closely related or, phenotypically similar to each other (Cadotte & Tucker, 2017; Webb et al., 2002). Habitat filtering and adaptive radiations have been described as the main factors that generate clustering patterns (Cadotte & Tucker, 2017; Emerson & Gillespie, 2008). In habitat filtering, restrictions imposed by environmental conditions may generate differential presence of particular traits in local assemblages with respect to the regional species pool (Cadotte & Tucker, 2017). In adaptive radiations, niche availability may promote rapid divergence of an ancestral taxon into several derived ecologically specialized species (Schluter, 2000). Interspecific interactions can also generate clustering patterns, competition may allow a given phenotype to exclude similar phenotypes due to differences in competitive ability (Mayfield & Levine, 2010), while mutualism may favor the establishment and success of certain species in a community (Martorell & Freckleton, 2014). Due to tight interactions between plants and pollinators such as hummingbirds, mutualism is a common process between these two groups, in which plants provide the necessary resources for the successful establishment of different hummingbird species, and pollination services maintain and promote plant diversification (Abrahamczyk et al., 2017; Bergamo et al., 2018).

In opposition to clustering, overdispersion occurs when coexisting species tend to be either phylogenetically distant or phenotypically dissimilar (Cavender-Bares et al., 2009; Webb et al., 2002). Phylogenetic and phenotypic overdispersion may occur when competitive interactions are linked to ecologically relevant traits that are highly evolutionarily conserved. Competitive interactions may result in either competitive exclusion (phylogenetic overdispersion) or character displacement (phenotypic overdispersion), both of which release competitive stress (Brown & Wilson, 1956; Webb et al., 2002; Emerson & Gillespie, 2008; Cavender-Bares et al., 2009; Bassar et al., 2017; Lara et al., 2011). If ecological traits are labile or convergent, habitat filtering may generate overdispersion due to the selection of traits scattered across the phylogeny (Cavender-Bares et al., 2009; Emerson & Gillespie, 2008; Webb et al., 2002). Given that the same factors may lead to contrasting patterns depending on trait evolution, it is necessary to include trait evolution for a proper interpretation of phylogenetic and phenotypic community structure patterns (Emerson & Gillespie, 2008;

Losos, 2008; Revell et al., 2008; Cavender-Bares et al., 2009).

The evolution of traits may imprint patterns able to be measured across the phylogeny through the estimation of the phylogenetic signal (Losos, 2008; Revell et al., 2008), which is a statistical measure of trait dependence among species due to their phylogenetic relationship (Revell et al., 2008). This measure may suggest if a trait is either conserved, convergent or shows a Brownian motion evolution pattern across the phylogeny (Losos, 2008; Pagel, 1999; Revell et al., 2008). Phylogenetic signal may be sensitive to changes in trait evolution and extinction rates across time (Aristide & Morlon, 2019; Revell et al., 2008); the combination of trait phylogenetic signal with other community structure measurements (Mayfield & Levine, 2010) provides information about the significance of a given trait in the evolution of natural communities (Webb et al., 2002).

Hummingbird evolution and their distributional patterns have been highly influenced by several factors operating at different scales, such as biogeographic history, past and current ecological conditions, and biotic interactions (Altschuler, 2006; Graham et al., 2012; McGuire et al., 2014; Weinstein et al., 2017; Martín Gonzalez et al., 2015; Maruyama et al., 2018; Rodríguez-Flores et al., 2019). Hummingbirds are distributed in almost all terrestrial environments from Alaska to Patagonia, and have established highly important mutualistic interactions with plants (Rodríguez-Flores et al., 2019; Stein, 1992; Temeles et al., 2009), such as pollination (Martín-Gonzalez et al. 2015; Maruyama et al., 2018; Rodríguez-Flores et al., 2019). Despite the relatively highly conserved morphology in hummingbirds, coexisting taxa form complex species assemblages (Brown & Bower, 1985; Ornelas et al., 2002; Lara et al., 2011; Abrahamczyk & Kessler, 2015; Rodríguez-Flores & Arizmendi, 2016; Bribiesca et al., 2019). These assemblages may be arranged by niche partitioning through different foraging strategies and competitive interactions between different species, generating distinctive phenotypic, and phylogenetic patterns at local and regional scales (Feinsinger & Colwell, 1978; Ornelas et al., 2002; Lara et al., 2011; Martín & Ghalambor, 2014; Martín Gonzalez et al., 2015; Rodríguez-Flores & Arizmendi, 2016; Wolowski et al., 2017). In addition, the evolution of short- and long-distance seasonal migration in some North American hummingbird species has been described as a strategy of competitive ecological release, both for intra- and interspecific competition (Licona-Vera & Ornelas, 2017; Magrath et al., 2020; Weinstein et al., 2017). Long-distance migratory species present changes in niche occupation across the latitudinal gradient. In wintering grounds, migratory taxa show a highly overlapped niche with resident species, therefore likely adopting a generalist strategy. In their breeding regions, these species presumably turn to a specialist strategy due to both the abundance of resources and a very low hummingbird species number (Magrath et al., 2020).

Here, we analyzed the phenotypic and phylogenetic structure of hummingbird assemblages across North American biogeographic regions and ecoregions to assess the relative significance of habitat filtering and interspecific competition in community assembly. Several factors make North American hummingbird assemblages particularly suitable for addressing this question. Nearctic and Neotropical biogeographic regions overlap in Mexico and Central America, resulting in highly diverse communities where different phylogenetic histories converge, likely to contain different phylogenetic structure patterns. Secondly, there is a north-to-south gradient of increase in both species' diversity and phylogenetic diversity, which suggests a gradient of phylogenetic structure ranging from clustering to overdispersion. Finally, migrant and resident species form mixed assemblages in Neotropical and the southernmost Nearctic ecoregions during the winter, potentially shifting the phylogenetic structure of resident communities. If inter-specific competition and habitat filtering have played significant roles in the assembly process of hummingbird communities at different regions across North America, we expect that: (1) phylogenetic and phenotypic structure values will gradually shift from an overdispersed pattern in Neotropical ecoregions to a clustered pattern toward the Nearctic; (2) migration will not affect phylogenetic and phenotypic structuring patterns in Neotropical and Transitional ecoregions because migratory species will have a generalist foraging strategy while wintering to avoid competition with closely related resident species; and (3) proportion of species in high diversification rates clades, and phylogenetic diversity, will all show a positive (interspecific competition) or negative (habitat filtering) relationship with phylogenetic and phenotypic structure values, depending of which factor is predominant across ecoregions.

Material and methods

Species composition

To calculate the phenotypic and phylogenetic structure of hummingbirds across North America (here defined as continental Mexico, USA, and Canada), we used level II ecoregions. The scale of these climatic and geological units reflects the distribution of natural communities at a subcontinental scale, appropriate for our study. Ecoregions level II were chosen because, comparatively, level I ecoregions are too coarse a scale for some of the patterns we were interested in (Bailey, 2004; Olson et al., 2001), while level III ecoregions are appropriate for local monitoring and decision-making studies (Omernik & Griffith, 2014). We grouped the ecoregions into three biogeographic regions (Morrone et al., 2017): (1) Nearctic, (2) Transitional, and (3) Neotropical.

We established hummingbird species composition for each ecoregion using distributional range maps in Nature Serve (BirdLife International & NatureServe, 2014) and CONABIO (available at <http://www.conabio.gob.mx/informacion/gis>). We overlapped the species' range maps with the ecoregions map using ArcGis 10.1 (ESRI, 2012). These data were used to build the presence/absence matrix used for all subsequent analyses. Given that some hummingbird species in the Bees clade show long-distance seasonal migration (Licona-Vera & Ornelas, 2017), we ran all analysis considering two different datasets: a) breeding species assemblages, which included resident species and migratory species in their breeding ranges, and b) winter species assemblages, including resident species and migrant species in their wintering ranges. Since our analyses focused on continental North America, we excluded the island endemic *Cyanthus forficatus* from all analyses.

Phylogenetic and phenotypic data

We based our phylogenetic analyses on a molecular phylogenetic tree for hummingbirds reconstructed using mitochondrial and nuclear DNA markers (6461 nucleotides) that was previously published (McGuire et al., 2014), and kindly provided by J. McGuire. The original phylogenetic tree recovered nine clades, which we pruned to include only North American species. Some species distributed in our study region (i.e., *Lophornis brachylophus*, *L. helenae*, *Doricha enicura*, *Calothorax pulcher*, *Selasphorus ellioi*, *Cyanthus auriceps*, and *Pampa curvipennis*) were not included in the original phylogeny. We therefore estimated their corresponding branch lengths attaching each of these species to its closest relative available in the phylogenetic tree using the *bind.tip* function in *phytools* (Revell, 2012) for R (R Development Core Team, 2017); following Banks, 1990; Monroe et al., 1995; Licona-Vera & Ornelas, 2017; Stiles et al., 2017).

We collected morphological data from specimens in the Colección Nacional de Aves at the Instituto de Biología-UNAM and the Museo de Zoología "Alfonso L. Herrera" at the Facultad de Ciencias-UNAM. We measured nine morphological traits that are likely to be related to foraging strategies, flying efficiency, and habitat use (see Wolf et al., 1972 for details; Feisinger & Colwell, 1978; Zeffler et al., 2003; Temeles et al., 2009; Claramunt et al., 2012; Graham et al., 2012; Jönsson et al., 2015): length of the exposed culmen; angle, length, width, and depth of the bill; tarsus length, wing chord, secondary length of the wing (distance from carpal joint to the tip of the first secondary feather), and length of central rectrices (Fig. S1). We measured the angle of the bill using the length of the bill (a straight line from the base to the tip of the bill) and the line resulting from bill deviation (Fig. S1B). We also estimated two composite morphological traits: bill curvature and hand-wing



index (HWI). Following Temeles et al. (2009), we calculated bill curvature using measurements from the bill angle and bill length with the formula:

$$K = \frac{1}{\frac{\frac{1}{2}C}{\sin(\text{radians } A)}}$$

where K is the curvature, C is the length from the base to the tip of the bill, and A is the angle of the bill. We calculated HWI as a measure of wing shape (Claramunt et al., 2012), using wing chord and secondary length of wing as follows:

$$HWI = 100 * \left(\frac{\text{wing chord} - \text{secondary length of wing}}{\text{wing chord}} \right)$$

In addition, we obtained the weight of each specimen from the specimen label. All morphological data are available from the first author upon request. We measured only mature male specimens to avoid variation in the morphological data due to sex- or age-associated differences (Rodríguez-Flores & Stiles, 2005; Temeles et al., 2009).

Considering the phylogenetic non-independence of our morphological dataset, we performed a phylogenetic principal component analysis (PCA; Revell, 2009) using the *phy.pca* function in phytools (Revell, 2012) for R (R Development Core Team, 2017). Phylogenetic PCA requires of a phenotypic trait matrix and a phylogenetic tree. Before analyses, we transformed raw morphological measurements using the natural logarithm. The first PCA axis (PC1) explained 60.87% of variance and was related to body size, the second axis (PC2) explained 10.99% and was related to bill curvature, and the third axis (PC3) explained 8.05% of the variance and was related to the wing shape. The cumulative variance explained by PC4–PC6 was 15.03% and was mainly related to bill size and the length of the central rectrices (Tables S1 and S2). Using phylogenetic PCA scores per species (PC1 to PC6), we calculated a Euclidean distance matrix, which was used for phenotypic structure analyses of hummingbird assemblages. We built a phylogenetic heatmap using *phylo.heatmap* function in phytools (Revell, 2012) for R (R Development Core Team, 2017) which allowed us to show the dispersion of each PC axis using the standard deviation (SD) for each species.

Phylogenetic and phenotypic mean pairwise distance (mpd) and mean nearest taxon distance (mntd)

To estimate the phylogenetic and phenotypic structure of hummingbird assemblages in each ecoregion, we considered four metrics: phylogenetic MPD and MNTD, and phenotypic pMPD and pMNTD. MPD averages the pair-wise distances among all pairs of co-occurring taxa throughout the

phylogenetic tree, while MNTD considers the mean distance between pairs of co-occurring closely related taxa (Webb et al., 2002). Similarly, pMPD averages morphological distances between all pairs of co-occurring taxa, while pMNTD averages distances in morphological characters for pairs of taxa. Both phenotypic structure metrics are estimated using a Euclidean distances matrix (Kembel et al., 2010). We estimated the significance of phylogenetic and phenotypic structure measurements by calculating standardized effect sizes (SES), which compares the observed phylogenetic and phenotypic structure measurements to a null model (Kembel et al., 2010; Webb et al., 2002). Relevant null models were obtained from the randomization of the species assemblages' matrix by drawing species from the corresponding pool (pruned phylogenetic tree or Euclidean matrix) with equal probability using the phylogeny pool model with 100 iterations, as implemented in picante (Kembel et al., 2010) for R (R Development Core Team, 2017). Hereafter, MPD and MNTD refer to the standardized effect sizes of these parameters rather than the raw parameters. The values of MPD and MNTD indicate the three possible patterns: MPD and MNTD values < -1.96 indicate clustering values; $x > 1.96$ indicate overdispersion, and values between $-1.96 < x < 1$ indicate a random pattern (Vamosi et al., 2009; Webb et al., 2002). Given that some trends may be overlooked within the random patterns, we also considered nonsignificant trends of clustering ($-1.96 < x < 0$) and overdispersion ($0 < x < 1.96$; Vamosi et al., 2009).

Using the species presences/absence matrix, we calculated phylogenetic and phenotypic structure metrics for the breeding and wintering season separately at two different geographic scales: the Nearctic, Transitional, and Neotropical biogeographic regions (Fig. S2); and at the level II ecoregions. Given that phylogenetic and phenotypic structure analyses require the conformation of an appropriate species group to serve as a relevant pool for null model comparisons (see Webb et al., 2002; Kembel, 2009), we used the relevant species pools for each analysis: (1) the pruned phylogenetic tree for the phylogenetic pattern, and (2) the morphological Euclidean matrix for the phenotypic pattern (Table S3).

We used DAMOCLES (Pigot & Etienne, 2015) for R (R Development Core Team, 2017) to test for phylogenetic and phenotypic structure patterns. DAMOCLES generates dynamic null models based on colonization, local extinction, and speciation processes. We built dynamic null models by drawing species from the corresponding pool (the pruned phylogenetic tree or the Euclidean matrix) with unequal probabilities and 100 iterations. Since DAMOCLES yields negative MPD and MNTD structure measurements, we multiplied results by -1, which allowed us to compare these with values derived from Picante (Kembel et al., 2010). Due to a low species richness in several ecoregional assemblages, we built null models using equal probabilities to draw species

from the species pool, which are as equally efficient as random draw models (Pigot & Etienne, 2015). We obtained the mean and standard deviations from 100 iterations of each of these null models using Picante (Kembel et al., 2010) for R (R Development Core Team, 2017).

It has been suggested that a more accurate phylogenetic structure process may be inferred by coupling phenotypic and phylogenetic structure information, as well as by estimating trait phylogenetic signal (Cadotte & Tucker, 2017). Using of all these results allows for a better inference of processes implicated in the phylogenetic structuring of community assemblages (Kraft et al., 2007). We therefore estimated the phylogenetic signal of each selected morphological trait using Pagel's λ (Pagel, 1999), which measures the statistical dependence of trait values among species given their phylogenetic relationship (Revell et al., 2008). Values of λ tending to 0 indicate lability or convergence of the traits, while significant values closer/equal to 1 indicate that trait evolution conforms to Brownian motion (Freckleton et al., 2002; Symonds & Blomberg, 2014). Phylogenetic signal analyses were calculated using the *phylosig* function in phytools (Revell, 2012) for R (R Development Core Team, 2017).

Data analysis

To determine whether the arrival of migratory species into wintering grounds shifts the phylogenetic and phenotypic structuring patterns across biogeographic regions, we performed a paired t test (Dytham, 2011) of the ecoregions' structure scores between the breeding and winter seasons. Since both measures were calculated from pairwise comparisons, ecoregions inhabited by less than two species were discarded from this test.

Since interspecific competition cannot be measured at the biogeographic or ecoregion scales, we used three variables (species richness, phylogenetic diversity, and proportion of species in high-diversification rate clades) to indirectly measure the relative influence of interspecific competition and habitat filtering in the structuring patterns of hummingbird assemblages. However, although both interspecific competition and habitat filtering may generate similar values for species richness, phylogenetic and phenotypic structure values would be different depending on the main assembly process and the evolution of the traits (Aristide & Morlon, 2019). We performed linear regression models (LM; Crawley, 2007) for each phylogenetic structure measure within each season. For each season, we evaluated the influence of 1) hummingbird species richness, 2) phylogenetic diversity (measured following Faith, 1992), and 3) the proportion of species in high-diversification rate clades (Emeralds, Mountain Gems, and Bees clades; McGuire et al., 2014). The proportion

of species in high-diversification rate clades allowed us to indirectly measure the age of the different assemblages, as the Emerald, Bee, and Mountain Gem clades are the youngest in the hummingbird phylogeny (McGuire et al., 2014). Therefore, hummingbird communities mainly composed of species from any of these three clades would indicate that the assemblage is younger than assemblages composed by species from other clades. On the other hand, the relationship between phylogenetic diversity and MPD, MNTD, pMPD, pMNTD may be influenced by the phylogenetic signal. When a trait is conserved, competition may promote communities with species not closely related; and phylogenetic diversity and phylogenetic structuring measures tend to increase together. In the case of traits convergent evolution, phylogenetic diversity and structuring measures would not be different (Webb et al., 2002; Emerson & Gillespie, 2008; see Kembel et al., 2010).

We compared among LMs including all possible combinations of the three explanatory variables (species richness, phylogenetic diversity, and proportion of species in high-diversification rate clades), including the intercept-only null model (Burnham et al., 2001). We obtained 32 LMs per phylogenetic structure measure in each ecoregion, for a total of 256 models in total. We used the corrected Akaike information criterion (AICc) to choose the best supported models. We also calculated ΔAIC (< 2.00) and the weight of the model as part of model evaluation (Johnson & Omland, 2004). We performed model selection using *MuMIn* (Barton, 2018), as implemented in R (R Development Core Team, 2017).

Results

Morphological and phylogenetic data

We compiled a list of 58 species for hummingbirds in North America (based on Gill et al., 2021; Table S3). Our pruned phylogenetic tree included 55 hummingbird species, and we measured a total of 803 specimens from 55 hummingbird species (Table S3; Figs. S2 and S4). Morphological data showed that phylogenetically closely related species are highly similar to each other (Fig. 1). The Bees and Coquettes clades included species with small body-sizes and showed similar positive SD values. Species in the Emeralds clade varied in body-size (negative and positive values of SD; Fig. 1), while the Mountain Gems clade included larger body-sized (negative SD values) species. On the other hand, the SD of the shape and size of the bill (PC2, PC4, PC5, PC6), and the wing shape (PC3) showed high variation within hummingbird clades.

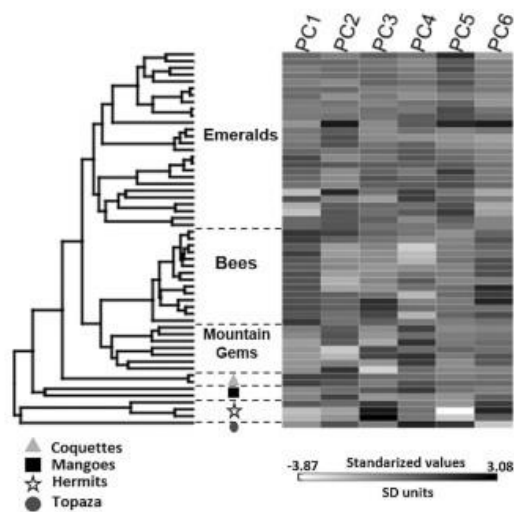


Fig. 1 Phylogenetic heatmap of the pruned phylogenetic tree (see Methods) based on McGuire et al. (2014) for North American hummingbird species and the matrix of the PC from phylogenetic PCA scores. Colors indicate standard deviation (SD) values for each PC axis by species

Phylogenetic and phenotypic structure patterns across North America

Phylogenetic and phenotypic structure measures of the Neotropical and Transitional biogeographic regions showed a random structure across North America in both seasons (Table 1). Contrast values for MPD and pMPD in the Nearctic region showed a clustered pattern in both seasons. At the ecoregional scale, we obtained 105 hummingbird assemblages which can be generally grouped into the three biogeographic regions (Fig. 2). In general, phylogenetic MPD and MNTD for the wintering and breeding seasons showed mostly clustered pattern in western Nearctic ecoregions (Fig. 2); and random patterns in ecoregions from the southern Nearctics, Transitional, and the Mexican and northern Central American

Neotropics ecoregions. There was an overdispersed pattern in MPD values in ecoregions in the southern Gulf of Mexico (Pantanos de Centla and Veracruz Dry Forest ecoregions; Tables S4 and S5). The wintering and breeding assemblages differed in MPD pattern in Balsas Dry Forests in the Neotropics and for the Sierra Madre Occidental pine forest in the Transitional biogeographic region (Fig. 2). The clustered pattern in the breeding season was maintained during the winter in some of the western Nearctic ecoregions (Fig. 2; Table S4).

Phenotypic structure patterns showed some similarities with the phylogenetic patterns above (Fig. 2). During the breeding season, pMPD showed a clustered pattern in western Nearctic ecoregions (USA, Canada, northern Baja California, and the Sonora desert); there were random patterns in some western and southern Nearctic ecoregions and most of the Transitional and Neotropical ecoregions (Table S4). In the winter season, the pMPD of most of the ecoregions recovered as clustered shifted to random structure patterns. In the case of pMNTD during the breeding season, the western Nearctic ecoregions (Columbia Plateau, Northwestern Pacific Coast, California Coast, and the Chihuahua Desert) showed a clustered pattern; we found no patterns of phenotypic overdispersion. During the winter season, almost all ecoregions that had clustered patterns during the breeding season shifted to random patterns, while the Sonora-Sinaloa Transitional Subtropical Dry Forest ecoregion shifted from a random to clustered phenotypic pattern (Table S5).

Boxplots by biogeographic region showed that Nearctic ecoregions had a nonsignificant trend toward clustering (negative values) in both the phylogenetic and phenotypic structure (Fig. 3). For Transitional ecoregions, MPD and MNTD showed positive and negative values, suggesting overdispersion and clustering tendencies; however, pMPD showed a trend toward more positive values while pMNTD showed mainly negative values. Neotropical ecoregions showed both positive and negative values for all MPD, MNTD, pMPD, suggesting clustering, but pMNTD suggested overdispersion for both breeding and wintering communities. Paired t test results (Table 2) and boxplots (Fig. 3) indicated that migratory species significantly shifted their phylogenetic patterns among seasons, except MNTD in the

Table 1 Phylogenetic (MPD and MNTD) and phenotypic (pMPD and pMNTD) structure values of hummingbird assemblages at biogeographic regions (Neotropical, Transitional, and Nearctic) estimated using the *bootstrap* function in *DAMOCLES* (Pigot & Etienne, 2015)

	MPD		MNTD		pMPD		pMNTD	
	breeding	winter	breeding	winter	breeding	winter	breeding	winter
Neotropical	0.3464 random	0.1084 random	-0.5225 random	1.0923 random	-1.7355 random	-1.681 random	-1.1377 random	-1.1045 random
Transitional	0.8809 random	0.9835 random	0.6432 random	0.6216 random	0.2692 random	0.3890 random	0.5932 random	0.6666 random
Nearctic	-3.0621 cluster	-2.2942 cluster	-1.5287 random	-1.2610 random	-2.9740 cluster	-2.408 cluster	-1.3493 random	-0.8975 random

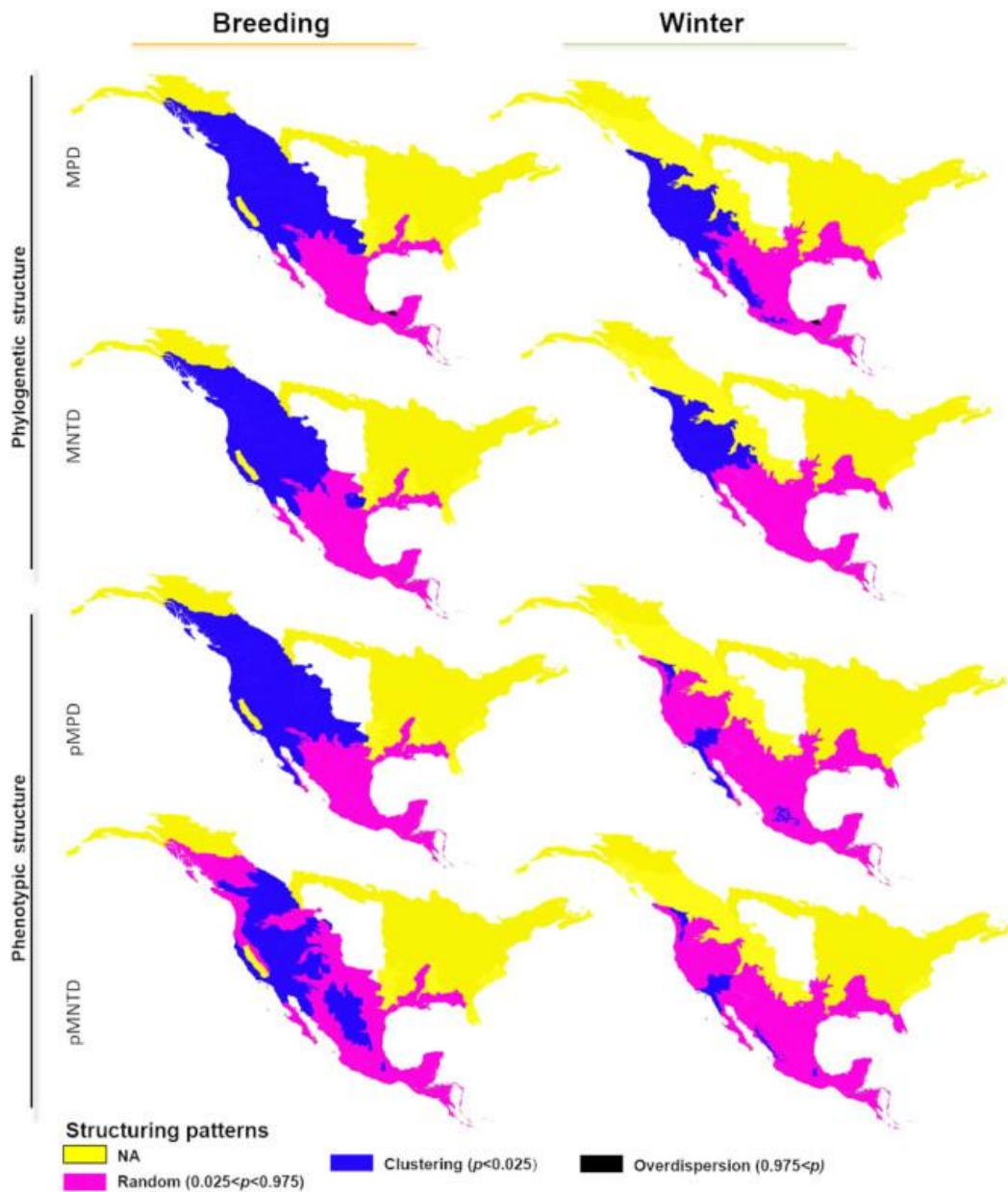


Fig. 2 Geographic patterns of phylogenetic and phenotypic MPDs and MNTDs across North America according to seasons considered (breeding and winter)

Nearctic. The phenotypic structure (pMPD and pMNTD) shifted at Nearctic ecoregions, but not in Transitional and Neotropical ecoregions.

Values of λ for body size (PC1) and wing shape (PC3) suggested that the evolution of these traits is conserved, while bill curvature (PC2) is a convergent trait, showing

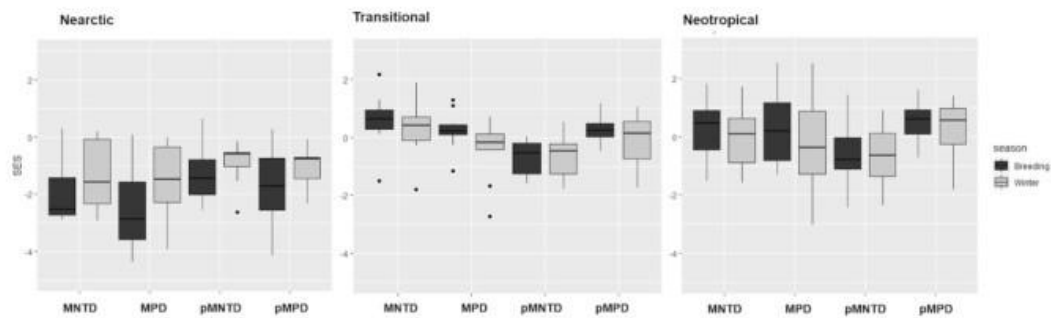


Fig. 3 Boxplots of MPD, MNTD, pMPD, and pMNTD between breeding and winter seasons by biogeographic region

a nonsignificant λ value different from 0 (Table 3). Traits related to bill size (PC4 and PC6) showed λ values that suggest convergence; λ values of the length of rectrices (PC5) suggest that this trait is conserved.

LMs showed that species richness was negatively related to both phylogenetic and phenotypic MPD and MNTD values in both seasons (Table 4). For the breeding season, the best models explaining MPD, pMPD, and pMNTD included significant effects for species richness and phylogenetic diversity (Table 5). However, MNTD was better explained by species richness, phylogenetic diversity, and proportion of species in high-diversification rate clades. In general, the best models indicated that phylogenetic and phenotypic structuring measures were negatively related to species richness, and positively related to phylogenetic diversity (Table 5).

Table 2 Paired t tests between breeding and winter season for MPD, MNTD, pMPD, and pMNTD at the ecoregions level

	t value	p value	df
Nearctic ecoregions			
MPD	-3.267	0.0027*	29
MNTD	-1.296	0.2051	29
pMPD	-2.199	0.0359*	29
pMNTD	-2.769	0.0097*	29
Transitional ecoregions			
MPD	3.741	0.0046*	9
MNTD	6.164	0.0001*	9
pMPD	2.070	0.0683	9
pMNTD	-0.075	0.9417	9
Neotropical ecoregions			
MPD	2.627	0.0170*	18
MNTD	2.124	0.0477*	18
pMPD	2.067	0.0533	18
pMNTD	-0.112	0.9117	18

*significant values

For the winter season, the best-supported models MPD included species richness, phylogenetic diversity, and the proportion of species in high-diversification rate clades, while MNTD included species richness and phylogenetic diversity (Table 4). For pMPD, the best model included only the proportion of species in high-diversification rate clades, while for pMNTD, in addition to species richness and phylogenetic diversity, proportion of species in high-diversification rate clades has a strong positive effect (Table 5).

Discussion

Our analyses suggest that present-day North American hummingbird communities have been structured by historical and ecological processes that have shaped their morphological characters. Our results showed that the different phylogenetic and phenotypic structure patterns detected in hummingbird assemblages may be explained, in part, by the lability of traits such as bill size and shape, as well as of conserved traits such as body size and wing shape. Both the Pagel λ values of the traits and the SD of PC1 (Fig. 1) suggested that body size is a conserved trait in North American hummingbirds, except for the Emeralds, which showed high variability. Bill curvature (PC2) and bill size (PC4 and PC6) are apparently labile traits, for which both extreme positive and extreme SD negative values were observed across our pruned phylogeny. Variation in these traits may be the result of character displacement processes allowing for resources

Table 3 Quantification of the phylogenetic signal using Pagel's λ values for each selected morphological trait

Trait	λ value	p value
PC1	0.991	<0.001*
PC2	0.741	0.051
PC3	0.961	<0.001*
PC4	0.584	0.001*
PC5	0.951	<0.001*
PC6	0.806	<0.001*

*significant values

Table 4 AICc scores of best performing linear models ($\Delta AIC < 2.00$). SR = species richness, PD = phylogenetic diversity, Prop = Proportion of species in high-diversification rate clades

Model	Coefficient estimated			AICc	$\Delta AICc$	Weight
	SR	Prop	PD			
Breeding						
MPD ~ SR + PD	-0.713		0.081	100.5	0.00	0.545
MPD ~ SR + Prop + PD	-0.760	1.319	0.087	100.8	0.36	0.454
MNTD ~ SR + Prop + PD	-0.478	1.415	0.061	69.6	0.00	0.643
MNTD ~ SR + PD	-0.427		0.061	70.8	1.18	0.356
pMPD ~ SR + PD	-0.380		0.045	154.85	0.00	0.749
pMNTD ~ SR + PD	-0.223		0.026	154.14	0.00	0.378
Winter						
MPD ~ SR + Prop + PD	-0.490	-1.474	0.062	113.40	0.00	0.658
MNTD ~ SR + PD	-0.3770		0.057	106.84	0.00	0.783
pMPD ~ SR + Prop + PD	-0.188	0.026	0.026	136.15	0.00	0.448
pMPD ~ Prop		6.849		137.91	1.75	0.186
pMNTD ~ SR + Prop + PD	-0.248	2.996	0.034	118.88	0.00	0.682

partition and species co-occurrence, thus reducing inter-specific competition (Bassar et al., 2017; López-Segoviano et al., 2018; Martín González et al., 2018). Interestingly, Emeralds showed a wide range of SD values, indicating variation in bill curvature and size ranging from long, curved bills like in *Campylopterus hemileucurus* to short, straight bills, as in *Abeillia abeillei*. This contrasts with previous findings in which Emerald species have been considered

generalist species with mostly straight bills (Rodríguez-Flores et al., 2019). Thus, our findings underline the need to quantitatively assess potentially ecologically relevant characters in specialized groups.

Hummingbird assemblage structure at the biogeographic scale showed that most of the Transitional and Neotropical ecoregions presented a random structure, which may be due to either the masking of local phylogenetic structure patterns given the large geographic scale (Table 1; Swenson et al., 2006), or to the diversity of other biotic groups with similar ecologies not included in studies focused on single taxonomic groups (Wilcox et al., 2018). The Nearctic biogeographic region, however, showed clustered patterns in MPD and pMPD: only some small body-sized species in the Bees clade range into higher latitudes (Table 1; Figs. 1–2). Values for MNTD and pMNTD showed a random pattern (Figs. S3–S4), which together with clustered patterns for MPD and pMPD, indicate that some closely related species did not range to northern regions (e.g., *S. sasin* and *S. platycercus*), and that co-occurring species show slightly morphological differences (e.g., differences in the SD of PC2 to PC6 between *S. rufus* and *S. calliope*; Figs. 1 and S4). Another important factor that may influence our assemblage structure results at the biogeographic scale is the distributional range and seasonal availability of flowering plants. The high species richness of flowering plants in the Neotropics has likely favored a high number of specialized hummingbird-flower interactions (Martín González et al., 2015), while at high latitudes in North America, drastic seasonal temperature changes may have favored generalist species, as in Bees, which show a mainly generalist morphology.

In comparison, at the ecoregional level, the smaller geographic scale, which has higher resolution in terms of habitat heterogeneity and climatic conditions, showed more detailed patterns. Nearctic ecoregions showed that clustered

Table 5 Estimated coefficient and p values of the best-supported linear models. SR = species richness, PD = phylogenetic diversity, Prop = proportion of species in high diversification rates clades

Model	Coefficient estimated		
	SR	Prop	PD
	p value	p value	p value
Breeding			
MPD ~ SR + PD	-0.713		0.081
	<0.001*		<0.001*
MNTD ~ SR + Prop + PD	-0.478	1.415	0.061
	<0.001*	0.069	<0.001*
pMPD ~ SR + PD	-0.38		0.045
	<0.001*		<0.001*
pMNTD ~ SR + PD	-0.223		0.026
	<0.001		<0.001
Winter			
MPD ~ SR + Prop + PD	-0.49	-1.474	0.062
	<0.001*	0.4126	<0.001*
MNTD ~ SR + PD	-0.29		0.057
	<0.001*		<0.001*
pMPD ~ SR + Prop + PD	-0.188	0.026	0.026
	0.0154*	0.2694	0.014*
pMNTD ~ SR + Prop + PD	-0.248	2.996	0.034
	<0.001*	0.1193	<0.001*

patterns for MPD, MNTD, and pMPD (Tables 1 and S4; Fig. 2), predominate at northwestern ecoregions, while pMNTD showed both random and clustered patterns for several ecoregions. Clustering patterns in both the phylogenetic and phenotypic structure in these ecoregions may be explained by habitat filtering (see Webb et al., 2002; Mayfield & Levine, 2010). This is exemplified by species in the Bees clade, which have similar body size and bill curvature, the extreme climatic conditions in northernmost Temperate Forests and western deserts may have favored the assembly of closely related and phenotypically similar species, generating clustering in both phylogenetic and phenotypic structure patterns (Figs. 1 and S3). Similar phylogenetic patterns have been found in high-elevation Andean hummingbirds, where only a few clades have been able to diversify (García-Moreno et al., 1999; Graham et al., 2009; McGuire et al., 2014). On the other hand, pMNTD in northwestern Nearctic ecoregions (Fig. 2) showed phenotypic random patterns, suggesting that species in these assemblages (e.g., *Selasphorus rufus*, *S. calliope*, and *Archilochus alexandri*) are similar in body size (PC1), bill curvature (PC2), and wing shape (PC3; Figs. 1 and S4), but not in bill size (PC4-PC6), therefore suggesting that, in addition to habitat filtering, ecological differentiation via character displacement has probably reduced interspecific competition (Mayfield & Levine, 2010). Furthermore, due to their mutualistic interactions, plant species may have facilitated the colonization of northernmost regions by species in the Bees clade, likely due, in part, to the generalist habits of these species (Rodríguez-Flores et al., 2019). Most Nearctic desert ecoregions showed phylogenetic (MPD and MNTD) and phenotypic (pMPD and pMNTD) clustered patterns, which may be due to habitat filtering promoted by the extreme environmental conditions, which some species of the Bees clade are able to manage. However, the Chihuahuan and Baja California deserts showed random phylogenetic and phenotypic patterns (pMPD), but a clustered pattern in pMNTD (Table S4). This might be due to the regular presence of species from the Mountain Gems (e.g., *Eugenes fulgens*) or the Emeralds (e.g., *Cynathus latirostris*) which have medium to large body sizes (Figs. 1 and S4), which may be the result of the availability of floral resources and of the proximity of these ecoregions to environmentally different ecoregions such as the Sierra Madre Oriental and the Sierra Madre Occidental (St-Louis et al., 2009).

Phylogenetic and phenotypic metrics in Transitional ecoregions showed values closer to zero (random pattern; Fig. 3). MPD, MNTD, and pMPD scores ranged from positive (i.e., overdispersion) to negative (i.e., clustered) values, but pMNTD values tended to be only negative (i.e., toward a clustered pattern; Figs. 2–3). This combination of assemblage structure patterns may have been promoted by the mixing of Nearctic and Neotropical biotas along the elevational

gradient of the Mexican Highlands (see Sánchez-González & Navarro, 2009; Escalante et al., 2013). Hummingbird assemblages in medium elevations show a species composition including species from tropical lowlands and from temperate highlands exhibiting both a high species richness assemblage, and a higher degree of feeding specialization and niche partitioning (López-Segoviano et al., 2021). The biotic mixing and habitat heterogeneity across the elevational gradient may explain overdispersed patterns by allowing species from different lineages to coexist, while trait lability and habitat filtering would explain the distribution of phenotypically similar species toward higher elevations.

Mexican Neotropical ecoregions showed a phylogenetic random pattern (Fig. 3) which may be due to the presence of species from mainly South American clades (i.e., Topazas, Hermits, Mangoes, and Coquettes) that are distantly related to the primarily North American Bees, Mountain Gems and the Emeralds clades (McGuire et al., 2014). Two ecoregions, however (Pantanos de Centla and Veracruz Dry Forest), showed an overdispersed phylogenetic (MPD) pattern (Fig. 3, Table S4). This may be explained by the presence of many Emerald clade species and other distantly related South American taxa, such as the Topazas and Hermits. Similarly, in the Tehuacan Valley ecoregion, clustered (pMNTD) and overdispersed (pMPD) trends were observed, suggesting the co-occurrence of highly and intermediate phenotypically similar species, which may be a response to niche partitioning by body size, and therefore probably to phenotypic repulsion to reduce strong interspecific competition (Mayfield & Levine, 2010); but, simultaneously allowing phenotypically highly similar species to coexist, likely mediated by character displacement, such as foraging strategies (Lara et al., 2011; López-Segoviano et al., 2018; Ornelas et al., 2002; Wolowski et al., 2017).

Neotropical and Transitional regions showed similar structure values, which may be due to factors such as a lower species richness in Neotropical assemblages in comparison with Transitional ecoregions. For example, Neotropical ecoregions showed higher variability in the community structure values, suggesting a finer niche partition likely associated with interspecific competition (Martin-González et al., 2015). However, due to the generally broader scales of our study, some factors operating at local scales, such as niche partitioning mediated by floral abundance and seasonal availability or local movements linked to flowers' phenology, may not be easily interpreted from our data.

We evaluated whether phylogenetic and phenotypic structure patterns may be explained by factors indirectly related to interspecific competition or habitat filtering. Values of λ phylogenetic signal of body size (PC1) and wing shape (PC3) indicate that these are conserved traits. In the case of the proportion of species in high-diversification rate clades, assemblages mainly composed of species from only

one of the three North American clades (Bees, Emeralds and Mountain Gems) may indicate that the assemblage is younger than mixed assemblages (i.e., composed of species from all clades). Interspecific competition in young lineages with high rate of diversification may generate high trait disparity between co-occurring species (Aristide & Morlon, 2019). On the other hand, when traits are conserved, habitat filtering favors fewer and more highly similar species from the same clade, and negative values in both phylogenetic and phenotypic structure measures may be thus obtained, however habitat filtering may keep a lower species richness depending on ecological conditions (p.e., seasonal flower availability). Thus, with increase in species richness, phylogenetic diversity and the proportion of species in high-diversification rate clades should present negative relationships (Emerson & Gillespie, 2008; Webb et al., 2002). In the case of convergent traits, habitat filtering favors highly similar species from different clades, and overdispersion values in phylogenetic structure and clustered in phenotypic structure. The proportion of species in high-diversification rate clades should have negative and positive relationship with phylogenetic and phenotypic structure, respectively (see Emerson & Gillespie, 2008).

Our results partially fit these patterns. The best supported models for MPD and MNTD for the breeding season included species richness and phylogenetic diversity (Table 5), but the coefficients were negative and positive respectively, which may be due to inclusion of most species in North American ecoregions in only three clades (Emeralds, Bees, and Mountain Gems; McGuire et al., 2014), therefore pulling toward MPD and MNTD negative values in ecoregions with high species richness. For pMPD and pMNTD, the best supported models included species richness and phylogenetic diversity, and only for pMNTD, proportion of species in high-diversification rate clades (Table 4). In these cases, species from the Bee clade increased the species richness in the northernmost ecoregions, showing relatively minor phenotypic differences with other clades, such as the Emeralds (Fig. 1). Breeding season models and structuring pattern suggest that habitat filtering may had been the main assembly process in the northernmost ecoregions where habitat conditions are highly variable among seasons. Conversely, in the southern ecoregions, overdispersion patterns and positive coefficient of phylogenetic diversity indicate the accumulation of phylogenetic histories from different clades, suggesting that factors, such as the diversity and abundance of resources or niche partitioning, may drive the assembly process (Weinstein & Graham, 2016; Wolowski et al., 2017; Martín-González et al., 2018).

The role of migratory behavior in the assembly process

The evolution of migratory behavior is a relatively recent trait in North American hummingbirds (Licona-Vera & Ornelas, 2017). It has been suggested that migratory movements may have evolved in different avian lineages to avoid competition (Laube et al., 2013; Salewski & Bruderer, 2007); however, migration in hummingbirds has been related to resource availability (Malpica & Ornelas, 2014; Licona-Vera & Ornelas, 2017). In North America, migrant hummingbird species modify the structure of hummingbird communities in ecoregions from the southernmost Nearctic to the Neotropics, and migrants adjust their niche width during winter season (Martín González et al., 2018). Therefore, it is necessary to evaluate differences in phylogenetic and phenotypic structure between assemblages in the breeding and winter season. At the scale of biogeographic regions, phylogenetic and phenotypic structure did not shift between the two seasons (Table 1). However, at the ecoregional level, our results showed that migratory species shift phylogenetic (MPD) and phenotypic (pMPD and pMNTD) structure patterns in several ecoregions in the Nearctic toward less negative (clustered) values compared to the winter season (Table 2; Fig. 3), indicating that migratory species (Bee clade) arrive to ecoregions with distantly related and phenotypically differentiated taxa, such as Emeralds and Mountain Gems. This pattern is similar to the ecological distribution patterns in *Sylvia* warblers, where the potential of habitat occupancy is greater where there are few congeneric species (Laube et al., 2013); and to Andean hummingbird co-occurrence patterns (Weinsten et al., 2017). However, migratory species movements did not significantly shift MNTD of Nearctic ecoregions, but tended to negative values, suggesting that winter assemblages are composed by not closely related. An interesting trend in northern Nearctic ecoregions during the wintering season is the presence of at least two migratory hummingbird species (Fig. 3), which may be due to the relatively recent range expansion related to climatic change and supplementary feeding by humans (Greig et al., 2017; Winker & Gibson, 2018).

Boxplots showed that in Transitional and Neotropical ecoregions, winter communities changed phylogenetically toward more negative values in MPD and MNTD (Figs. 2–3), due to the arrival of species from the Bees clade sharing wintering locations (e.g., *S. rufus* and *S. platycercus*). Values of pMPD and pMNTD in these bioregions did not change between seasons (Table 2). Given that migratory species are usually classified as generalists (Rodríguez-Flores & Arizmendi, 2016), the phenotypic structure of assemblages is not expected to change (see

Malpica et al., 2017), at least at the ecoregional scale, likely due to niche expansion in long distance migratory species, which feed from even no-ornithophilic species in their wintering grounds (Martín González et al., 2018; Waser et al., 2018), while more specialized species move across the elevational gradient (altitudinal migration) following seasonal flowering patterns (López-Segoviano et al., 2021).

The best models fitting the winter season assemblages showed negative relationships between species richness and phylogenetic and phenotypic structure measures (Tables 4–5). Phylogenetic diversity showed positive coefficients for phylogenetic (MPD and MNTD) and phenotypic structure (pMPD and pMNTD), while the proportion of species in high diversification rates clades coefficient were positive for phenotypic structure (pMPD and pMNTD) models and negative for phylogenetic structure (MPD) model. This combination of coefficients did not clearly fit predictions for competition or habitat filtering assembly processes; however, the negative coefficient of species richness in all models suggests that the habitat filtering may be the main factor for the assemblage of winter communities, since migratory species belong to the Bee clade and are phenotypically similar to each other (Fig. S4). For example, *S. platycercus*, *S. calliope*, and *S. rufus* co-occur during the winter season across their migratory grounds are phenotypically highly similar (although they differ slight in bill size PC4 and PC6, Fig. 1). The lability of traits such as bill curvature and size may be key to the rearrangement of winter communities, because bill traits are closely related to the partitioning of floral resources (López-Segoviano et al., 2021).

In summary, our results suggest that the assembly process of North American hummingbird assemblages may have been significantly influenced by either habitat filtering or interspecific competition, which may have operated differentially depending on time and scale in the North American biogeographic regions. Results from phylogenetic signal analysis and from the phenotypic dendrogram showed that curvature and size of the bill are labile, while body size and wing shape are conserved for most North American hummingbird species. Phylogenetic clustering patterns together with mostly random phenotypic structure suggest that migratory behavior and morphological differentiation may release competitive stress at local scales, while LM suggest that habitat filtering is the main factor in the assembly processes across North America. Finally, it is important to point out that hummingbirds have established an important mutualistic interaction with plants, which has been described as a main driver of their morphological evolution and diversity patterns, and that may be helpful to disentangle random structure across Transitional and Neotropical ecoregions, which are a highly heterogeneous mosaic of distinctive

habitats (Maruyama et al., 2018; Martín-Gonzalez et al., 2018; Rodriguez-Flores et al., 2019).

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Author's contribution AP-C and LAS-G conceived and designed the study; AP-C collected, analyzed the data, and wrote the manuscript; LAS-G supervised, edited, and wrote the manuscript. All authors discussed the results, contributed, and wrote the final manuscript.

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Code availability Not applicable.

Declarations

Ethics approval Not applicable.

Consent to participate The authors declare consent to participate in this paper.

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Conflict of interest The authors declare no conflicts of interest.

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1 Apéndices

2 Table S1 Phylogenetic principal component analysis (PCA) of the 11 morphological traits

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
Proportion of variance	0.60879	0.10997	0.08638	0.07322	0.04339	0.03383	0.01575	0.01345	0.01172	0.00278	0.00066
Cumulative proportion	0.60879	0.71876	0.80514	0.87837	0.92176	0.95560	0.97136	0.98482	0.99654	0.99933	1.00000

3

4 **Table S2** Loadings values by traits from PC1 to PC6 of phylogenetic PCA

	PC1	PC2	PC3	PC4	PC5	PC6
Weight	-0.737586	-0.407582	-0.262525	-0.129006	0.177340	0.398041
Tarsus	-0.519149	-0.429852	-0.239629	-0.026772	0.162257	0.036817
Bill length	-0.697345	-0.179704	-0.198458	-0.558225	0.215881	-0.247057
Bill width	-0.560590	-0.428967	-0.184943	-0.472157	0.217257	0.000641
Bill depth	-0.720813	-0.154018	-0.361209	-0.367954	0.097634	0.123038
Wing chord	-0.858717	-0.191976	-0.326475	0.045923	-0.033924	0.177547
Wing secondary length	-0.978264	-0.126014	-0.050993	0.034610	-0.151100	-0.020996
Hand-Wing Index	0.552345	0.390995	-0.724387	0.114303	-0.049544	-0.038961
Exposed culmen	-0.690795	-0.179934	-0.223630	-0.543581	0.230147	-0.244882
Bill curvature	0.469534	-0.879234	-0.056611	0.030539	-0.042183	-0.021748
Central Rectrices	-0.837321	-0.211180	-0.031377	0.339149	0.363849	-0.072307

5

6 **Table S3** North American hummingbird species list (see Gill et al. 2021). Species marked
 7 with X count with phylogenetic and morphological data

Species	Phylogenetic Data	Phenotypic Data
Topazes		
<i>Florisuga mellivora</i>	X	X
Hermits		
<i>Phaethornis mexicanus</i>	X	X
<i>Phaethornis longirostris</i>	X	X
<i>Phaethornis striigularis</i>	X	X
Mangoes		
<i>Colibri thalassinus</i>	X	X
<i>Heliostyris barroti</i>	X	
<i>Anthracothorax prevostii</i>	X	X
Coquette		
<i>Lophornis brachylophus</i>	Added	X
<i>Lophornis helenae</i>	Added	X
Mountain Gems		
<i>Eugenes fulgens</i>	X	X
<i>Heliomaster longirostris</i>	X	X
<i>Heliomaster constantii</i>	X	X
<i>Lampornis viridipalens</i>	X	X
<i>Lampornis amethystinus</i>	X	X
<i>Lampornis clemenciae</i>	X	X
<i>Lamprolaima rhami</i>	X	X
Bees		
<i>Doricha enicura</i>	Added	
<i>Doricha eliza</i>	X	X
<i>Tilmatura dupontii</i>	X	X
<i>Calothorax lucifer</i>	X	X
<i>Calothorax pulcher</i>	Added	X
<i>Archilochus colubris</i>	X	X
<i>Archilochus alexandri</i>	X	X
<i>Calypte anna</i>	X	X
<i>Calypte costae</i>	X	X
<i>Selasphorus calliope</i>	X	X
<i>Selasphorus rufus</i>	X	X
<i>Selasphorus sasin</i>	X	X
<i>Selasphorus platycercus</i>	X	X
<i>Selasphorus heloisa</i>	X	X
<i>Selasphorus ellioti</i>	Added	X
Species	Phylogenetic Data	Phenotypic Data

Emeralds

<i>Phaeoptila sordida</i>	X	X
<i>Cynanthus latirostris</i>	X	X
<i>Cynanthus doubledayi</i>	X	X
<i>Cynanthus auriceps</i>	Added	X
<i>Cynanthus canivetti</i>	X	X
<i>Basilinna leucotis</i>	X	X
<i>Basilinna xantusii</i>	X	X
<i>Pampa curvipennis</i>	Added	X
<i>Pampa excellens</i>	X	X
<i>Pampa rufa</i>	X	
<i>Abeillia abeillei</i>	X	X
<i>Campylopterus hemileucurus</i>	X	X
<i>Eupherusa ridgwayi</i>	X	X
<i>Eupherusa poliocerca</i>	X	X
<i>Eupherusa cyanophrys</i>	X	X
<i>Eupherusa eximia</i>	X	X
<i>Phaeochroa curvierii</i>	X	X
<i>Leucolia violiceps</i>	X	X
<i>Leucolia viridifrons</i>	X	X
<i>Saucerottia cyanocephala</i>	X	X
<i>Saucerottia beryllina</i>	X	X
<i>Saucerottia cyanura</i>	X	X
<i>Amazilia rutila</i>	X	X
<i>Amazilia yucatanensis</i>	X	X
<i>Amazilia tzacatl</i>	X	X
<i>Chlorestes candida</i>	X	X
<i>Chlorestes eliciae</i>	X	X

- 8 Added= refers to species not included in the Trochilidae phylogeny proposed by McGuire
9 et al. (2014), but attached to its sister species (see Methods).

10 **Table S4** Phylogenetic and phenotypic structure scores by ecoregion in breeding season. NA= one hummingbird species is recorded

Ecoregions	MPD		MNTD		pMPD		pMNTD	
	Scores	Pattern	Scores	Pattern	Scores	Pattern	Scores	Pattern
Nearctic								
Central Appalachian Forest	NA	NA	NA	NA	NA	NA	NA	NA
Cumberlands and Southern Ridge and Valley	NA	NA	NA	NA	NA	NA	NA	NA
Great Lakes	NA	NA	NA	NA	NA	NA	NA	NA
High Allegheny Plateau	NA	NA	NA	NA	NA	NA	NA	NA
Interior Low Plateau	NA	NA	NA	NA	NA	NA	NA	NA
Lower New England	NA	NA	NA	NA	NA	NA	NA	NA
North Central Tillplain	NA	NA	NA	NA	NA	NA	NA	NA
Northern Appalachian	NA	NA	NA	NA	NA	NA	NA	NA
Ouachita Mountains	NA	NA	NA	NA	NA	NA	NA	NA
Ozarks	NA	NA	NA	NA	NA	NA	NA	NA
Piedmont	NA	NA	NA	NA	NA	NA	NA	NA
Prairie-Forest Border	NA	NA	NA	NA	NA	NA	NA	NA
Southern Blue Ridge	NA	NA	NA	NA	NA	NA	NA	NA
St. Lawrence-Champlain Valley	NA	NA	NA	NA	NA	NA	NA	NA
Superior Mixed Forest	NA	NA	NA	NA	NA	NA	NA	NA
Western Allegheny Plateau	NA	NA	NA	NA	NA	NA	NA	NA
Chesapeake Bay Lowlands	NA	NA	NA	NA	NA	NA	NA	NA
Florida Peninsula	NA	NA	NA	NA	NA	NA	NA	NA
South Atlantic Coastal Plain	NA	NA	NA	NA	NA	NA	NA	NA
West Gulf Coastal Plain	NA	NA	NA	NA	NA	NA	NA	NA

Ecoregions	MPD		MNTD		pMPD		pMNTD	
	Scores	Pattern	Scores	Pattern	Scores	Pattern	Scores	Pattern
Willamette Valley-Puget Trough-Georgia	-3.255	Cluster	-2.744	Cluster	-2.157	Cluster	-1.346	Random
Basin Temperate Broadleaf Mixed Forests								
Aspen Parkland	NA	NA	NA	NA	NA	NA	NA	NA
Central Tallgrass Prairie	NA	NA	NA	NA	NA	NA	NA	NA
Crosstimbers and Southern Tallgrass	NA	NA	NA	NA	NA	NA	NA	NA
Fescue-Mixed Grass Prairie	NA	NA	NA	NA	NA	NA	NA	NA
Northern Tallgrass Prairie	NA	NA	NA	NA	NA	NA	NA	NA
Osage Plains	NA	NA	NA	NA	NA	NA	NA	NA
Mississippi River Alluvial Plain	-0.001	Random	-0.003	Random	0.600	Random	-0.623	Random
Arizona-New Mexico Mountains	-2.833	Cluster	-2.040	Cluster	-2.033	Cluster	-0.091	Random
California North Coast	-3.677	Cluster	-2.768	Cluster	-2.476	Cluster	-2.085	Cluster
Canadian Rocky Mountains	-3.662	Cluster	-2.619	Cluster	-2.678	Cluster	-2.019	Cluster
East Cascades-Modoc Plateau	-3.607	Cluster	-2.724	Cluster	-2.678	Cluster	-2.019	Cluster
East Gulf Coastal Plain	-0.043	Random	0.061	Random	0.060	Random	-0.623	Random
Gulf of Alaska Mountains and Fjordlands	NA	NA	NA	NA	NA	NA	NA	NA
Klamath Mountains	-3.258	Cluster	-2.795	Cluster	-2.157	Cluster	-1.346	Random
Sierra Nevada	-3.579	Cluster	-2.559	Cluster	-1.961	Cluster	-1.855	Random
Montane Cordillera	-3.351	Cluster	-2.762	Cluster	-2.157	Cluster	-1.346	Random
North Cascades	-3.617	Cluster	-2.735	Cluster	-2.678	Cluster	-2.019	Cluster
Pacific Northwest Coast	-3.265	Cluster	-2.782	Cluster	-2.309	Cluster	-1.777	Random
S.E Alaska-B.C Coastal Forest and	-2.213	Cluster	-2.251	Cluster	-2.309	Cluster	-0.787	Random
Southern Rocky Mountains	-2.791	Cluster	-2.311	Cluster	-2.524	Cluster	-1.627	Random
Utah High Plateaus	-2.882	Cluster	-2.647	Cluster	-2.704	Cluster	-1.453	Random

Ecoregions	MPD		MNTD		pMPD		pMNTD	
	Scores	Pattern	Scores	Pattern	Scores	Pattern	Scores	Pattern
Utah-Wyoming Rocky Mountains	-3.544	Cluster	-2.899	Cluster	-2.704	Cluster	-2.197	Cluster
West Gulf Coastal Plain	-0.053	Random	0.013	Random	-0.602	Random	-0.623	Random
Middle Rockies-Blue Mountains	-3.830	Cluster	-2.847	Cluster	-2.524	Cluster	-1.573	Random
Okanagan	-3.585	Cluster	-2.667	Cluster	-2.678	Cluster	-2.019	Cluster
West Cascades	-3.528	Cluster	-2.581	Cluster	-2.678	Cluster	-2.019	Cluster
Boreal Cordillera	NA	NA	NA	NA	NA	NA	NA	NA
Gulf Coast Prairies and Marshes	-1.139	Random	-1.773	Random	-1.201	Random	-0.954	Random
Edwards Plateau	-2.471	Cluster	-2.509	Cluster	-0.689	Random	-0.669	Random
Southern Shortgrass Prairie	-2.005	Cluster	-1.936	Random	-1.961	Random	-0.702	Random
California Central Coast	-3.659	Cluster	-2.591	Cluster	-3.010	Cluster	-1.994	Cluster
California South Coast	-4.370	Cluster	-2.788	Cluster	-3.027	Cluster	-2.242	Cluster
Great Central Valley	NA	NA	NA	NA	NA	NA	NA	NA
Apache Highlands	-1.760	Random	-1.086	Random	0.647	Random	-0.431	Random
Baja California Desert	-1.701	Random	-1.630	Random	-2.557	Cluster	-1.458	Random
Central Mexican Matorral	-0.244	Random	-0.127	Random	0.135	Random	-1.363	Random
Chihuahuan Desert	-1.678	Random	-0.850	Random	0.564	Random	-2.056	Cluster
Colorado Plateau	-3.591	Cluster	-2.618	Cluster	-2.565	Cluster	-2.260	Cluster
Columbia Plateau	-4.277	Cluster	-2.770	Cluster	-3.982	Cluster	-2.554	Cluster
Great Basin	-3.672	Cluster	-2.707	Cluster	-2.565	Cluster	-2.260	Cluster
Mojave Desert	-4.351	Cluster	-2.774	Cluster	-4.140	Cluster	-2.148	Cluster
Gulf of California Xeric Scrub	-1.067	Random	-1.656	Random	-1.583	Random	-1.020	Random
Meseta Central Matorral	0.070	Random	0.207	Random	0.230	Random	-1.514	Random
Sonoran Desert	-3.141	Cluster	-2.134	Cluster	-4.140	Cluster	-2.148	Cluster
Tamaulipan Thorn Scrub	-1.541	Random	-1.374	Random	-0.683	Random	-0.641	Random

Ecoregions	MPD		MNTD		pMPD		pMNTD	
	Scores	Pattern	Scores	Pattern	Scores	Pattern	Scores	Pattern
Wyoming Basins	-2.888	Cluster	-2.659	Cluster	-2.704	Cluster	-1.453	Random
Upper East Gulf Coastal Plain	NA	NA	NA	NA	NA	NA	NA	NA
Willamette Valley-Puget Trough- Georgia Basin Temperate Conifer Forests	-3.255	Cluster	-2.744	Cluster	-2.157	Cluster	-1.346	Random
Mid-Atlantic Coastal Plain	NA	NA	NA	NA	NA	NA	NA	NA
Upper West Gulf Coastal Plain	NA	NA	NA	NA	NA	NA	NA	NA
Bajío Dry Forests	-0.591	Random	0.296	Random	0.263	Random	-0.399	Random
Sierra De La Laguna Dry Forests	NA	NA	NA	NA	NA	NA	NA	NA
Sierra De La Laguna Pine-Oak Forests	-0.068	Random	0.039	Random	-1.077	Random	-1.009	Random
San Lucan Xeric Scrub	-0.089	Random	-0.059	Random	-1.077	Random	-1.009	Random
Transitional								
Sierra Madre Occidental Pine-Oak Forests	-1.169	Random	-1.490	Random	-0.460	Random	-0.150	Random
Sierra Madre Oriental Pine-Oak Forests	0.175	Random	0.610	Random	-0.374	Random	-1.565	Random
Chiapas Montane Forests	1.088	Random	2.184	Overdispersed	-0.022	Random	0.027	Random
Chimalapas Montane Forests	0.450	Random	0.124	Random	0.426	Random	-1.446	Random
Oaxacan Montane Forests	0.345	Random	0.638	Random	0.730	Random	-0.031	Random
Sierra Madre De Chiapas Moist Forests	-0.277	Random	1.028	Random	0.109	Random	-0.489	Random
Veracruz Montane Forests	0.135	Random	0.249	Random	0.342	Random	-0.605	Random
Sierra Madre De Oaxaca Pine-Oak Forests	1.292	Random	1.286	Random	1.174	Random	-0.704	Random
Sierra Madre Del Sur Pine-Oak Forests	0.247	Random	0.738	Random	0.518	Random	-0.363	Random
Trans-Mexican Volcanic Belt Pine-Oak Forests	0.085	Random	0.360	Random	0.118	Random	-1.593	Random

Ecoregions	MPD		MNTD		pMPD		pMNTD	
	Scores	Pattern	Scores	Pattern	Scores	Pattern	Scores	Pattern
Neotropical								
Sonoran-Sinaloan Transition Subtropical Dry Forest	-1.149	Random	-0.652	Random	0.561	Random	-1.744	Random
Pantanos De Centla	2.552	Overdispersed	1.349	Random	1.228	Random	-0.075	Random
Petén-Veracruz Moist Forests	1.717	Random	1.820	Random	1.496	Random	1.437	Random
Sierra De Los Tuxtlas	1.914	Random	1.102	Random	1.602	Random	0.041	Random
Balsas Dry Forests	-0.642	Random	-0.005	Random	0.039	Random	-1.925	Random
Veracruz Moist Forests	0.304	Random	-0.522	Random	0.890	Random	-1.060	Random
Central American Dry Forests	-0.959	Random	0.691	Random	0.353	Random	-1.270	Random
Chiapas Depression Dry Forests	-1.296	Random	-0.204	Random	0.726	Random	0.076	Random
Jalisco Dry Forests	0.281	Random	0.503	Random	0.470	Random	-0.800	Random
Sinaloan Dry Forests	-1.148	Random	-0.646	Random	0.055	Random	-1.086	Random
Southern Pacific Dry Forests	0.598	Random	0.813	Random	-0.152	Random	-0.975	Random
Veracruz Dry Forests	2.008	Overdispersed	1.008	Random	0.884	Random	0.548	Random
Yucatán Dry Forests	-0.719	Random	-0.265	Random	0.604	Random	-0.916	Random
Yucatán Moist Forests	0.470	Random	0.603	Random	0.673	Random	-1.126	Random
Central American Pine-Oak Forests	-0.353	Random	0.153	Random	0.119	Random	-0.535	Random
Tehuacan Valley Matorral	0.192	Random	0.454	Random	0.715	Random	-2.434	Cluster
Mesoamerican Gulf-Caribbean Mangroves	1.742	Random	1.772	Random	1.302	Random	0.010	Random
Northern Mesoamerican Pacific Mangroves	-0.050	Random	-0.567	Random	0.917	Random	-0.088	Random
Southern Mesoamerican Pacific Mangroves	-1.084	Random	-1.535	Random	0.585	Random	0.188	Random

12 **Table S5** Phylogenetic and phenotypic structure scores by ecoregion in winter season. NA= one or none hummingbird species is
13 recorded

Ecoregions	MPD		MNTD		pMPD		pMNTD	
	Scores	Pattern	Scores	Pattern	Scores	Pattern	Scores	Pattern
Nearctic								
Central Appalachian Forest	NA	NA	NA	NA	NA	NA	NA	NA
Cumberlands and Southern Ridge and Valley	NA	NA	NA	NA	NA	NA	NA	NA
Great Lakes	NA	NA	NA	NA	NA	NA	NA	NA
High Allegheny Plateau	NA	NA	NA	NA	NA	NA	NA	NA
Interior Low Plateau	NA	NA	NA	NA	NA	NA	NA	NA
Lower New England	NA	NA	NA	NA	NA	NA	NA	NA
North Central Tillplain	NA	NA	NA	NA	NA	NA	NA	NA
Northern Appalachian	NA	NA	NA	NA	NA	NA	NA	NA
Ouachita Mountains	NA	NA	NA	NA	NA	NA	NA	NA
Ozarks	NA	NA	NA	NA	NA	NA	NA	NA
Piedmont	NA	NA	NA	NA	NA	NA	NA	NA
Prairie-Forest Border	NA	NA	NA	NA	NA	NA	NA	NA
Southern Blue Ridge	NA	NA	NA	NA	NA	NA	NA	NA
St. Lawrence-Champlain Valley	NA	NA	NA	NA	NA	NA	NA	NA
Superior Mixed Forest	NA	NA	NA	NA	NA	NA	NA	NA
Western Allegheny Plateau	NA	NA	NA	NA	NA	NA	NA	NA
Chesapeake Bay Lowlands	NA	NA	NA	NA	NA	NA	NA	NA
Florida Peninsula	-0.066	Random	-0.070	Random	-0.758	Random	-0.547	Random
South Atlantic Coastal Plain	NA	NA	NA	NA	NA	NA	NA	NA
West Gulf Coastal Plain	NA	NA	NA	NA	NA	NA	NA	NA

Ecoregions	MPD		MNTD		pMPD		pMNTD	
	Scores	Pattern	Scores	Pattern	Scores	Pattern	Scores	Pattern
Willamette Valley-Puget Trough-Georgia	-2.291	Cluster	-2.282	Cluster	-0.727	Random	-0.599	Random
Basin Temperate Broadleaf Mixed Forests								
Aspen Parkland	NA	NA	NA	NA	NA	NA	NA	NA
Central Tallgrass Prairie	NA	NA	NA	NA	NA	NA	NA	NA
Crosstimbers and Southern Tallgrass	-0.056	Random	-0.032	Random	-0.758	Random	-0.547	Random
Fescue-Mixed Grass Prairie	NA	NA	NA	NA	NA	NA	NA	NA
Northern Tallgrass Prairie	NA	NA	NA	NA	NA	NA	NA	NA
Osage Plains	NA	NA	NA	NA	NA	NA	NA	NA
Mississippi River Alluvial Plain	-0.014	Random	-0.074	Random	-0.758	Random	-0.537	Random
Arizona-New Mexico Mountains	-1.490	Random	-1.705	Random	-0.727	Random	-0.599	Random
California North Coast	-2.204	Cluster	-2.336	Cluster	-0.727	Random	-0.599	Random
Canadian Rocky Mountains	NA	NA	NA	NA	NA	NA	NA	NA
East Cascades-Modoc Plateau	-2.227	Cluster	-2.251	Cluster	-0.727	Random	-0.599	Random
East Gulf Coastal Plain	-0.059	Random	-0.033	Random	-0.758	Random	-0.547	Random
Gulf of Alaska Mountains and Fjordlands	NA	NA	NA	NA	NA	NA	NA	NA
Klamath Mountains	-2.275	Cluster	-2.266	Cluster	-0.727	Random	-0.599	Random
Sierra Nevada	-2.228	Cluster	-2.345	Cluster	-0.727	Random	-0.599	Random
Montane Cordillera	NA	NA	NA	NA	NA	NA	NA	NA
North Cascades	NA	NA	NA	NA	NA	NA	NA	NA
Pacific Northwest Coast	-2.126	Cluster	-2.333	Cluster	-0.727	Random	-0.599	Random
S.E Alaska-B.C Coastal Forest and	NA	NA	NA	NA	NA	NA	NA	NA
Southern Rocky Mountains	NA	NA	NA	NA	NA	NA	NA	NA
Utah High Plateaus	NA	NA	NA	NA	NA	NA	NA	NA

Ecoregions	MPD		MNTD		pMPD		pMNTD	
	Scores	Pattern	Scores	Pattern	Scores	Pattern	Scores	Pattern
Utah-Wyoming Rocky Mountains	NA	NA	NA	NA	NA	NA	NA	NA
West Gulf Coastal Plain	-0.038	Random	-0.003	Random	-0.758	Random	-0.547	Random
Middle Rockies-Blue Mountains	NA	NA	NA	NA	NA	NA	NA	NA
Okanagan	NA	NA	NA	NA	NA	NA	NA	NA
West Cascades	-2.307	Cluster	-2.243	Cluster	-0.727	Random	-0.599	Random
Boreal Cordillera	NA	NA	NA	NA	NA	NA	NA	NA
Gulf Coast Prairies and Marshes	-0.057	Random	-0.035	Random	-0.758	Random	-0.547	Random
Edwards Plateau	-0.015	Random	-0.069	Random	-0.758	Random	-0.547	Random
Southern Shortgrass Prairie	NA	NA	NA	NA	NA	NA	NA	NA
California Central Coast	-3.208	Cluster	-2.670	Cluster	-1.461	Random	-1.526	Random
California South Coast	-3.935	Cluster	-2.919	Cluster	-2.154	Cluster	-2.622	Cluster
Great Central Valley	-2.238	Cluster	-2.331	Cluster	-0.727	Random	-0.599	Random
Apache Highlands	-1.486	Random	-1.236	Random	-0.738	Random	-0.990	Random
Baja California Desert	-1.959	Random	-1.940	Random	-2.148	Cluster	-1.540	Random
Central Mexican Matorral	-1.336	Random	-0.664	Random	-2.347	Cluster	-1.195	Random
Chihuahuan Desert	-1.193	Random	-0.565	Random	-0.385	Random	-0.905	Random
Colorado Plateau	-2.330	Cluster	-2.390	Cluster	-0.727	Random	-0.599	Random
Columbia Plateau	-2.344	Cluster	-2.391	Cluster	-0.727	Random	-0.599	Random
Great Basin	-3.336	Cluster	-2.684	Cluster	-1.461	Random	-1.526	Random
Mojave Desert	-3.334	Cluster	-2.486	Cluster	-1.461	Random	-1.526	Random
Gulf of California Xeric Scrub	-1.057	Random	-1.584	Random	-1.571	Random	-1.028	Random
Meseta Central Matorral	-0.650	Random	-0.129	Random	-1.589	Random	-1.224	Random
Sonoran Desert	-3.202	Cluster	-1.620	Random	-0.089	Random	-0.887	Random
Tamaulipan Thorn Scrub	-0.809	Random	-0.839	Random	-0.757	Random	-0.1461	Random

Ecoregions	MPD		MNTD		pMPD		pMNTD	
	Scores	Pattern	Scores	Pattern	Scores	Pattern	Scores	Pattern
Wyoming Basins	NA	NA	NA	NA	NA	NA	NA	NA
Upper East Gulf Coastal Plain	-0.448	Random	-0.041	Random	-0.758	Random	-0.547	Random
Willamette Valley-Puget Trough- Georgia Basin Temperate Conifer Forests	NA	NA	NA	NA	NA	NA	NA	NA
Mid-Atlantic Coastal Plain	NA	NA	NA	NA	NA	NA	NA	NA
Upper West Gulf Coastal Plain	NA	NA	NA	NA	NA	NA	NA	NA
Bajío Dry Forests	-1.313	Random	0.180	Random	-1.976	Cluster	-1.367	Random
Sierra De La Laguna Dry Forests	NA	NA	NA	NA	NA	NA	NA	NA
Sierra De La Laguna Pine-Oak Forests	-1.193	Random	-1.474	Random	-1.571	Random	-1.028	Random
San Lucan Xeric Scrub	-1.102	Random	-1.544	Random	-1.571	Random	-1.028	Random
Transitional								
Sierra Madre Occidental Pine-Oak Forests	-2.717	Cluster	-1.789	Random	-1.757	Random	-0.337	Random
Sierra Madre Oriental Pine-Oak Forests	-0.130	Random	0.469	Random	-0.795	Random	-1.407	Random
Chiapas Montane Forests	0.695	Random	1.878	Random	-0.574	Random	0.523	Random
Chimalapas Montane Forests	0.114	Random	-0.137	Random	0.771	Random	-0.518	Random
Oaxacan Montane Forests	0.105	Random	0.487	Random	0.289	Random	-0.125	Random
Sierra Madre De Chiapas Moist Forests	-0.411	Random	0.763	Random	-0.010	Random	-0.415	Random
Veracruz Montane Forests	-0.231	Random	0.014	Random	0.592	Random	-1.772	Montane
Sierra Madre De Oaxaca Pine-Oak Forests	-0.310	Random	0.782	Random	1.052	Random	-0.815	Random
Sierra Madre Del Sur Pine-Oak Forests	-0.367	Random	0.354	Random	0.469	Random	-0.203	Random
Trans-Mexican Volcanic Belt Pine-Oak Forests	-1.674	Random	-0.266	Random	-1.163	Random	-1.666	Random

Ecoregions	MPD		MNTD		pMPD		pMNTD	
	Scores	Pattern	Scores	Pattern	Scores	Pattern	Scores	Pattern
Neotropical								
Sonoran-Sinaloan Transition Subtropical Dry Forest	-1.306	Random	-1.092	Random	0.242	Random	-1.280	Random
Pantanos De Centla	2.529	Overdispersed	1.721	Random	1.143	Random	-0.193	Random
Petén-Veracruz Moist Forests	1.641	Random	1.246	Random	0.976	Random	0.913	Random
Sierra De Los Tuxtlas	1.846	Random	0.916	Random	1.349	Random	0.392	Random
Balsas Dry Forests	-2.240	Cluster	-1.139	Random	-1.007	Random	-0.777	Random
Veracruz Moist Forests	0.015	Random	0.013	Random	0.904	Random	-1.262	Random
Central American Dry Forests	0.002	Random	0.351	Random	0.550	Random	-0.643	Random
Chiapas Depression Dry Forests	-1.620	Random	-0.291	Random	0.275	Random	0.055	Random
Jalisco Dry Forests	-1.562	Random	-0.226	Random	-0.992	Random	-1.421	Random
Sinaloan Dry Forests	-3.027	Cluster	-1.587	Random	-1.810	Random	-2.102	Cluster
Southern Pacific Dry Forests	-0.488	Random	0.070	Random	-0.058	Random	-0.834	Random
Veracruz Dry Forests	1.180	Random	-0.690	Random	0.811	Random	0.200	Random
Yucatán Dry Forests	-0.552	Random	0.108	Random	0.964	Random	-1.846	Random
Yucatán Moist Forests	0.560	Random	1.022	Random	0.991	Random	-1.771	Random
Central American Pine-Oak Forests	-0.529	Random	0.179	Random	-0.368	Random	-0.204	Random
Tehuacan Valley Matorral	-0.245	Random	0.105	Random	-1.423	Random	-2.364	Cluster
Mesoamerican Gulf-Caribbean Mangroves	1.648	Random	1.287	Random	1.308	Random	0.872	Random
Northern Mesoamerican Pacific Mangroves	-0.257	Random	-1.045	Random	0.706	Random	0.495	Random
Southern Mesoamerican Pacific Mangroves	-1.245	Random	-1.392	Random	-0.115	Random	-0.050	Random

Fig. S1 Morphological measures. a) Measurement of the length of the exposed culmen (i), and the depth of the bill (ii); b) measurement of the bill length (iii), and the bill angle (iv) using the iii as the base line (0°) and the base of the bill as the origin; c) measurement of the length of one the central rectrices (CR; v); d) measurement of the width of the bill (vi), the secondary length of wing (vii), and the wing chord (viii)

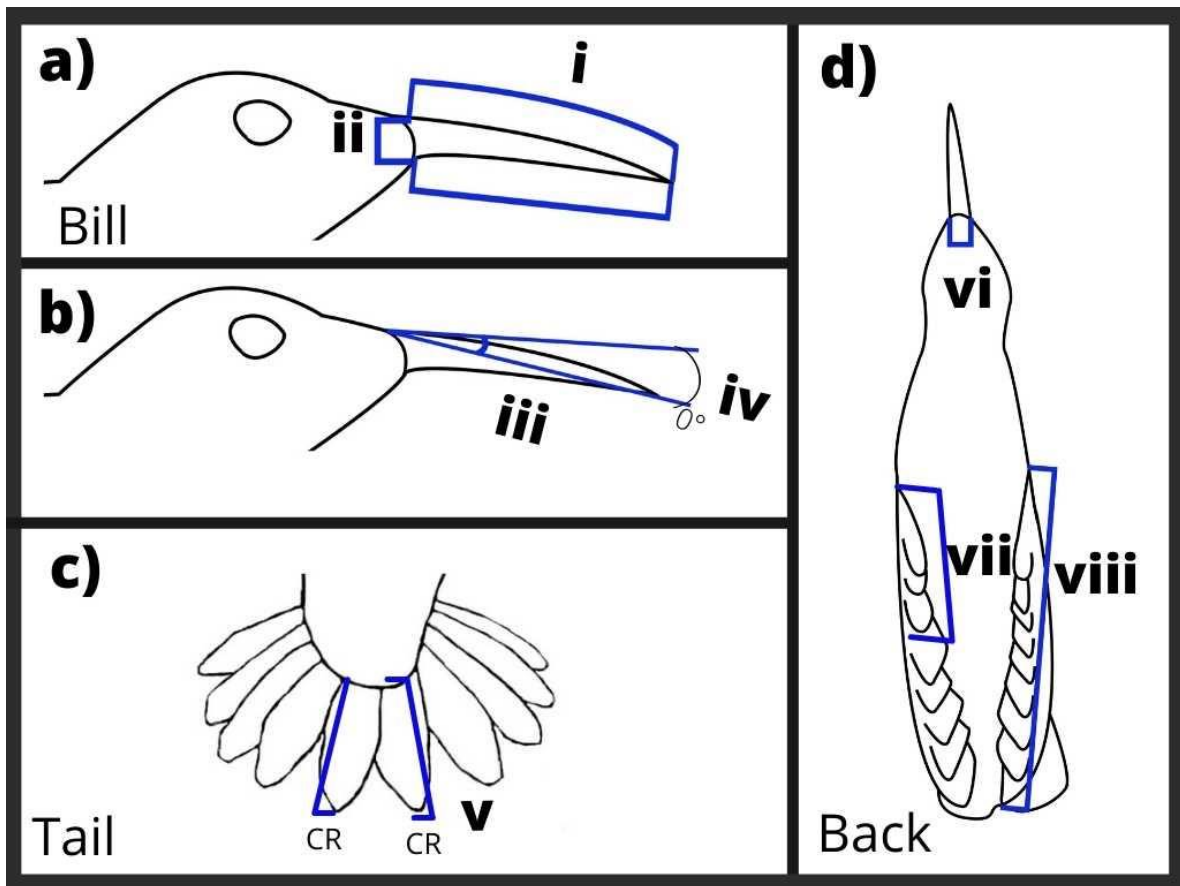


Fig. S2 Major geographic regions grouping 105 level II ecoregions according to biogeographic affinity

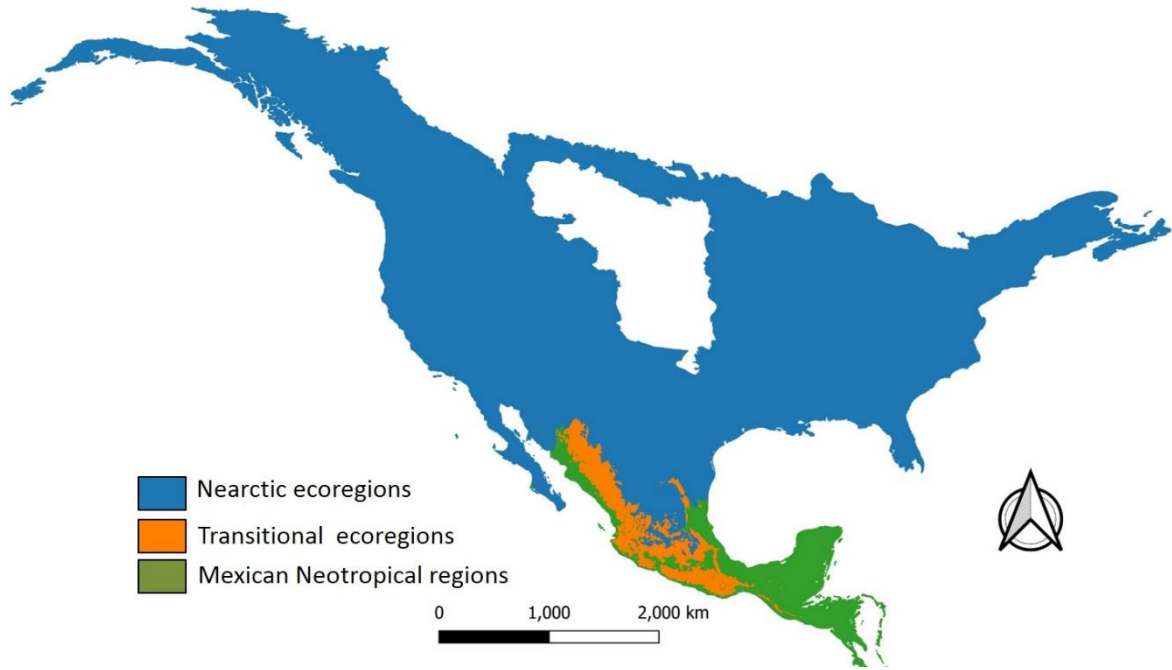


Fig. S3 Trochilidae phylogenetic tree proposed by McGuire et al. 2014 modified for North American species

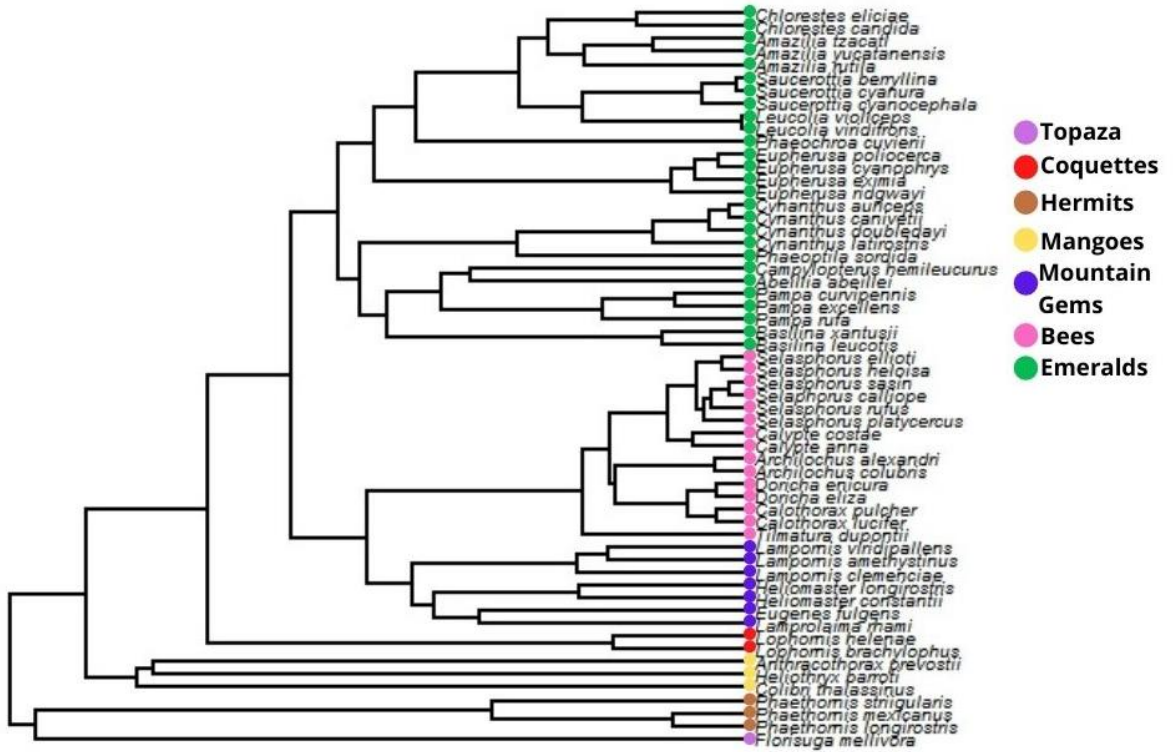
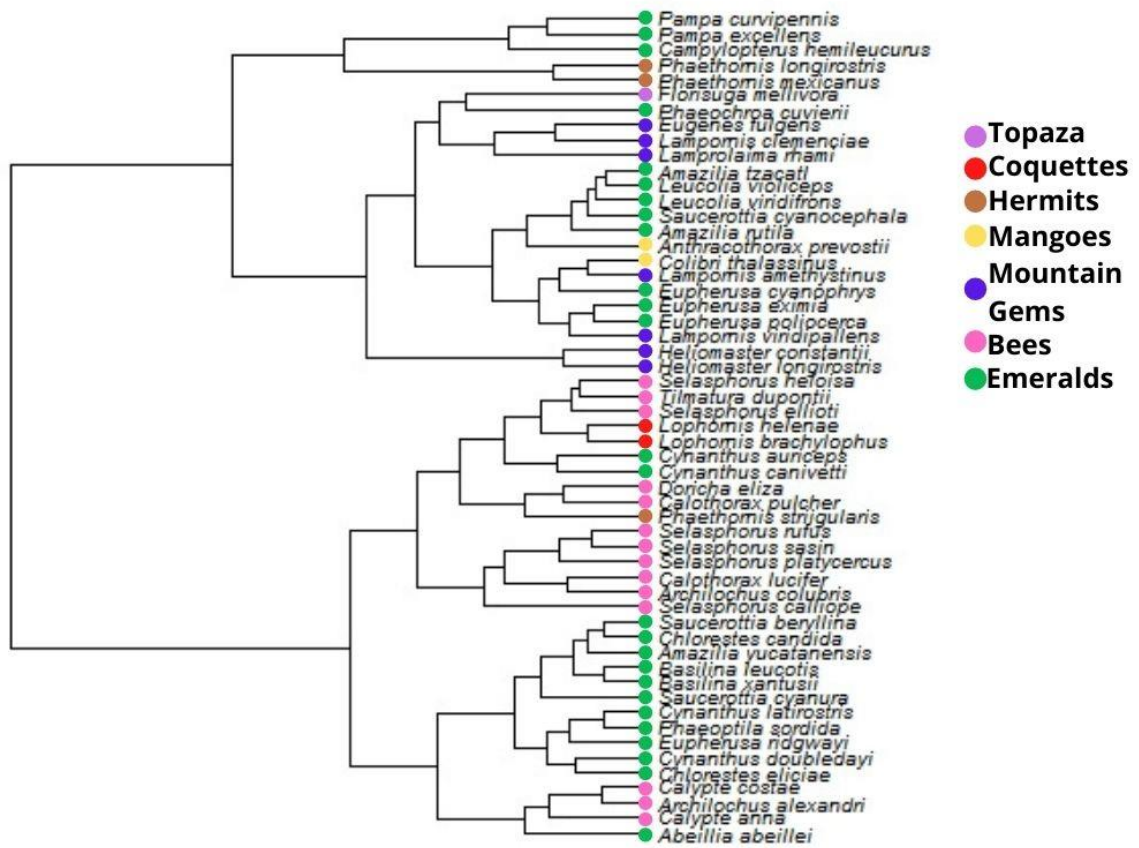


Fig. S4 Cluster dendrogram of morphological similarity based in the Euclidean matrix and grouped by complete linkage



Capítulo 2: Ecological opportunity as a promoter of morphological evolution in a likely North American hummingbird species radiation in North America.

Ecological opportunity as a promoter of morphological evolution in a likely hummingbird species radiation in North America

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Abstract

Aim

To analyze the morphological evolution in a nearly endemic radiation of hummingbirds in North America as a probable result of the influence of the three ecological opportunity conditions (access to a new geographic space, absence of competitors, and evolutionary innovation).

Location

Mainland North America (Mexico, USA and Canada).

Taxon

Hummingbirds (Aves: Trochilidae).

Methods

To analyze morphological evolution in North American hummingbirds, we assessed the three ecological opportunity conditions based on a molecular phylogenetic tree of hummingbirds and 11 morphological traits. We performed a phylogenetic principal component analysis (PPCA) and built disparity-through-time (DTT) plots to inspect the

evolution of traits. To evaluate the role of potential competitors, we estimated lineage diversity through time and standardized independent contrasts (IC) and assessed their relationship with morphological evolution rate via regression models.

Results

Our results showed that in North American hummingbirds, species in the Bees and Mountain Gems clades occupy relatively well-differentiated morphospaces, while Emeralds and Hermits occupy a wider range of body sizes. In addition, Bees and Mountain Gems showed a wide variation in bill curvature and tarsus length, in comparison to straighter bills in other clades (excepting Hermits). DTT plots suggest that body size is a conserved trait in the Bees + Mountain Gems clade, while bill and wing shape are highly labile traits. DTT values of bill traits and wing shape suggest shifts in concert with several Emerald invasions from South American. Regression models indicate that lineage diversity is related to the increase of body size, bill traits, tarsi length and wing shape variance in Bees and Mountain Gems.

Main conclusions We found that in Bees and Mountain Gems, the three conditions for ecological opportunity have promoted several pulses of morphological diversification, for which some traits are key in primary niche partitioning. Our analysis suggests that the arrival of the common ancestor of Bees and Mountain Gems in North America may have promoted niche partitioning mainly related to body size. In addition, the presence of competitors may have influenced morphological evolution, especially upon the arrival of the Emeralds into the region. Our results suggest a priority effect in which Bees and Mountain Gems may have constrained the colonization of species of small and large body sizes, leaving the intermediate size to be occupied by Emeralds.

Keywords: niche filling model, priority effect, species radiation, Trochilidae.

Introduction

Throughout the assembly process, evolutionary and/or ecological changes may lead to ecological opportunity in biotic communities, which may generate ecological release (Yoder et al., 2010). Ecological opportunity, which refers to the relaxation of natural selection over one or more ecological traits (Yoder et al., 2010), may be originated due to: (1) access to a new geographic area, (2) absence of antagonist species, and (3) the evolution of key innovations for accessing to new resources (Schluter, 2000; Mahler et al., 2010). Relaxation in natural selection may increase either the rate of lineage diversification or phenotypic variance, both of which may be achieved through changes in demography (e.g., the increase of population density), or through the increase in trait variation within populations (Yoder et al., 2010). These changes may lead to character displacement (Bassar et al., 2017), a process in which co-occurring species with similar ecological requirements diverge in at least one trait (Brown & Wilson, 1956; Bassar et al., 2017), promoting phenotypic diversity and ecological niche partitioning (Schluter, 2000; Webb et al., 2002). When both character displacement and lineage diversification are followed by speciation occurring in a short time span, an adaptive radiation may be advocated (Glor, 2010; Yoder et al., 2010). As speciation proceeds, niches are filled up and ecological opportunity decreases, producing lineage and phenotypic diversification to slow down (Losos & Mahler, 2010).

With nearly 338 species, the New World hummingbirds (Aves: Trochilidae) are one of the richest bird families. The family is divided into nine clades (McGuire et al., 2007; McGuire et al., 2014) indicating a great diversification largely associated with significant orogenic events, such as the Andean uplift (Bleiweiss, 1998a; McGuire et al., 2014). The extensive hummingbird diversification is also expressed in a wide ecological distribution, covering almost all habitats whose (mostly) nectar resources exploit through an extensive morphological diversity (Bleiweiss, 1998b; Altshuler & Dudley, 2002; Stiles, 2008; Abrahamczyk & Kessler, 2015), which allow different hummingbird species to

coexist (Rodríguez-Flores & Arizmendi, 2016; López-Segoviano et al., 2008; Abrahamczyk & Kessler, 2015; González et al., 2018; Maruyama et al., 2018; Rodríguez-Flores et al., 2019). Biogeographic history and past ecological conditions have both played significant roles in hummingbird lineage diversification, but also on the evolution of morphological traits, which have influenced community assembly processes and the shaping of different biotic interactions (Martin & Ghalambor, 2014; Rodríguez-Flores & Arizmendi, 2016, Bribiesca et al. 2019).

North America is inhabited by a few hummingbird clades of relatively recent arrival, some of which show accelerated diversification rates and a high species richness, such as the nearly endemic Bees and Mountain Gems clades. The ample morphological diversity and wide ecological distribution suggest that these taxa may be considered as an adaptive radiation (McGuire et al., 2014; Rodríguez-Flores et al., 2019). Due to these characteristics, we expect that the ecological opportunity may be reflected in morphological disparity among clades followed by a niche filling process that decreased the morphological disparity towards the present (Mahler et al., 2010).

In this study we assessed the influence of the ecological opportunity in the evolution of morphological traits through time, as well as on diversification and the assembly process of North American hummingbird communities. We approached this through the analyses of the three proposed conditions for the recognition of ecological opportunity: (1) the access to a new geographic area, (2) the absence of competitors, and (3) the development of key innovations, all of which may indicate an adaptive radiation at the regional scale. We estimated the phylomorphospace of hummingbird assemblages in three biogeographic regions of North America (Neotropical, Transitional and Nearctic, Morrone et al. 2017), and analyzed changes in the morphological space of assemblages over time using plots of disparity through time (DTT). We also estimated the accumulation of lineage richness over time to evaluate the role of absence/presence of competitors in the evolution of morphological disparity.

Materials and Methods

Study area

North America (here considered as Mexico, USA and Canada) is a biotically complex area in which two biogeographic regions abut in its southern portion (Morrone et al., 2017): the Nearctic, from central and northern Mexico to Alaska and northern Canada; and the Neotropical region, ranging from central Mexico to southern South America. These two regions overlap in the mountains of central Mexico (Morrone et al. 2017), which is inhabited by a mixing of species with different biogeographic origins, but that has also promoted the evolution *in situ* of a high number of endemic species, mostly distributed in semihumid and temperate highland forests (Espinosa et al., 2008; Escalante et al., 2013). This area is therefore biotically distinctive, allowing its recognition as a Transitional region (Morrone et al., 2017).

Morphological and Phylogenetic Data

Our study is based on morphological data from adult male specimens in the Colección Nacional de Aves, Instituto de Biología, and in the Museo de Zoología “Alfonso L. Herrera”, Facultad de Ciencias, both at the UNAM. We measured 12 traits, 9 of these directly from skin specimens: (1) length of the exposed culmen; (2) angle, (3) length, (4) width, and (5) depth of the bill; (6) tarsus length, (7) wing chord, (8) secondary length of wing (distance from carpal joint to the tip of the first secondary feather), and (9) length of central rectrices. Two additional traits were calculated using measurements from the original traits (see below for details): (10) bill curvature and (11) hand-wing index (HWI). All of these traits are likely related to foraging strategies, flying efficiency, and habitat use (see Wolf et al., 1972 for details; Feisinger & Colwell, 1978; Zeffer et al., 2003; Temeles et al., 2009; Claramunt et al., 2012; Graham et al., 2012; Jønsson et al., 2015). We also obtained the (12) weight of each specimen as recorded from the specimen label.

To calculate bill curvature, we used measurements from the bill angle and bill length with the formula (Temeles et al., 2009):

$$K = \frac{1}{\frac{\frac{1}{2}C}{\text{sen}(\text{radians } A)}}$$

where K is the curvature, C reflects the length between the base and tip of the bill, and A corresponds to the angle of the bill.

We estimated HWI as a measure of wing shape (Claramunt et al., 2012) using the wing chord and the second length of wing measurements via the following formula:

$$HWI = 100 * \left(\frac{\text{wing chord} - \text{second length of wing}}{\text{wing chord}} \right).$$

We used a published molecular phylogenetic tree for hummingbirds (McGuire et al., 2014), kindly provided by J. McGuire. Given that some North American species were not included in the original phylogenetic tree (e.g. *Lophornis brachylophus*, *L. helenae*, *Doricha enicura*, *Calothorax pulcher*, *Selasphorus ellioti*, *Cynanthus auriceps*, and *Pampa curvipennis*), we added them by attaching each of these taxa to its putative sister taxon or closest relative (e.g. *L. delattrei*, for *L. brachylophus* + *L. helenae*; *D. eliza*; *Calothorax lucifer*, *S. heloisa*; *C. canivetti*, and *P. excellens*, respectively; Banks, 1990; Monroe et al., 1995; Licona-Vera & Ornelas, 2017; Stiles et al., 2017) using the *bind.tip* function in phytools (Revell, 2012) for R (R Development Core Team, 2017). After adding these taxa, we pruned the original phylogenetic tree to get a modified phylogeny including only North American taxa.

To both maximize the variance and reduce the dimensionality of our morphological trait matrix, we performed a phylogenetic principal component analysis (PPCA; Revell, 2009), which corrects the non-independence of morphological data due

to shared genealogic history of closely related species (Revell, 2009). PPCA requires of a phenotypic trait matrix for which we natural log transformed the average of measures by species, and of a phylogenetic tree, for which we used the pruned tree of North American hummingbirds (see above). We estimated PPCA using the *phy.pca* function in phytools (Revell, 2012) for R (R Development Core Team, 2017). The first component (PC1) accumulated 60.79% of variance and was mainly related to body size, while PC2 accumulated 10.88% and was mainly related to bill curvature and tarsus length. PC3 was related to the shape of the bill and accumulated 8.59% of the variance, and PC4 was related to the shape of the wing and accumulated a 7.42% of the variance (Tables S1-S2). We used the four principal components and our modified phylogenetic tree to build phylomorphospaces using the *phylomorphospace* function (Sidlauskas, 2008) in phytools (Revell, 2012) for R (R Development Core Team, 2017). These projections are useful to differentiate clades with broad morphological diversification from clades showing a relatively limited diversification in a multivariate space (Sidlauskas, 2008).

Ecological opportunity

Three conditions have been proposed as drivers of ecological opportunity (Schluter, 2000; Losos & Mahler, 2010; Yoder et al., 2010): (1) access to a new geographic area, (2) absence of antagonist species, and (3) the evolution of innovations for accessing to new resources. Given that phylogenetic analyses have suggested that the colonization process of North America started with the arrival of the common ancestor of Bees and Mountain Gems (McGuire et al., 2014), to analyze the effect of access to a new geographic area (1), we performed morphological evolution analyses and node-based methods, which estimate probabilities of lineage presence and trait diversity for each node in the phylogeny (Pagel, 1999; Harmon et al., 2008). To approach morphological evolution, we performed Disparity through time (DTT) analyses, which estimate disparity

from an average Euclidean pairwise distance for a given phylogeny (in our study, the modified phylogenetic tree); and for each node also (Harmon et al., 2003). We used the *dtt* function in *geiger* (Harmon et al., 2008) for R, in which values approaching to 0 indicate that the total variation of a given trait is split between the different subclades, suggesting that trait evolution may be conserved; while values close to 1 indicate that each subclade has a significant portion of the variation, suggesting trait lability or evolutionary convergence (Harmon et al., 2003). We calculated disparity using the four main components (PC1-PC4) separately. To test the significance of the DTT values, we used the *dtt* function to construct null models by running 1,000 simulations of Brownian motion trait evolution for each plot, which allowed us to assess if the disparity of our morphological data differ from the disparity expected due to random evolution (Harmon et al., 2003; Harmon et al., 2008). Using both values from null model comparisons and observed values, we calculated a morphological disparity index (MDI), which quantifies the overall difference in relative disparity of a clade compared to a null model. Negative MDI values indicate a higher degree of partition of morphological variance among subclades than expected under a Brownian motion model, suggesting that trait evolution is conserved; while positive MDI values indicate high degree of overlap of morphological variance among subclades, suggesting lability of the trait and possibly, evolutionary convergence (Harmon et al., 2003).

Despite its South American origin, Emeralds is the richest clade in North America due to different colonization events followed by *in situ* diversification processes (García-Moreno et al., 2006; García-Deras et al., 2008; Ornelas et al., 2014; Rodríguez-Gómez and Ornelas, 2013; Zamudio-Beltrán and Hernández-Baños, 2015; Zamudio-Beltrán and Hernández-Baños, 2018). We therefore performed a separate DTT analysis including the Emeralds, Bees and Mountain Gems clades considering the probable date of each colonization event (McGuire et al., 2014) to explore their possible effects in the morphological evolution of Bees + Mountain Gems. We expected DTT values to

decrease after each colonization event, suggesting morphological differentiation probably due to niche partitioning (Jønsson, et al., 2015). We considered the date of divergence as the date of invasion into North America from its South American sister clade, and estimated node dates using depth of the nodes with the *node.depth.edgelen* function in ape (Paradis, 2006).

To evaluate the effect in morphological evolution of the absence of competitors from other hummingbird lineages (2), we required of the estimation of the variation in the number of potentially competitor species over time. To do this, we estimated lineage diversity through time using a modification of a method proposed by Mahler et al., (2010) as follows: we reconstructed ancestral presences in the three considered biogeographic regions through building a matrix of current presences using potential distribution maps of each species from NatureServe (BirdLife International and NatureServe, 2014) and CONABIO (Navarro and Peterson, 2007), which allowed us to establish the species composition of each region by the overlapping of distribution maps and the biogeographic regions using ArcGis 10.1 (ESRI, 2012). We performed the reconstruction of ancestral presences using the *ace* function as implemented in ape (Paradis, 2006) for R (R Development Core Team, 2017), in which the presence/absence in each region is considered as a discrete character, allowing the calculation of a probability of presence via a maximum likelihood approach (Pagel, 1994; Paradis, 2006). Unlike Mahler et al. (2010), we performed the reconstruction of ancestral presences using a 2 x 2 matrix with unequal transition rates, in which the *absence* to *presence* transition had a higher weight (Pagel, 1994). We favored this scheme because of the wide distributional range of many species, as well as due to the migratory behavior in some Nearctic species, which spans more than one biogeographic region. The probability of presence at each node obtained from the reconstruction allows the establishment of a marginal probability (per node) of presence (see Mahler et al. 2010) in each biogeographic region. Then, for each biogeographic region, we estimated lineage accumulation at each node using the sum

of marginal probabilities of ancestral nodes. We did not include species from Topazas, Hermits, Mangoes, Coquettes and Emeralds clades because most diversification events in these groups occurred primarily outside North America, which may lead to biases in lineage accumulation estimations in our study area. Although our modification to the method admittedly underestimates current lineage diversity due to exclusion of more recent invasions and *in situ* diversification processes, it allowed us to estimate the increase of lineage accumulation during the first stages of hummingbird colonization of North America.

To evaluate if morphological evolution is negatively related with lineage accumulation in North American hummingbirds, we used standardized phylogenetic independent contrasts (PIC; Felsenstein, 1985). We calculated PIC using the *pic* function in *ape* (Paradis, 2006) for R (R Development Core Team, 2017). PIC quantifies differences between closely related clades, estimating values of the morphological attribute of interest in each node and weighting it with phylogenetic distance (Felsenstein, 1985). For PIC calculation, we used our modified phylogenetic tree, as well as PPCA scores. We calculated PIC for the first four (PC1-PC4) separately, and by biogeographic region. We then performed linear regression models for each PC explained by lineage diversity and included an additional model using relative time as explanatory variable. To calculate relative time, we used the depth of the nodes obtained with the *node.depth.edgelen* function in *ape* (Paradis, 2006), which we transformed to a proportional measure. We used lineage accumulation as the explanatory variable and PICs as the dependent variable for linear regression models. Linear regressions models were assessed via corrected Akaike Information Criterion (AICc), ΔAIC (<2.00) and the weight of the models (Johnson & Omland, 2004). For model selection, we used MuMIn (Bartón, 2018) for R (R Development Core Team, 2017). According to a hypothesis of radiation driven by ecological opportunity, we expect linear models of PICs variation explained by lineage diversity to show a better fit in comparison to models explained by

time. Also, we expect models of conserved traits to show a positive association, while models of convergent traits may be associated negatively (see Felsenstein, 1985; see Webb et al., 2002).

Results

We measured a total of 803 specimens of 55 species. Our pruned phylogenetic tree however, included 58 hummingbird species (Fig. S1). The most diverse clades were Mountain Gems (seven species), Bees (15 species) and Emeralds (27 species), these latter represented more than 80% of the species richness in North America.

Phylomorphospace plots showed that most clades occupy relatively well defined morphospaces along PC1 (body size; Fig. 1; Fig. S2). North American Bees and Mountain Gems occupy relatively well-differentiated morphological spaces, while the Emeralds and Hermits clade spanned a wide range of body sizes. Most species in the Emeralds clade are located in between Bees and Mountain Gems clades, although *Cynanthus canivetii*, *C. auriceps* and *Abeillia abeillei* overlapped with the small body-sized Bees; while *Amazilia rutila*, *A. tzacatl*, *Leucolia violiceps*, *Saucerottia cyanocephala* and *Eupherusa eximia* overlapped with species in the large-sized Mountain Gems clade (Fig. S2). Some Emeralds species (e.g., *Pampa excellens*, *Campylopterus hemileucurus*) show a trend toward larger body-sizes, comparable to large Hermit species. Migratory species in the Bees clade showed a large body-size in comparison to resident Bee species. For bill curvature and tarsus length (PC2), the North American Bees and Mountain Gems clades showed the widest range of variation, while clades like Emeralds, Coquettes, Mangoes and Topazes showed mostly straighter bills and longer tarsi. In addition, within the Bees clade, migratory species showed major proportion of variance (i.e., curved bills). Regarding bill shape (PC3), the Emeralds showed a reduced variation, while Bees, Mountain Gems and Mangoes showed a higher

variance in comparison to the rest of the clades, with the Hermits clade showing values towards more curved bills (Fig. S3). For wing shape (PC4), three groups were apparent. The largest group includes species with intermediate wing shapes, such as Emeralds, Hermits, Coquettes and some species in the Mangoes (*Colibri thalassinus*) and Mountain Gems (*Heliomaster longirostris*, *Lampornis amethystinus* and *Lamprolaima rhami*) clades. A second group included several migratory species (*Selasphorus sasin*, *S. calliope*, *S. rufus*, *Archilochus colubris*, *Calothorax lucifer*; Fig. S4) with wide wing shapes which tended to separate from the rest, although some of their closest relatives (*S. platycercus*, *A. alexandrei*, *C. pulcher*) were nested within the main group of intermediate wing shape. The third group included species from Topazas (one species), Mountain Gems (four species), Mangoes (one species), and Emeralds (two species) with a slender wing shape.

As it may be expected, geographic patterns (Fig. S5) based on PPCA showed that the morphological variation tended to decrease towards the Nearctics, in which hummingbird species showed small to medium body sizes (PC1), straighter bills and a more limited bill shape variation than hummingbirds in Neotropical and Transitional regions (see bill traits in PC2, and PC3). Regarding wing shape (PC4), morphometric variation showed almost the same variation across all regions. This might be unexpected given the lower species number in the Nearctic species assemblage, but this pattern may be likely due to the different wing shapes in migratory and resident species inhabiting this biogeographic region (Fig. S4).

The DTT plot for the Bees + Mountain Gems clade (Fig. 2A) showed a steady pattern of morphological space partition (values close to 0) for body size (PC1) suggesting that this trait has been conserved among species in these clades since the early colonization of North America; other morphological traits (PC2-PC4) however, showed high lability. As expected, bill traits (PC2 and PC3) showed highly similar patterns, with two pulses of differentiation at older and medium relative times (relative

time 0.6). Bill shape (PC3) at older times (relative time >0.6) showed high differentiation regarding bill curvature (PC2), suggesting niche partitioning toward the present. For wing shape (PC4), most variation was partitioned within species in the same clade suggesting convergence at recent times but a conservative pattern at older times (relative time 0.0-0.4) probably related with the differentiation of body size between the Bees and Mountain Gems and their different feed strategies (e.g., territoriality and trap lining) as well as the evolution of migratory behavior within the Bees clade. MDI values (Table 1) of Bees + Mountain Gems showed that body size (PC1) evolution is significantly different from a Brownian motion evolution (MDI= -0.3241, *p-value* =0.015), indicating that this trait is conserved; however, bill traits, tarsus length and wing shape (PC2-PC4) were not. When the Emeralds clade was added to the DTT analysis (Fig. 2B), disparity patterns between relative time 0 and 0.2 showed that all traits tended to 1.0, suggesting high trait lability and probably convergent evolution; but after the relative time 0.2 DDT body size values decrease, and around relative time 0.4 body size showed a conserved pattern. Bill traits (PC2 and PC3) showed DTT values that suggest convergence in older and towards recent times (since relative time 0.7). Similarly, wing shape (PC4) showed convergence (higher portion of variation) within clades at older and towards recent times (especially since relative time 0.7). MDI values of Bees + Mountain Gems + Emeralds clade indicate that bill traits (PC2 and PC3), wing shape (PC4), and body size (PC1) were not significant different from a Brownian motion evolution (Table 1). On the other hand, when the Bees and Mountain Gems clade are considered together with the possible date of invasions from species in the Emerald clade (Fig. 2C), DTT plots suggest that disparity values of bill traits (PC2 and PC3) and wing shape (PC4) shifted in coincidence with several Emerald invasions, mostly at relative intermediate times (~0.6). These shifts took different directions; while bill curvature and wing shape increased their DDT values suggesting high lability (i.e., convergence); bill shape values shifted from high disparity to a Brownian evolution pattern. During the last invasion (between 0.8 and 1.0) match

with a decrease of DTT values for bill curvature and wing shape, but DTT values keep above the mean DTT values suggesting convergent evolution.

The estimation of lineage diversity accumulation over time for the Bees + Mountain Gems clade showed high rates of lineage accumulation in the three biogeographic regions of North America (Fig. 3). As expected, lineage accumulation in the Neotropical region is higher since earlier stages. Lineage accumulation showed highly similar values in the Transitional and the Nearctics, but with higher diversity in the Transitional region at intermediate times (relative time between 0.6 and 0.8). Lineage accumulation seem to have reached saturation at relatively recent times (~0.2).

The regression models for PIC of PC axes showed that models explained by the diversity of lineages in each region had a better fit than the model explained by time (Table S2). In addition, all these models presented positive relationships between PIC with relative time or lineage diversity, respectively (Fig. S6). The PIC model of PC3 explained by time presented a negative relationship, but with a better fit than those explained by lineage diversity, however the weight of the model was less than 50%.

Discussion

In hummingbirds, factors such as interspecific competition, habitat filtering, and the distribution and abundance of resources among others, all may have influenced morphological evolution and diversification of lineages, both locally and regionally (Weinstein & Graham, 2016; Martín González et al., 2018; Rodriguez-Flores et al., 2019). Our results are consistent with a study of hummingbird-plant interaction networks at the continental scale, in which the wing and bill traits were found to be labile in North American taxa (Rodriguez-Flores et al., 2019).

According to our results, ecological opportunity has influenced the morphological evolution of Bees and Mountain Gems in North America. First, the DTT plot (Fig. 2A), suggests that the arrival of the common ancestor of these two clades to a new geographic region may have promoted niche partitioning related to body size, similar to other mainland radiations in other vertebrates such as ovenbirds, woodcreepers (Derryberry et al., 2011), and cichlids (Arbor & López-Fernández 2013). In these North American hummingbirds, body size differentiation probably allowed for the partitioning of the morphological space into small (Bees) and large (Mountain Gems) species. Thus, niche partitioning may have led to a reduced interspecific competition (see Yoder et al., 2010; Jønsson et al., 2012; Bassar et al., 2017) by promoting the evolution of different feeding strategies (e.g., territoriality and trap-lining), which allowed different hummingbirds species to co-occur (Brown & Bowers, 1985; Martin and Ghalambor, 2014; López-Segoviano et al., 2018; Bribiesca et al., 2019). In addition to body size, other traits may be also related to character displacement and niche partition, such as bill curvature, tarsus length and wing shape, all of which showed high values of disparity. Differences in bill curvature are related to feeding specialization (Izquierdo-Palma et al., 2021; Ocampo-Sandoval et al., 2021), variation in the tarsus length is related to perching time (Stiles, 2008) and probably to territoriality, and wing length may be also under ecological and sexual pressures derived from foraging and aerial fight performance. This pattern is similar to that reported in the Madagascan vangas adaptive radiation (Jønsson et al., 2012), in which, according to a niche filling model, body size is the first trait for niche space partitioning, followed by a second niche partitioning mediated by the bill shape.

The second source of ecological opportunity is related to the absence of competitive and predator species. Given the relatively frequent specialized use of resources in Trochilidae, we here considered other hummingbird lineages as potentially competitor species (Webb et al., 2002; see Mahler et al., 2010). Regression models

(Table 2; Fig. S6) showed that lineage diversity through time explained PIC in all traits, suggesting that the presence of competitors may have influenced morphological evolution, especially upon the arrival of the Emeralds into the region. According to our expectations, body size (a conservative trait) showed a positive relationship between PICs and lineage diversity in the regression models in the three regions (Fig. S6). This may be due to the arrival of lineages from South America, particularly Emeralds, which likely occupied the available morphological spaces (mainly medium body sizes, Fig. 1), limiting Bees (small body size) and Mountain Gems (larger body size) clades to cover the morphological space outside intermediate sizes (Fig. 1). This pattern is similar to that described by Jønsson et al., (2015) for passerine birds and the colonization and diversification in the Oriental and Australian regions, therefore describing a priority effect. In the priority effect, the early arrival and diversification of a lineage may constrain the diversification processes for secondary colonization lineages (see Fukami, 2015; Jønsson et al., 2015). Our results suggest that this priority effect may have occurred in two separated events. First, Bees and Mountain Gems may have constrained the colonization of species of small and large body sizes, leaving the intermediate size as the available morphological space, which was occupied by Emeralds. Second, for the body size partition among Bees, Mountain Gems and Emeralds, a priority effect by these clades may have inhibited the diversification of other secondary colonizing North American lineages, such as Mangoes or Coquettes, or later invasions by different South American lineages. However, despite the constrained morphological space in body size, Emeralds are the richest clade of North America. The Emeralds clade arrived into North America ~7 million years after the diversification of the Bees and Mountain Gems clade (McGuire et al., 2014), probably first diversifying in the available morpho-ecological spaces, and then promoting the diversification of Bees and Mountain Gems clades, as suggested in the DTT plots. This suggest that a priority effect of the first colonizers (Bees+ Mountain Gems) did not inhibit the arrival of the second colonizers (Emeralds) but constrained their subsequent diversification (Schenk et al., 2013; Rowsey et al.,

2018). Although probably constrained to occupy mostly intermediate morphological spaces, Emeralds became the richest clade in North America, which may be related to both generalist feeding strategies and being highly aggressive during competitive interactions (Bribiesca et al., 2019; Rodriguez-Flores et al., 2019). Thus, our results suggest that the strength of the priority effect in the involved clades may depend on their capacity to diversify, expanding their niche space and their abilities to compete against species with similar ecological requirements (see Jønsson et al., 2015); and also suggest that ecological opportunity may not be drastically diminished by the presence of potential competitors, but the competitors should be equally efficient, and the niche overlap (e.g. the partition of body size axis) should be low for co-occurrence (see Mayfield & Levine, 2010).

As suggested above, the increase of competitor species may have promoted changes in the curvature and shape of the bill, tarsus, and shape of the wing (PC2-PC4). However, contrary to our expectations, these traits showed a positive relationship between PICs and lineage diversity (Table S2; Fig. S6) despite the trend to convergence in DTT plots (Fig. 2A). DTT plots showed that these traits (especially bill curvature and wing shape) changed over time, suggesting high lability. This may indicate that after partition of the morphospace related with body size, a secondary niche partition may have occurred, probably driven by the tarsus, bill shape and wing shape (see also Jønsson et al., 2012). In birds, bill shape is related to diet and foraging behavior; and in hummingbirds especially, the shape and curvature of the bill are closely related to floral resources acquisition and is thus susceptible to high diet specialization (Temeles et al., 2009). Similarly, wing shape may be related with this secondary niche partition. DTT plots (Fig. 2C) showed that the variance in this trait was partitioned among clades at the beginning of Bees and Mountain Gems diversification (~0.2 and 0.6 of relative time), but with a final trend (after several invasions events, around of 0.6 of relative time) to partitioning the variance within clades. Flight is implicated in many relevant behaviors for

hummingbird, such the feeding strategies and courtships display (Stiles et al., 2005; Stiles, 2008; see Claramunt et al., 2012). Additionally, wing shape is related to the flight efficiency during long-distance migration (Mönkkönen, 1995), which is apparently a character recently evolved in North American hummingbirds (Licona-Vera & Ornelas 2017). Our results seem to support this (Fig.1, Fig. S4): four species traveling long migratory distances showed a differentiated wing shape from resident species.

Finally, the third source of ecological opportunity is related to the evolution of key innovations, which may promote novel evolutionary adaptations (Schluter, 2000). The migratory behavior may be also considered as an evolutionary novelty in North American hummingbirds because this trait may have evolved from sedentary ancestors, allow migratory species to access to different resources at northern habitats (Licona-Vera & Ornelas, 2017). A migratory behavior is also likely related to wing shape variation (Fig. 1; Lo Valvo et al., 1988; Mulvihill & Chandler, 1990; Fiedler, 2005), and other physiological traits, as hyperphagia and Zugunruhe (Zink, 2011). Within the Bees clade, some species in *Selasphorus*, *Archilochus*, *Calothorax*, and *Calypte* have independently evolved a latitudinal migratory behavior (Licona-Vera and Ornelas, 2017). Phylomorphospaces showed that migratory species occupy a delimited space in body size (PC1); while in bill curvature and tarsus (PC2) axes, as well as in wing shape (PC4; Fig. 1) variance overlap with non-migrant species. The wing shape variance of migratory species may be due to difference in the distance traveled and the different strategies along migratory routes (Zink 2011). The long-distance migrants *S. sasin*, *S. rufus*, *S. calliope*, *A. colubris* and *C. lucifer* tended to show wide wings (negative values of PC4 axis), while short- and intermediate-distance migrants *C. costae*, *C. anna*, *A. alexandri* and *S. platycercus* showed intermediate shapes, suggesting that a specific phenotype may serve as an adaptive response.

Factors like interspecific competition or habitat filtering may have promoted the evolution of migratory behaviors. In some hummingbird species, periodic movements

(latitudinal migration or altitudinal movements) to avoid competitive stress are common. In addition to latitudinal migration, some hummingbird species exhibit altitudinal migration (e.g., *Colibri thalassinus*, *Selasphorus heloisa*, *Saucerotia beryllina*, *Leucolia violiceps*, *Tilmatura dupontti*), which is linked to resource availability and a decreased competitive stress (Rodríguez-Flores & Arizmendi, 2016; López-Segoviano et al., 2018; Ortega-Álvarez et al. 2018). Habitat filtering (see Webb et al., 2002) may be related to evolution of migratory movements and may have also promoted changes in morphological traits. In the northern Nearctics, where migratory species spend the summer, extreme climatic changes during the winter season may acts as a selective force (filter) that few species are able to inhabit (Cadotte & Tucker, 2017), which has likely limited the expansion of the Bees clade to the northern Nearctics, due to the highly limited availability of floral resources in these habitats (Licona-Vera & Ornelas, 2017).

Although we did not evaluate if Bees and Mountain Gems are the result of an adaptive radiation in North America, as proposed by McGuire et al. (2014), our results support that the morphological evolution in these lineages may have been driven by ecological opportunity, generating niche partitioning patterns highly similar to other continental adaptive radiations (see Derryberry, et al., 2011; Price et al., 2014). However, invasions posterior to initial colonization events likely affected their diversification process. North American hummingbirds present several radiation pulses related with different conditions of ecological opportunity, a pattern possible in continental radiations in which the geographic space is extensive and highly heterogeneous (Derryberry, et al., 2011). The evolution of hummingbirds in the American continent is a constant sequence of radiation pulses, related with the uplift of mountain ranges (e.g., the Andes, Mexican Highlands), the arrival to North America and the expansion to coldest regions through facilitation and evolution of migratory behavior (McGuire et al., 2014; Licona-Vera & Ornelas, 2017; Rodriguez-Flores et al., 2019).

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Table 1. Morphological disparity index (MDI) by component in the different hummingbird clades.

Clade	Component	MDI	<i>P</i>
Bees+ Mountain Gems	PC1	-0.3241	0.015*
	PC2	0.0342	0.477
	PC3	-0.0452	0.359
	PC4	0.1258	0.638
Bees+ Mountain Gems+ Emeralds	PC1	-0.0331	0.356
	PC2	0.1908	0.912
	PC3	0.1248	0.824
	PC4	0.2427	0.955

* Significant *p-values*.

Table 2. Comparison of regression models of four main components (PC1-PC4). The models were ordered by component and value of $\Delta AICc$. LD = lineage diversity.

Trait	Model	Coefficient	AICc	$\Delta AICc$	Model Weight
PC1	LD Nearctic	0.1535	96.764	0	0.312
	LD Neotropical	0.1030	97.020	0.256	0.274
	LD Transitional	0.1308	97.184	0.419	0.253
	Relative Time	0.7845	98.110	1.345	0.159
PC2	LD Nearctic	0.0969	70.654	0	0.308
	LD Neotropical	0.0677	70.864	0.209	0.278
	LD Transitional	0.0880	71.040	0.385	0.254
	Relative Time	0.8634	71.992	1.337	0.158
PC3	LD Nearctic	0.2738	61.876	0	0.262
	LD Neotropical	0.009	61.998	0.121	0.262
	LD Transitional	0.0050	62.012	0.135	0.245
	Relative Time	-0.0065	62.013	0.137	0.245
PC4	LD Nearctic	0.1626	60.651	0	0.382
	LD Neotropical	0.1160	61.206	0.554	0.289
	LD Transitional	0.1521	61.848	1.196	0.210
	Relative Time	1.9689	63.014	2.362	0.117

Figure 1. Phylomorphospace of North American hummingbirds considering PC1, PC2, PC3 and PC4. Species in each clade is identified by color. See Supplementary Figures S2 – S4 for species names.

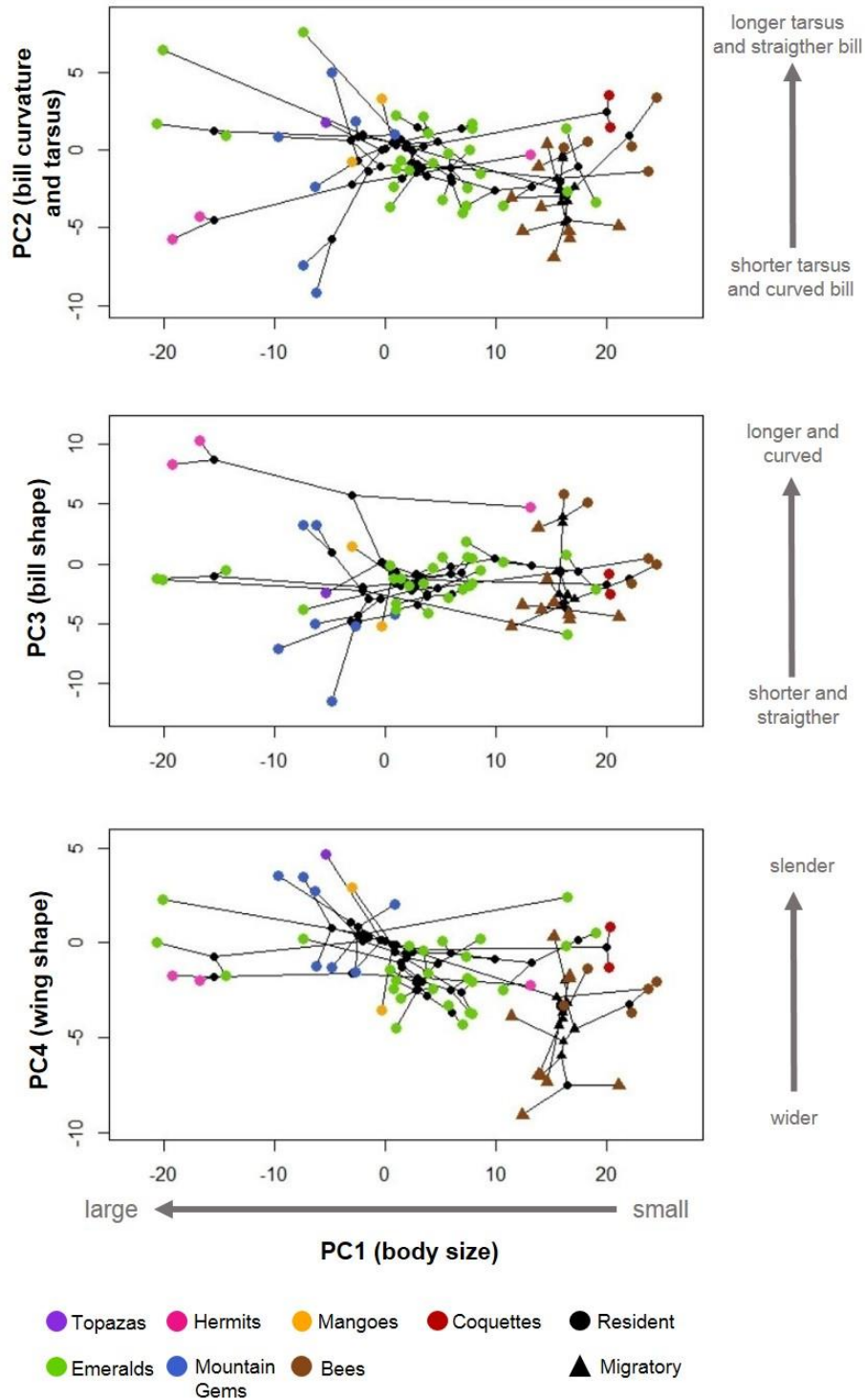


Figure 2. Morphological Disparity through Time (DTT) plots for the main hummingbird clades (Bees, Mountain Gems and Emeralds) present in North America. Solid lines represent the relative disparity values calculated from the species data for each node in the phylogeny. The light grey dotted line represents the average of the relative disparity calculated from the simulated data based on Brownian motion evolution.

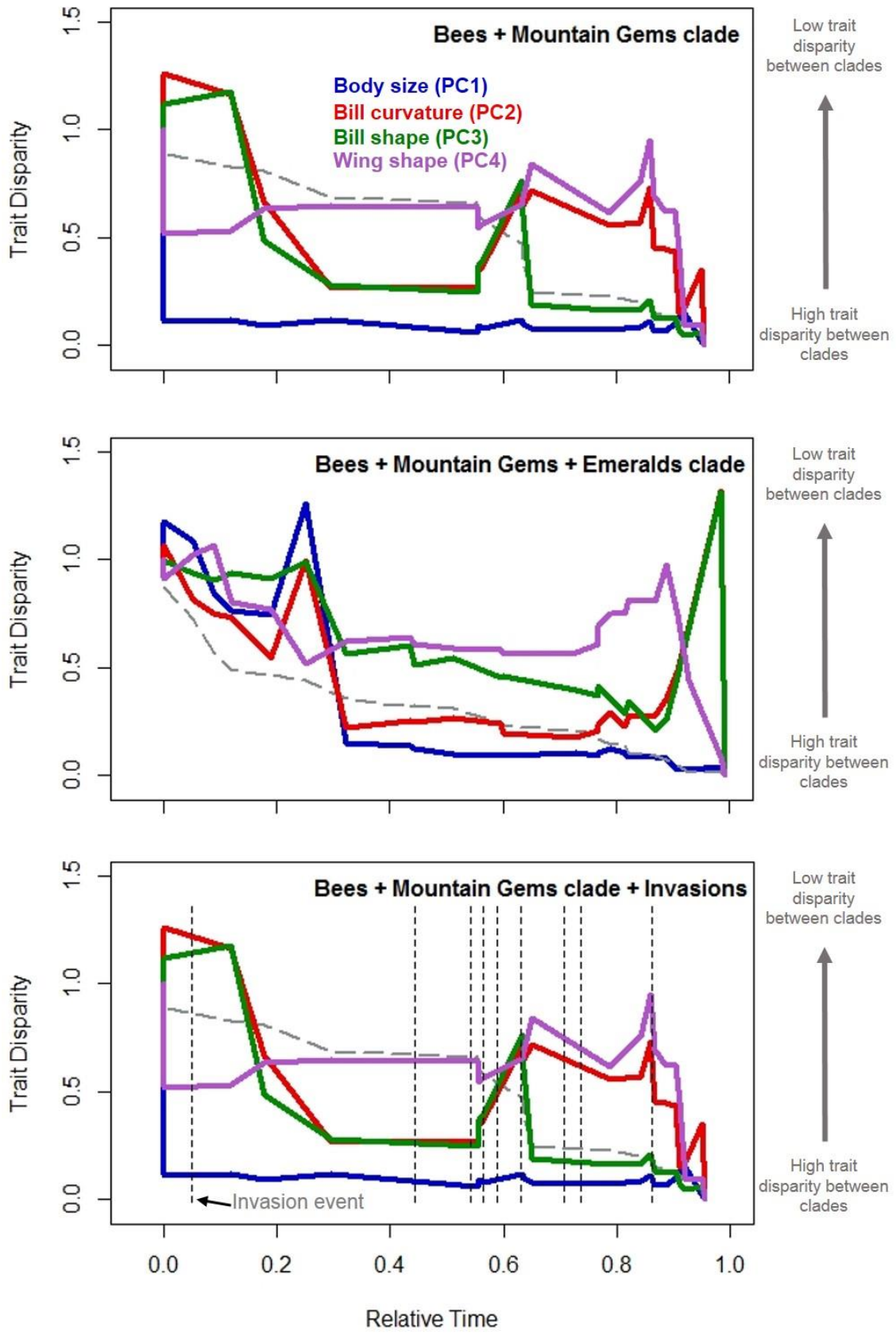
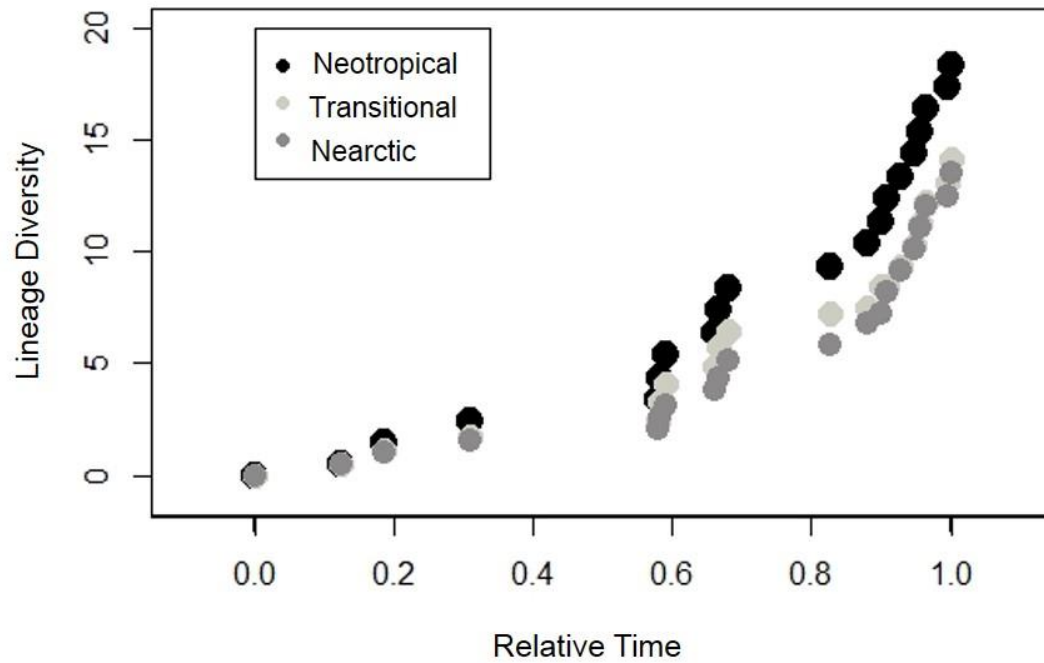


Figure 3. Lineage diversity accumulation through time for Bees + Mountain Gems clade in the three biogeographic regions of North America: Neotropical (black), Transitional (light gray), and Nearctic (dark gray).



Data availability statement

Data are available from the authors upon request.

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Apéndices

Table S1. Phylogenetic principal components (PCA) for the 11 morphological traits.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
% varianza	0.60794	0.1089	0.0859	0.0742	0.0440	0.0337		0.0135			
		9	5	7	5	3	0.01589	7	0.36477	0.17521	0.00069
% accumulated	0.60794	0.7169	0.8028	0.8771	0.9212	0.9549		0.9844			
		3	8	6	1	5	0.97084	1	0.99651	0.99930	1.00000

Table S2. Factor loadings by traits from PC1 to PC6 of phylogenetic PCA.

	PC1	PC2	PC3	PC4
Weight	-0.891167	0.191278	-0.139473	0.139328
Tarsus	-0.693213	0.472137	-0.077161	-0.018003
Bill length	-0.831703	-0.332997	0.380854	-0.041393
Bill width	-0.800089	0.03333	0.349373	-0.098815
Bill depth	-0.859917	-0.112260	0.135407	0.263742
Wing chord	-0.876141	0.080656	-0.328099	0.244875
Wing secondary length	-0.891535	0.199755	-0.291941	0.035892
Hand-Wing Index	0.534724	0.059633	0.218445	0.801750
Exposed culmen	-0.827358	-0.330217	0.377204	-0.023440
Bill curvature	0.156157	0.809022	0.487140	-0.098799
Central Rectrices	-0.885440	0.035845	-0.120178	-0.043883

Figure S1. Trochilidae phylogenetic tree proposed by McGuire et al. (2014) modified for North American species.

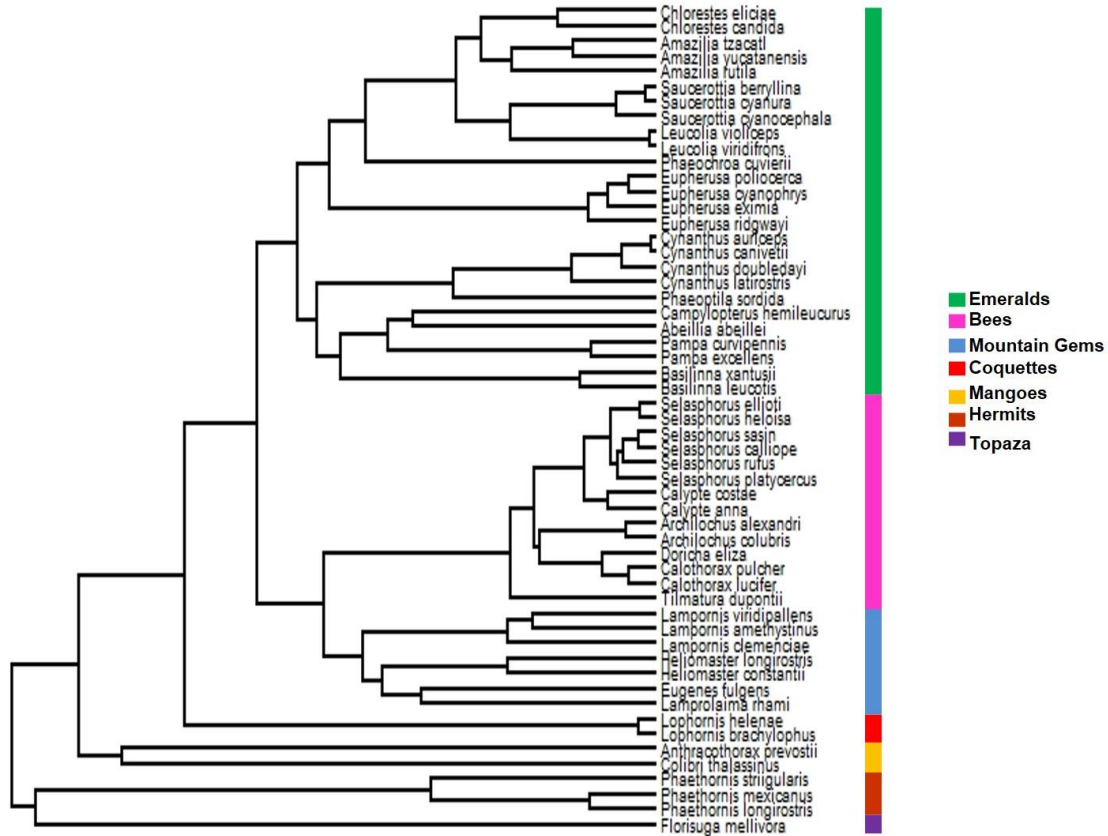


Figure S2. Phylomorphospace of North American hummingbirds of body size and bill curvature and tarsus length. Each clade is distinguished by color. Each species is indicated at the tips.

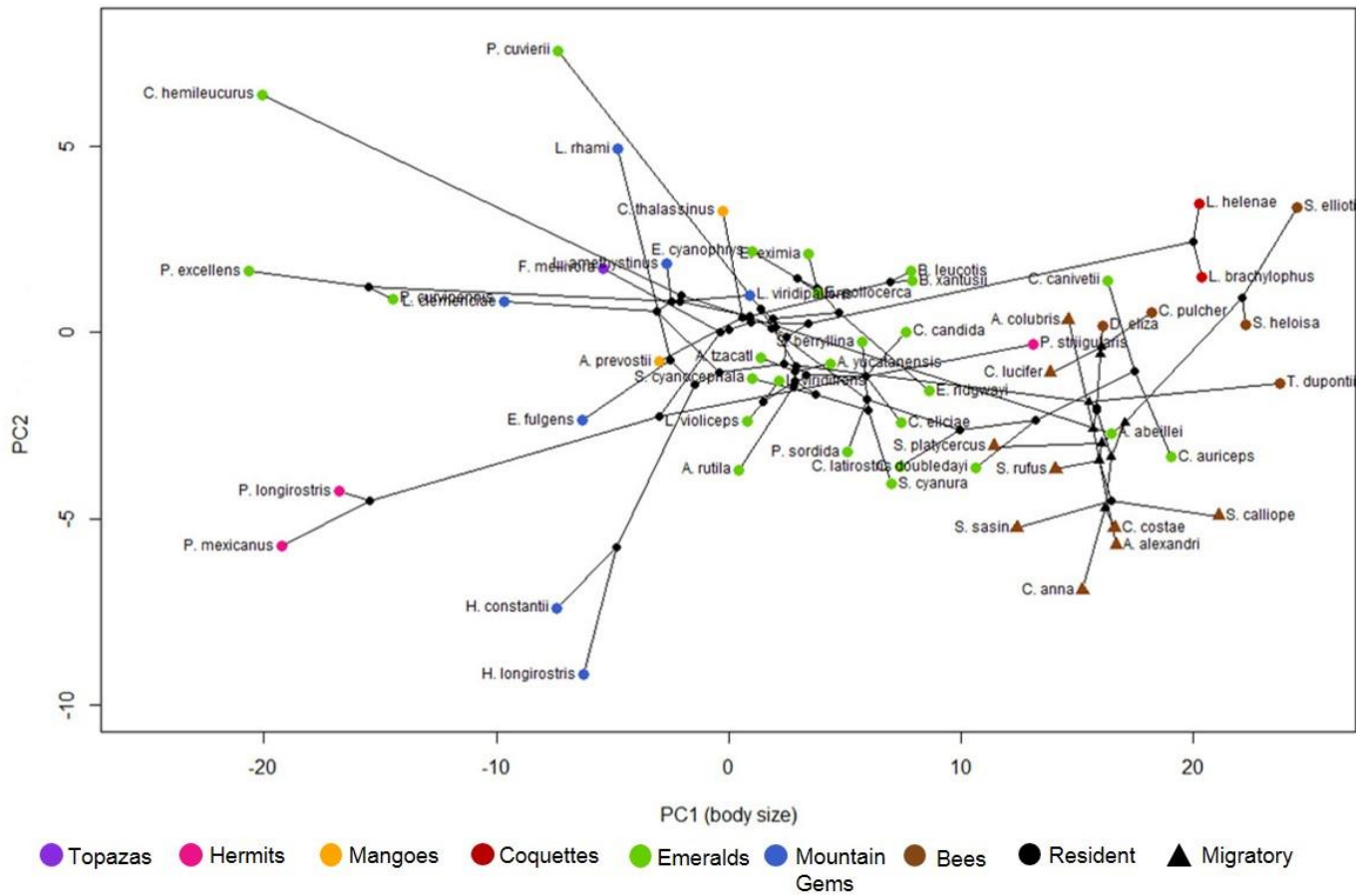


Figure S3. Phylomorphospace of North American hummingbirds of body size and bill shape. Each clade is distinguish by color. Each species is indicated at the tips.

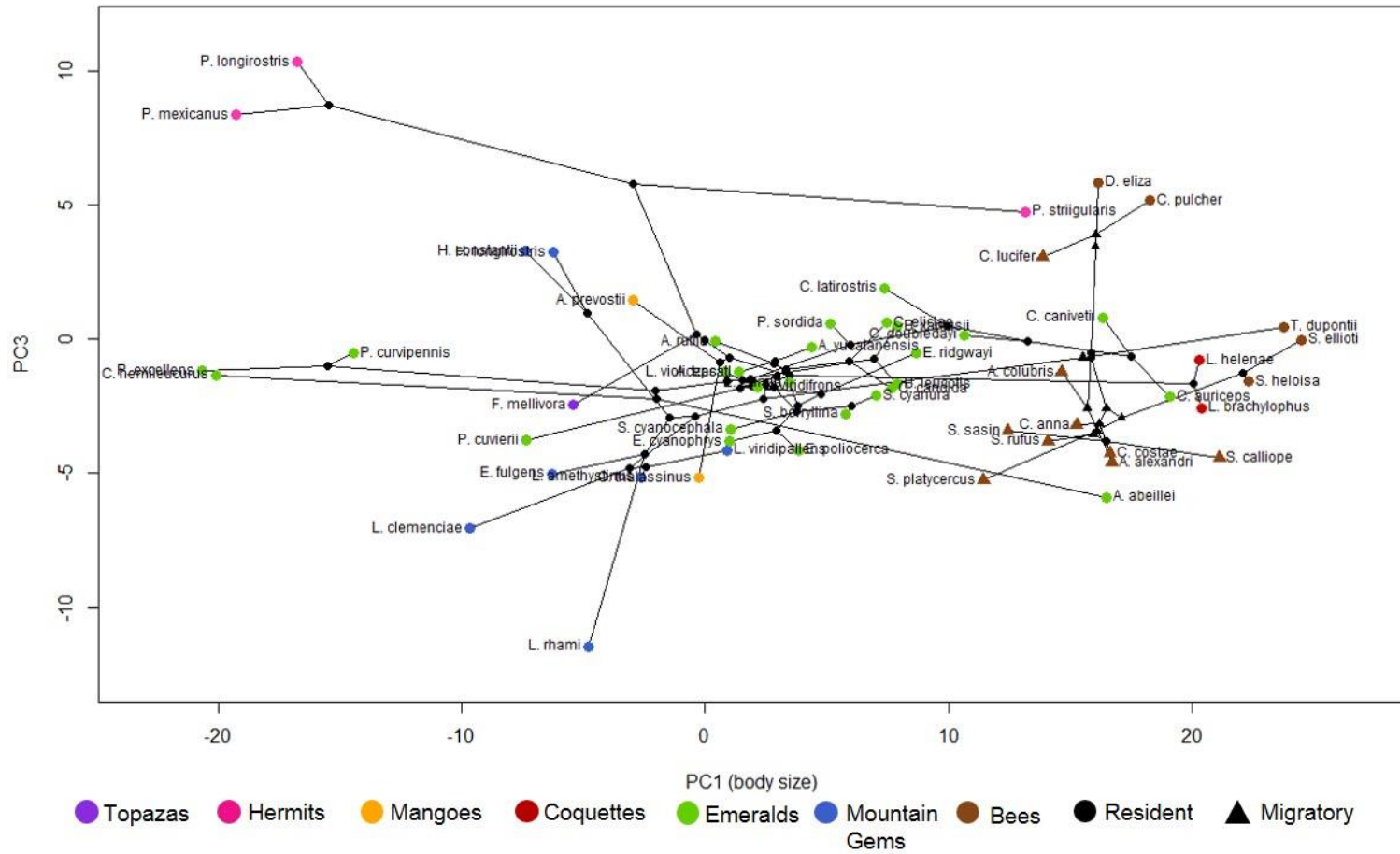


Figure S4. Phylomorphospace of North American hummingbirds of body size and wing shape. Each clade is distinguish by color. Each species is indicated at the tips.

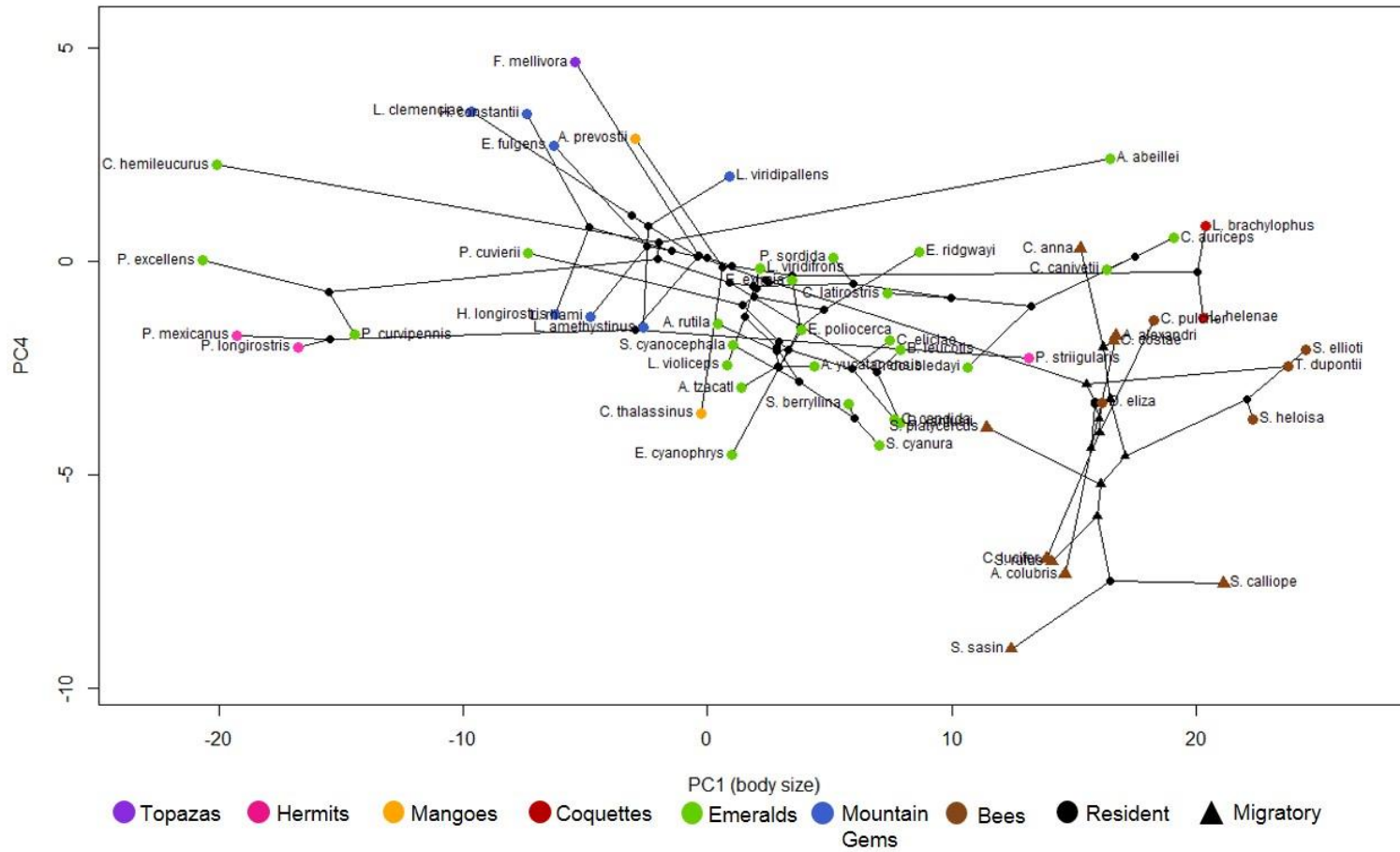


Figure S5. PC1 versus PC2, PC3 and PC4 plots show the morphological space occupied by each hummingbird species in each region of North America: (1) Neotropical, (2) Transitional, and (3) Nearctic. Triangles indicate migratory species.

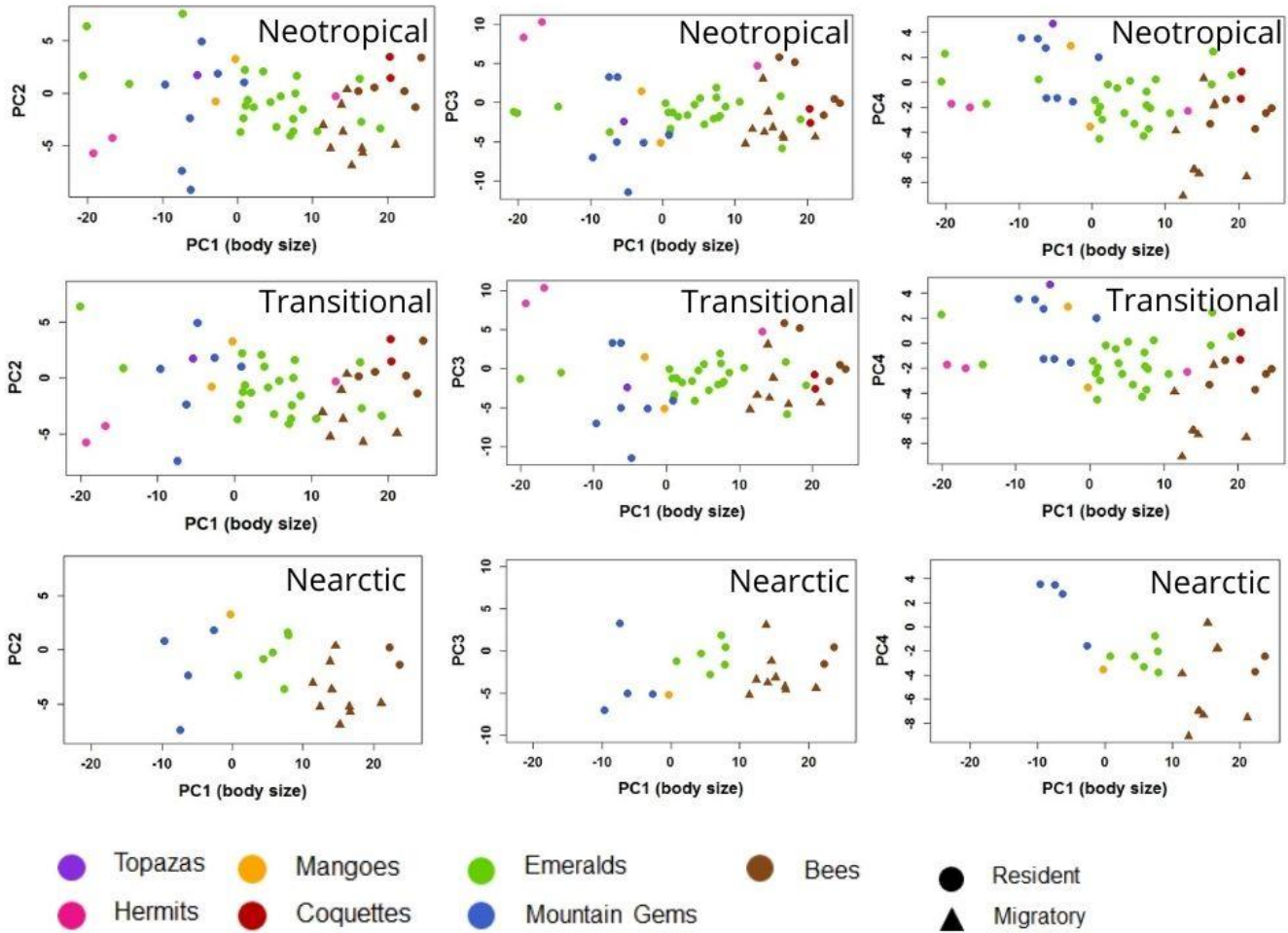
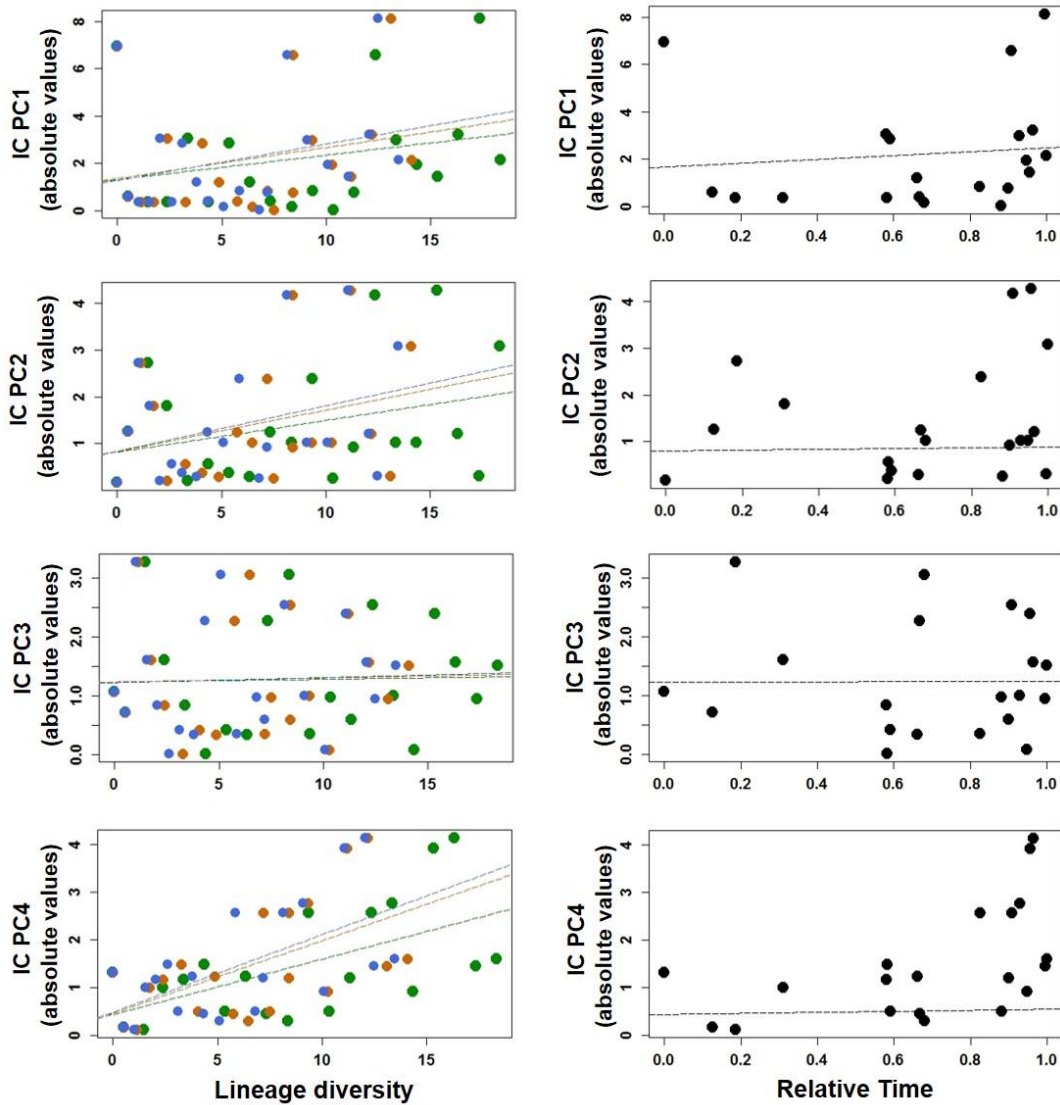


Figure S6. Absolute values of the standardized independent contrasts (CI) of the first four components (PC1-PC4) resulting from the phylogenetic PCA explained by lineage diversity (left) and relative time (right). In the lineage diversity charts, they show the lineage diversity for each biogeographic region of North America: Neotropical (green), Transitional (orange), and Nearctic (blue). The dotted lines show the expected values according to the regression models.



Discusión General

Los resultados de este estudio sugieren que el proceso de estructuración de los ensamblajes de colibríes norteamericanos ha sido influenciado por diferentes factores como el filtrado de hábitat, interacciones mutualistas, competencia interspecífica y oportunidad ecológica.

El gradiente latitudinal en la estructuración filogenética

En Norteamérica, los ensamblajes de colibríes muestran un gradiente geográfico latitudinal en su estructura filogenética y fenotípica que va desde una estructura agrupada en la región noroeste de Estados Unidos y Canadá (región Neártica), hasta estructuras sobredispersas en pequeñas ecorregiones (solo en caso de la estructura filogenética) en la costa este de México (región Neotropical); aunque la mayoría de las ecorregiones en México (regiones Transicional y Neotropical) no son diferentes de lo esperado por el azar (Puga-Caballero et al. 2022). Los parones filogenéticos agrupados junto con la falta de estructura fenotípica (azar) sugieren que las condiciones ecológicas en altas latitudes ejerce un efecto de filtrado de hábitat (ver Webb et al., 2002; Mayfield & Levine, 2010). Esto puede deberse a que las especies pertenecientes al clado Abejas dominan los ensambles hacia las regiones con mayor latitud, además que estas especies tienen entre un tamaño corporal y forma de pico muy similares, pero que presenta mayor variación en otros atributos, como la forma del ala. Este grupo de colibríes son dominantes en los bosques templados y desiertos occidentales (ecoregiones noroeste de México), lo que genera que los patrones filogenéticos y parte de los fenotípicos (pMPD) resulten en agrupamiento. Este patrón es similar a lo reportado en los Andes, donde unos pocos clados de colibríes dominan dichos ensamblajes (Graham et al., 2009; McGuire et al., 2014). Por su parte, la estructuración azarosa observada en la región

Transicional pueden haber sido promovidos por la mezcla de biotas neárticas y neotropicales a lo largo del gradiente altitudinal del altiplano mexicano (ver Sánchez-González & Navarro, 2009; Escalante et al., 2013), puesto que la heterogeneidad del hábitat a lo largo del gradiente de elevación permite que especies de diferentes linajes puedan coexistir, mientras que la labilidad de algunos atributos y el filtrado del hábitat explicarían la distribución de especies fenotípicamente similares hacia elevaciones más altas. La región neotropical mexicana mostró principalmente estructuración azarosa, lo que puede deberse a la presencia de especies de clados sudamericanos (es decir, Topazas, Ermitaños, Mangos y Coquetas) que son parientes lejanos de los clados Abejas y Gemas de Montaña (McGuire et al., 2014). Para completar el gradiente, dos ecorregiones, Pantanos de Centla y Bosque Seco Veracruzano, mostraron un patrón filogenético (MPD) sobredisperso, que puede deberse a la presencia de una gran cantidad de especies filogenéticamente lejanas.

En cuanto a los patrones geográficos durante la estación invernal, los resultados mostraron que los movimientos migratorios no cambian significativamente la estructura observada, lo que puede deberse a que las especies migratorias arriban a ensamblajes dominados por especies filogenéticamente lejanas y fenotípicamente poco similares. Las especies migratorias suelen clasificarse como generalistas (Rodríguez-Flores & Arizmendi, 2016), lo que les podría permitir evitar interacciones competitivas intensas con otras especies.

Morfoespacio filogenético y variación fenotípica

La variación morfológica de los colibríes sugirió que el tamaño corporal es el atributo más importante para separar a los principales clados presentes en Norteamérica. Esto puede

deberse a que la diferenciación de tamaño corporal es uno de los primeros mecanismos para la diferenciación ecológica entre especies cercanamente relacionadas (Derryberry et al., 2011; Arbor & López-Fernández 2013). Estos resultados concuerdan con lo reportado por López-Segoviano et al., (2018), acerca que el tamaño corporal está relacionado con el reparto de nicho ecológico, en especial sobre los recursos florales, y por Bribiesca et al., (2019) que asocian este atributo con la abundancia y el nivel de dominancia que ejercen sobre otras especies de colibríes.

Por otro lado, el morfoespacio que ocupan los siete clados de colibríes presentes en Norteamérica se sobrelapa al menos parcialmente en los atributos forma y tamaño de pico, y forma del ala. Tanto los valores de λ , el Mapa de calor (“heatmap”) filogenético y las gráficas DTT sugieren que estos atributos son convergentes dentro de los clados principales de colibríes. Esto puede deberse a que la labilidad estos atributos permite un reparto del nicho ecológico secundario al que se lleva a cabo a través del tamaño corporal. Estos resultados son similares a los obtenidos por Jønsson et al. (2012) acerca de la radiación adaptativa de los vangas de Madagascar, en la que de acuerdo un modelo de llenado de nicho, el tamaño del cuerpo es el primer atributo cuya variación permite la repartición del espacio ecológico, seguido de una segunda partición dado por la variación en la forma del pico.

Oportunidad ecológica

Patrones similares a los de este estudio han sido asociados con alguna fuente de oportunidad ecológica (Jønsson et al., 2012; Price et al., 2014): la relajación de la selección natural sobre uno o más rasgos ecológicos (Yoder et al., 2010) y sus fuentes son: (1) acceso a una nueva área geográfica, (2) ausencia de especies antagonistas, y (3) la evolución de innovaciones

clave para acceder a nuevos recursos (Schluter, 2000; Mahler et al., 2010). De acuerdo a la historia biogeográfica propuesta para la familia Trochilidae (McGuire et al. (2014), los colibríes comenzaron a colonizar Norteamérica a través de la llegada de un ancestro común de las Abejas y las Gemas de Montaña. El resto de los clados que actualmente habitan en esta región, Esmeraldas, Ermitaños, Coquetas, Mangos y Topazas arribarían posteriormente en distintos eventos independientes; lo que sugiere que el clado formado por Abejas + Gemas de Montaña han experimentado momentos de oportunidad ecológica.

Las gráficas DTT sugieren que la llegada del ancestro común de Abejas y Gemas de Montaña a una nueva región geográfica pudo haber promovido la partición de nichos relacionada con el tamaño corporal, similar a otras radiaciones del continente (Derryberry et al., 2011). La diferenciación del tamaño del cuerpo probablemente permitió la partición del espacio morfológico en especies pequeñas (Abejas) y grandes (Gemas de Montaña). Esta partición del nicho ecológico pudo haber sido promovida por competencia interespecífica entre linajes (ver Yoder et al., 2010; Jønsson et al., 2012; Bassar et al., 2017), en la que se desarrollaron diferentes estrategias de alimentación (p. e. territorialidad y trap-lining), permitiendo liberar el estrés competitivo (Brown and Bowers, 1985; Martin and Ghalambor, 2014; López-Segoviano et al., 2018; Bribiesca et al., 2019). Este proceso de diferenciación fenotípica que permite la coexistencia de especies, se le conoce como desplazamiento de carácter (Brown & Wilson, 1956). Igualmente, la variación observada en los otros atributos evaluados como la curvatura del pico, la longitud del tarso y la forma del ala, pueden estar relacionados con el desplazamiento del carácter y la partición del nicho. Así, las diferencias en la curvatura del pico están relacionadas con la especialización alimentaria (Izquierdo-Palma et al., 2021; Ocampo-Sandoval et al., 2021); mientras que la variación en la longitud

del tarso está relacionada con el tiempo de percha (Stiles, 2008) y probablemente con la territorialidad. Por su parte, la longitud del ala puede estar bajo presiones ecológicas y sexuales derivadas de la búsqueda de alimento y el desempeño de la lucha aérea.

La segunda fuente de oportunidad ecológica está relacionada con la ausencia de especies competitivas y depredadoras. Los modelos de regresión (capítulo 2) mostraron que la diversidad de linajes a lo largo del tiempo explicó la variación de los contrastes independientes en el tamaño corporal, de los atributos de pico y la forma del ala, lo que sugiere que la presencia de competidores puede haber influido en la evolución morfológica. Los contrastes independientes del tamaño corporal (un carácter conservado) mostraron una relación positiva entre los valores de $\ln(\text{tamaño corporal})$ y la diversidad de linajes en las tres regiones. Esto puede deberse a la llegada de linajes de América del Sur, particularmente Esmeraldas, que probablemente ocuparon los espacios morfológicos disponibles (principalmente tamaños de cuerpo medianos), generando una selección direccional en los clados preexistentes, Abejas (tamaño de cuerpo pequeño) y Gemas de Montaña (tamaño de cuerpo más grande). Por otra parte, los resultados sugieren que un efecto de prioridad ocurrió en dos eventos separados. Primero, la presencia de Abejas y Gemas de Montaña pudo haber limitado la colonización de especies de tamaño corporal pequeño y grande, dejando el tamaño intermedio como el espacio morfológico disponible, que fue ocupado por el clado de Esmeraldas. Segundo, la repartición del rango de tamaño corporal entre Abejas, Gemas de Montaña y Esmeraldas, tuvo un efecto de prioridad en el que se inhibió la diversificación de otros linajes colonizadores secundarios, como Mangos o Coquetas, o invasiones posteriores de diferentes linajes sudamericanos. Aunque probablemente limitadas a ocupar en su mayoría espacios morfológicos intermedios, las Esmeraldas se convirtieron en el clado más rico en

Norteamérica, lo que puede estar relacionado tanto con las estrategias de alimentación generalistas como con su gran agresividad y dominancia durante las interacciones competitivas (Bribiesca et al., 2019; Rodríguez-Flores et al., 2019). Así, estos resultados sugieren que la fuerza del efecto de prioridad en los clados involucrados puede depender de su capacidad para diversificarse, expandir su espacio de nicho y sus habilidades para competir contra especies con requisitos ecológicos similares (ver Jønsson et al., 2015).

El comportamiento migratorio en los colibríes de Norteamérica puede considerarse como la tercera fuente de oportunidad ecológica, evolución de innovación ecológica (ver Schluter, 2000). Este atributo, que pudo haber evolucionado a partir de ancestros sedentarios, permitió a las especies migratorias acceder a diferentes recursos en los hábitats del Neártico (Licona-Vera y & Ornelas, 2017). Los movimientos migratorios probablemente también están relacionados con la variación en la forma del ala y otros rasgos fisiológicos, como hiperfagia y Zugunruhe (Zink, 2011). Los filomorfoespacios mostraron que las especies migratorias ocupan un espacio delimitado en el tamaño corporal y en la forma del ala. La variación de la forma del ala de las especies migratorias puede deberse a la diferencia en la distancia recorrida y las diferentes estrategias a lo largo de las rutas migratorias (Zink 2011). Los migrantes de larga distancia como *Selaphorus sasin*, *S. rufus*, *S. calliope*, *Archilochus colubris* y *Calothorax lucifer* tendieron a mostrar alas anchas, mientras que los migrantes de corta e intermedia distancia *Calypte costae*, *C. anna*, *A. alexandri* y *S. platycercus* mostraron formas intermedias, lo que sugiere que un fenotipo específico puede servir como una respuesta adaptativa. La evolución del comportamiento migratorio puede estar relacionado con competencia interespecífica o el filtrado de hábitat. En algunas especies de colibríes, son comunes movimientos geográficos estacionales como migración latitudinal o

movimientos altitudinales probablemente para evitar el estrés competitivo. Además de la migración latitudinal, algunas especies de colibríes exhiben migración altitudinal (p. ej., *Colibri thalassinus*, *Selasphorus heloisa*, *Saucerotia beryllina*, *Leucolia violiceps*, *Tilmatura dupontti*), que está probablemente relacionada con la disponibilidad de recursos y una disminución del estrés competitivo (Rodríguez-Flores & Arizmendi, 2016; López-Segoviano et al., 2018; Ortega-Álvarez et al. 2018). Las condiciones extremas en la parte norte de la región Neártica limitan la disponibilidad de recursos florales en estos hábitats, pudieron promover un filtrado de hábitat en el que se favorece a los colibríes generalistas que son capaces de explotar recursos de las especies de flores que puedan encontrarse a lo largo de la ruta migratoria (ver Rodríguez-Flores et al., 2019)

Conclusiones Generales

Los resultados de este estudio muestran que una gran variedad de factores puede estar involucrados en el proceso de estructuración de una comunidad. Los ensamblajes de colibríes norteamericanos están influenciados por la disponibilidad y abundancia de recursos, por la competencia interespecífica y por la historia biogeográfica de los principales clados. Igualmente, los resultados sugieren que el tamaño corporal es un atributo ecológico clave en el reparto del nicho ecológico, mientras que los atributos del pico y la forma del ala permiten una repartición más fina del nicho.

El filtrado de hábitat y la competencia interespecífica están distribuidos en un patrón que refleja un gradiente latitudinal, en el que las condiciones extremas de la región Neártica promovieron patrones filogenéticos y fenotípicos agrupados, mientras que en las regiones Transicional y Neotropical los ensamblajes presentan patrones estocásticos.

Los resultados también respaldan que la evolución morfológica de los colibríes norteamericanos puede haber sido impulsada por oportunidades ecológicas, generando patrones de partición de nichos muy similares a otras radiaciones adaptativas continentales (ver Derryberry, et al., 2011; Price et al., 2014). Igualmente, la historia de la colonización de Norteamérica por la familia Trochilidae ha influido en la diversificación y distribución morfológica de sus linajes a través del efecto de prioridad. Los colibríes norteamericanos presentan varios pulsos de radiación relacionados con diferentes condiciones de oportunidad ecológica, patrón posible en radiaciones continentales en las que el espacio geográfico es extenso y altamente heterogéneo (Derryberry, et al., 2011). La evolución de los colibríes en el continente americano es una secuencia constante de pulsos de radiación, relacionados con el levantamiento de las cadenas montañosas (por ejemplo, los Andes, las tierras altas

de México), la llegada a América del Norte y la expansión a las regiones más frías a través de la facilitación y evolución del comportamiento migratorio (McGuire et al., 2014; Licona-Vera and Ornelas, 2017; Rodriguez-Flores et al., 2019).

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