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ECOLOGÍA DE METACOMUNIDADES DE PARÁSITOS HAEMOSPORIDIOS AVIARES EN DIFERENTES AMBIENTES

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RESUMEN

La identificación y comprensión de los factores ecológicos y evolutivos que delimitan la diversidad y distribución de organismos parásitos en sus hospederos y a lo largo del medio ambiente constituye una línea de investigación fundamental dentro de las ciencias de la salud animal. Bajo la crisis ambiental global, la distribución e interacciones entre especies de parásitos y hospederos se han visto afectadas produciendo un aumento en la prevalencia de enfermedades infecciosas emergentes. Sin embargo, es poco el conocimiento que se tiene sobre los factores que regulan naturalmente a las poblaciones y comunidades de organismos parásitos, por lo que la respuesta a la emergencia de enfermedades que amenazan la salud animal, humana y la conservación de especies puede ser deficiente. En esta tesis se buscó identificar los principales factores que delimitan la diversidad, distribución y composición de comunidades de parásitos haemosporidios aviares a través de comunidades de aves y de distintos ambientes. Se encontró que múltiples procesos (ecológicos, espaciales y evolutivos) interactúan para gobernar la diversidad y distribución de los haemosporidios aviares. Sin embargo, la importancia relativa de cada proceso varió de acuerdo con la escala espacial y región de estudio. A escalas locales y de paisaje, los procesos ecológicos (i.e., variación climática) representaron determinantes clave para la diversidad y distribución de haemosporidios aviares; mientras que a escalas regionales los determinantes espaciales (i.e., distancias geográficas entre sitios) aumentaron su poder explicativo. Adicionalmente, a escalas regionales se observó una fuerte correlación entre los procesos evolutivos (i.e., gradientes de disimilitud filogenética de hospederos aviares) y la diversidad filogenética de los haemosporidios aviares. Continuar con el estudio de la ecología de los parásitos haemosporidios aviares, y de sus vectores transmisores es necesario para la protección de especies de aves nativas susceptibles. El uso de teorías ecológicas (e.g., ecología de metacomunidades), así como herramientas estadísticas robustas que nos permitan modelar a estos complejos sistemas parasitarios será de utilidad para identificar los factores clave que delimiten su diversidad y distribución, y con eso su potencial de invasión hacia nuevas regiones y especies.

INTRODUCCIÓN

Los organismos parásitos son considerados componentes fundamentales de los ecosistemas y representan a más del 50% de las especies biológicas descritas (Poulin 2014). Debido a su alta biomasa, alta diversidad e interacción con especies de hospederos, los parásitos tienen efectos directos e indirectos sobre la estructura y dinámica de las poblaciones y comunidades biológicas (Hudson et al. 2006; Poulin and Morand 2000). Por ejemplo, las comunidades de parásitos (i.e., el conjunto de diferentes especies de parásitos que coexisten en tiempo y espacio) (Begon 2006) pueden influenciar el comportamiento de sus hospederos, regular patrones demográficos, alterar interacciones inter-específicas y modificar la co-existencia de especies, entre otros (Thomas et al. 2006). A su vez, las especies de hospederos también tienen efectos directos sobre la estructura y composición de las comunidades de parásitos, regulando así su posibilidad de colonización, dispersión e interacción con nuevos hospederos, y por lo tanto determinando sus patrones de diversidad y distribución en tiempo y espacio (Guégan et al. 2005).

Conocer los mecanismos y factores que regulan la diversidad y distribución de los parásitos sobre las comunidades de hospederos es de utilidad para la modelación de enfermedades infecciosas, así como para la planeación de estrategias de protección de la salud animal y la conservación de la biodiversidad (Gutiérrez et al. 2019; Mihaljevic et al. 2018; Roche and Guégan 2011). Pese a que existen amplios estudios ecológicos y epidemiológicos para algunos sistemas parasitarios (e.g., rabia en murciélagos hematófagos), para la mayoría aún se desconocen aspectos ecológicos fundamentales; por ejemplo, no se conoce cómo varía la diversidad de parásitos sobre sus hospederos y sobre su espacio geográfico, y tampoco se conocen las barreras que determinan los límites en su distribución. En este sentido, estudios recientes se han enfocado en determinar las barreras geográficas (e.g., cordilleras-ríos) y ambientales (e.g., condiciones climáticas) que delimitan la distribución de los parásitos en el espacio y con esto su potencial de invasión hacia nuevas regiones (Clark et al. 2017). Otros estudios se han enfocado en determinar características intrínsecas, ecológicas y filogenéticas de las comunidades de hospederos que se asocian al potencial de transmisión y a la variación en la composición de especies de las comunidades parasitarias (e.g. barreras inter-especie) (Krasnov et al. 2010).

Hasta hace algunas décadas, las aproximaciones utilizadas para comprender las barreras que delimitan la distribución de los parásitos se enfocaban únicamente en el efecto de procesos y condiciones ambientales locales (e.g., interacciones bióticas, uso y respuesta a recursos locales) sobre la riqueza y composición de comunidades aisladas de parásitos (Poulin 2007). Sin embargo, debido a que los parásitos forman parte de metacomunidades (i.e., el conjunto de comunidades locales conectadas entre sí por la dispersión de especies) se ha reconocido la necesidad de considerar también los efectos de factores ecológicos regionales (e.g., heterogeneidad ambiental, dispersión de hospederos, macro-clima etc.) sobre la riqueza, composición y conectividad de múltiples ensambles de parásitos (Dümmer, Ristau, and Traunspurger 2016; Mihaljevic 2012; Poulin 2007).

El objetivo de esta tesis fue utilizar la ecología de metacomunidades para estudiar al modelo 'parásitos haemosporidios-aves' a través de distintos tipos de ambientes. La pregunta ecológica central se basó en identificar y entender cuáles son los factores que delimitan la diversidad, distribución y composición de comunidades de haemosporidios a través de comunidades de aves y de gradientes ambientales, geográficos y de disimilitud de hospederos. Para ello se realizaron estudios de campo y moleculares para determinar la diversidad de parásitos y hospederos en distintos hábitats y regiones biogeográficas. Los parásitos haemosporidios aviares se distribuyen a nivel mundial infectando a múltiples familias de aves (Svensson-Coelho et al. 2014). Comúnmente, estos parásitos producen infecciones crónicas, pero también pueden producir infecciones agudas, afectando las tasas de reproducción y sobrevivencia de poblaciones enteras de aves (Merino et al. 2000). Debido a su amplia diversidad genética (Bensch et al. 2009), los haemosporidios aviares tienen la capacidad de saltar frecuentemente entre especies aviares demostrando su alta adaptabilidad para infectar a nuevos hospederos susceptibles (Ferreira-Junior et al. 2018). Bajo la actual crisis ambiental global y debido a la amenaza que las enfermedades infecciosas representan para la salud animal y humana, el estudio ecológico del sistema 'parásitos haemosporidios-aves' es de importancia para la salud animal y la conservación de la biodiversidad.

El primer capítulo de esta tesis doctoral se centró en el estado de Veracruz. Se realizó un estudio de campo a través de un gradiente altitudinal en donde se evaluó la estructura de la
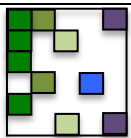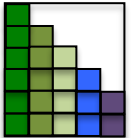
metacomunidad de haemosporidios aviares y de sus hospederos, así como los factores ambientales y las características ecológicas y filogenéticas de los hospederos asociadas a dichas estructuras metacomunitarias. En el segundo capítulo, se modelaron dos componentes de la beta diversidad (taxonómica y filogenética) de parásitos haemosporidios aviares dentro y entre la región biogeográfica Neártica y Neotropical de México. Se evaluó la asociación entre gradientes ambientales, geográficos y de disimilitud de hospederos y los componentes de la beta diversidad de parásitos. Para este capítulo se utilizaron los datos generados en el capítulo anterior (región Neotropical), datos generados por el Instituto Potosino de Investigación Científica y Tecnológica (IPICYT) (región Neártica) (Ortega-Guzmán et al. unpublished), así como datos sobre la diversidad y distribución de haemosporidios aviares producidos por el Instituto de Ecología A.C. (INECOL) en proyectos anteriores (región Neotropical) (Hernández-Lara et al. 2017; Hernández-Lara et al. 2020). Ambos capítulos de esta tesis fueron producto del proyecto Problemas Nacionales CONACYT (2015-01-1628) "Relaciones ecológicas entre aves y parásitos haemosporidios en un gradiente ambiental en el centro de México", co-dirigido por el Dr. Leonardo Chapa Vargas (IPICYT) y el Dr. Diego Santiago Alarcón (INECOL).
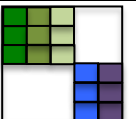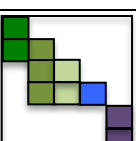
REVISIÓN DE LITERATURA

La teoría ecológica de metacomunidades

La ecología de metacomunidades representa una teoría útil para comprender la interdependencia y contribución de procesos locales y regionales sobre el ensamblaje y distribución de las comunidades biológicas (Leibold et al. 2004; Leibold and Chase 2018). Esta teoría ha permitido estudiar, mediante distintas propuestas estadísticas, algunos de los patrones más comunes de distribución y orden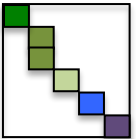ación de especies en el espacio (i.e., las estructuras idealizadas de la metacomunidad, ver Tabla 1) (Leibold and Mikkelson 2002; Leibold and Chase 2018). Al ser consideradas como un concepto multi-escala (Leibold et al. 2004), las metacomunidades constituyen un nivel de organización adecuado para el estudio de la distribución y conectividad de las comunidades parasitarias y de sus hospederos (Mihaljevic 2012). Por ejemplo, permiten estudiar la distribución y composición de comunidades locales de simbiontes dentro de un hospedero individual (i.e. los parásitos detectados en cada órgano representan una comunidad local), o entre hospederos de una comunidad (i.e. los parásitos detectados en cada especie de hospedero representan una comunidad local) (Mihaljevic 2012).

Tabla 1. Estructuras idealizadas de la metacomunidad, con sub-estructuras y sus definiciones. Dentro de las matrices gráficas, las especies se encuentran representadas por las columnas, y los sitios o comunidades locales por las filas. Modificado de Suzán et al. (2015)

Estructura idealizada	Sub-estructura hipotética	Definición
Aleatoria	Aleatoria	Las especies se distribuyen aleatoriamente, respondiendo de manera diferente al mismo gradiente ambiental (Simberloff 1983)
No - Aleatoria	Anidada	Los ensambles de especies que ocupan una menor proporción del gradiente ambiental se encuentran contenidos dentro de los ensambles de especies que tienen mayor distribución, exhibiendo pérdida de la riqueza entre los sitios (Patterson and Atmar 1986)

No - Anidadas	 Checkerboard	Las especies se excluyen mutuamente a través del gradiente ambiental (Diamond 1975)
	 Clementsiana	Las especies exhiben recambio en grupos que poseen las mismas restricciones ambientales a través del gradiente ambiental (Clements 1916)
	 Gleasoniana	Las especies exhiben recambio gradual respondiendo de manera individual hacia el gradiente ambiental (Gleason 1926)
	 Evenly spaced	Las especies exhiben un recambio más uniforme a través del gradiente ambiental que lo esperado por el azar (Tilman 1982)

Dentro de la ecología de metacomunidades, una aproximación frecuentemente utilizada para inferir los procesos ecológicos que determinan el ensamblaje de las comunidades se centra en la identificación de las estructuras idealizadas de la metacomunidad a través de gradientes ambientales (Leibold and Chase 2018). Estas surgen a partir de teorías e hipótesis ecológicas clásicas sobre el ensamblaje de las comunidades biológicas (i.e., desde las ideas opuestas de Gleason (1926) y Clements (1916) sobre las respuestas individualistas vs. grupales de las especies hacia el gradiente ambiental, hasta el principio de ensamblaje por exclusión competitiva propuesto por Diamond (1975) y los patrones de anidamiento de especies propuestos por Patterson y Atmar (1986)) (Leibold and Mikkelson 2002). Por esta razón, cada estructura idealizada de la metacomunidad asume que la distribución y composición de especies está asociada en menor o mayor medida a uno o más procesos ecológicos (e.g., interacciones bióticas, especialización al hábitat, tolerancia a condiciones abióticas, capacidad de dispersión).

La identificación de las estructuras idealizadas de la metacomunidad dentro de los sistemas parásito-hospedero ha permitido realizar inferencias y poner a prueba hipótesis sobre la forma en la que un grupo de parásitos responde ante la variación en la composición de las comunidades de sus hospederos y ante el medio ambiente (Mihaljevic et al. 2018; Richgels et al. 2013). Por ejemplo,

podríamos esperar que grupos de parásitos que presenten fuertes asociaciones hacia un tipo de hospedero (e.g., parásitos con alta especificidad de hospedero) exhiban estructuras Clementsianas (i.e., que presenten un recambio grupal de especies con restricciones y especializaciones ambientales similares a través de un gradiente ambiental), o anidadas (i.e., que la riqueza de las comunidades de parásitos con alta especificidad de hospedero disminuya a través de un gradiente, dejando contenidas a dichas comunidades dentro de comunidades de parásitos con mayor riqueza de especies) (Willig et al. 2011); mientras que grupos de parásitos que respondan de manera idiosincrática al infectar a diferentes especies de hospederos (e.g., parásitos generalistas) presenten una estructura Gleasoniana (i.e., que presenten un recambio gradual de especies que respondan de manera individual al gradiente ambiental) (Dallas and Presley 2014).

A partir de la metodología cuantitativa propuesta por Leibold y Mikkelson (2002) (i.e., el análisis de los elementos de la estructura de la metacomunidad EMS) y mejorada por Presley et al. (2010), ha sido posible determinar cuál de las estructuras idealizadas de la metacomunidad refleja de mejor manera la ordenación de distintas comunidades observadas en la naturaleza (e.g., comunidades de murciélagos, roedores, aves, anfibios, plantas, helmintos, virus, bacterias, entre otros) y qué procesos ecológicos podrían asociarse a dichas estructuras metacomunitarias (Presley and Willig 2010; Newton et al. 2012; López-González et al. 2012; Mihaljevic et al. 2018; Nieto-Rabiela et al. 2018; Cardoso et al. 2020). Por ejemplo, Richgels et al. (2013) encontró una metacomunidad anidada de tremátodos sobre hospederos caracoles a través de charcas, en donde filtros locales bióticos (i.e., la biomasa de los hospederos) y abióticos (i.e., el área de las charcas) explicaron significativamente la variación en la composición de las metacomunidades parasitarias. En contraste, Dallas y Presley (2014) encontraron metacomunidades Clementsianas de helmintos, ectoparásitos y coccidios sobre hospederos roedores, en donde la variación en la composición de los parásitos fue explicada mayormente por rasgos de historias de vida de las especies de roedores (e.g., masa corporal y longevidad).

Además del estudio e identificación de las estructuras idealizadas de la metacomunidad, la ecología de metacomunidades se ha enfocado en explicar la coexistencia de especies en el espacio a través de modelos teóricos metacomunitarios (Leibold and Chase 2018). Los modelos teóricos metacomunitarios (descritos también como paradigmas o arquetipos) asumen diferencias en

cuanto a la influencia que tienen los procesos locales y regionales sobre el ensamblaje de las comunidades biológicas (Leibold et al. 2004; Leibold and Chase 2018). Por ejemplo, el modelo de filtrado ambiental (SS 'species sorting') asume que las condiciones ambientales locales determinan la coexistencia local y composición de especies (Cottenie et al. 2003; Leibold and Chase 2018). Bajo este modelo metacomunitario, la heterogeneidad ambiental y las tasas intermedias de dispersión promueven la partición de nichos y distribución diferencial de las especies a través del paisaje (Leibold et al. 2004). De forma similar, el modelo de efectos de masa (ME 'mass-effects') asume que la heterogeneidad ambiental permite la persistencia de especies competidoras al crear variación en condiciones bióticas y abióticas (Amarasekare and Nisbet 2001; Leibold and Chase 2018). Sin embargo, este modelo está caracterizado por asumir que las especies poseen altas tasas de dispersión que promueven dinámicas fuente-sumidero entre comunidades locales (Leibold et al. 2004). De esta forma, las especies que se consideran competidoras inferiores pueden coexistir con competidoras superiores al mantener altas tasas de dispersión desde otras comunidades locales (Leibold et al. 2004).

Contrario a lo propuesto por los modelos SS y ME, el modelo metacomunitario de dinámica de parches (PD 'patch dynamics') asume homogeneidad ambiental y espacial en donde la ocurrencia de las especies no depende de procesos locales determinísticos (e.g., selección de nicho) (Leibold and Chase 2018). Al considerar que las comunidades son idénticas ambiental y espacialmente, la importancia del nicho ecológico disminuye (Leibold et al. 2004). Además, este modelo asume que las especies tienen distintas capacidades de dispersión, por lo que no todas las especies tienen acceso a las mismas comunidades locales (Leibold and Chase 2018). Por esta razón, el modelo predice que la coexistencia de especies dependerá de trade-offs competencia-colonización (Tilman 1994). Es decir, los competidores inferiores podrán persistir si son colonizadores superiores capaces de llegar a sitios de reclutamiento, y los colonizadores inferiores podrán persistir si son competidores superiores favorecidos por el uso de recursos y si son capaces de desplazar a otras especies de una comunidad local (Leibold and Chase 2018).

Finalmente, el modelo metacomunitario neutral (NT) asume que las especies son ecológicamente equivalentes (Hubbell 2001; Leibold et al. 2004). Bajo esta hipótesis, se predice que la coexistencia de especies está determinada por límites en la dispersión y estocasticidad

demográfica (Leibold et al. 2004). El modelo neutral asume homogeneidad ambiental, por lo que las especies pueden estar presentes o ausentes en las comunidades locales sin importar las características de los sitios (Leibold and Chase 2018).

Actualmente, se reconoce que los modelos teóricos metacomunitarios no son mutuamente excluyentes (Brown et al 2016). Si bien algunos estudios empíricos han mostrado que el ensamblaje de numerosas comunidades biológicas está determinado mayoritariamente por procesos/modelos determinísticos (e.g., el modelo de filtrado ambiental SS) (Cottenie 2005), otros han propuesto que los procesos determinísticos y neutrales actúan en conjunto (e.g., los modelos SS y NT podrían operar al mismo tiempo) (Chase and Myers 2011). Por esta razón la tipificación de los distintos modelos teóricos metacomunitarios sobre comunidades empíricas debe ser cautelosa (Leibold and Chase 2018). Dentro de los sistemas parásito-hospedero, la tipificación de modelos teóricos metacomunitarios se ha realizado en menor medida que la identificación de las estructuras idealizadas de la metacomunidad. Por lo tanto, la consideración e integración de modelos determinísticos/neutrales, procesos locales/regionales, y factores bióticos/abióticos es fundamental para comprender los determinantes de la diversidad, distribución y composición de las comunidades y metacomunidades parasitarias (Rigaud et al. 2010).

Los parásitos haemosporidios aviares

Los haemosporidios aviares (Phylum: Apicomplexa, Orden: Haemosporida) constituyen un modelo ideal para aplicar una aproximación de ecología de metacomunidades al estudio de comunidades parasitarias. Los haemosporidios aviares son organismos intracelulares transmitidos por vectores dípteros y se encuentran representados por 3 géneros principales: *Plasmodium*, *Haemoproteus* y *Leucocytozoon* (Valkiūnas 2005; Santiago-Alarcon et al. 2012a, 2016). Su detección molecular a través de genes mitocondriales conservados (e.g., citocromo b) indica que poseen una amplia distribución geográfica (se encuentran en todos los continentes menos en la Antártida) y una alta diversidad de linajes genéticos (>4000; (Bensch et al. 2009)) (Ferraguti et al. 2018; Hellgren et al. 2009; Pacheco et al. 2018). Pese a que algunos linajes genéticos exhiben una alta especificidad de hospedero, otros son considerados generalistas (particularmente linajes del género *Plasmodium*) debido a que saltan entre diferentes especies de hospederos comúnmente siendo capaces de

infectar a numerosas especies de aves (e.g., *Plasmodium relictum* >400 especies de aves) que se encuentran alejadas filogenéticamente (Križanauskienė et al. 2006; Svensson-Coelho et al. 2013; Hellgren et al. 2015; Martínez-de la Puente et al. 2020).

El ciclo de vida y desarrollo de los haemosporidios aviares es similar para los géneros *Plasmodium*, *Haemoproteus* y *Leucocytozoon* (Valkiūnas 2005). Se lleva a cabo dentro de los vectores dípteros (i.e., reproducción sexual: gametogonia y esporogonia) y dentro de hospederos aviares (i.e., reproducción asexual: merogonia) (Valkiūnas 2005). Para que su ciclo de transmisión sea exitoso, las aves deben entrar en contacto con los esporozooitos contenidos dentro de las glándulas salivales de un vector infectado, y posteriormente un nuevo vector debe entrar en contacto con los gametocitos maduros que se encuentren dentro de la sangre de un hospedero aviar infectado (Santiago-Alarcon and Marzal 2020). El contacto e inoculación de estos estadios infecciosos se lleva a cabo durante la alimentación hematófaga de los vectores dípteros sobre las aves, y resulta en la infección del sistema digestivo del vector (Paul et al. 2002) y/o en la infección de los tejidos del hospedero aviar (i.e., merogonia exo-eritrocítica: infección de tejido hepático, pulmonar, renal, cardiaco, entre otros) (Hernández-Lara et al. 2021).

Posterior a la merogonia exo-eritrocítica, los haemosporidios aviares tienen la capacidad de invadir los eritrocitos del hospedero vertebrado (i.e., merogonia eritrocítica), resultando en una infección que se caracteriza por tres fases: la fase aguda, en donde de la parasitemia (i.e., intensidad de la infección en sangre) comienza a incrementar; la fase de crisis, en donde la parasitemia llega a su pico máximo; y la fase crónica, en donde el número de parásitos circulando en sangre disminuye hasta niveles en donde la infección puede no ser detectable (Valkiūnas & Atkinson 2020). Posteriormente, los haemosporidios aviares pueden entrar a una fase de latencia en donde los gametocitos desaparecen por completo de la circulación sanguínea, pero la infección se mantiene en estadios exo-eritrocíticos dentro de los tejidos de las aves (Hernández-Lara et al. 2021). En ocasiones, las fases de latencia pueden activarse bajo estímulos de inmunosupresión (e.g., en la época reproductiva de las aves) o bajo la presencia de vectores transmisores, y regresar a estadios eritrocíticos produciendo parasitemias secundarias capaces de infectar a nuevos vectores susceptibles (LaPointe et al. 2012; Santiago-Alarcon and Marzal 2020).

Las fases de infección agudas y de crisis, así como las infecciones exo-eritrocíticas, tienen

efectos importantes sobre la salud de los hospederos aviares (Knowles et al. 2010). Por ejemplo, la destrucción de los eritocitos por medio del sistema inmune produce una importante reducción en la eficiencia del transporte de oxígeno en la sangre (LaPointe et al. 2012). Así mismo, las infecciones agudas pueden producir anorexia, reducción de la masa corporal y reducción en los niveles de actividad, afectando el éxito reproductivo y la sobrevivencia de poblaciones de aves (Palinauskas et al. 2008). En infecciones exo-eritrocíticas se ha reportado daño tisular importante como hepatomegalia y esplenomegalia, así como el bloqueo de capilares cardiacos y cerebrales (Hernández-Lara et al. 2021). La severidad de las infecciones puede ser variable, y depende, en general, del linaje de haemosporidio y de los rasgos de historia de vida de las especies de aves infectadas (Palinauskas et al. 2008). Las poblaciones de aves silvestres suelen presentar infecciones de fase crónica (LaPointe et al. 2012), con pocos ejemplos descritos de daños directos a la salud. Sin embargo, las poblaciones que se han visto frecuentemente afectadas son las que carecen de una adaptación evolutiva a los parásitos haemosporidios aviares (i.e., poblaciones inmunológicamente susceptibles: aves domésticas, aves silvestres en cautiverio, avifauna con distribución restringida a islas) (LaPointe et al. 2012).

El papel que juegan la ecología de las comunidades de vectores y aves es fundamental para la reproducción, desarrollo y sobrevivencia de los haemosporidios aviares en tiempo y espacio. Por un lado, las comunidades de vectores son las responsables de la reproducción sexual y transmisión local de haemosporidios entre poblaciones de aves silvestres (Gager et al. 2008). Los patrones de distribución, estacionalidad y actividad de los vectores pueden determinar el acceso de ciertas especies de parásitos haemosporidios a ciertas poblaciones de aves susceptibles. Por otro lado, las comunidades de aves son las responsables de la reproducción asexual, y las encargadas de dispersar a los haemosporidios a nivel regional, a través de la altitud, latitud y a través del tiempo (Pérez-Tris and Bensch 2005; Ellis et al. 2015). Las infecciones crónicas y latentes de las aves permiten el mantenimiento a largo plazo de los haemosporidios aviares en distintos ambientes, y facilitan la extensión de sus rangos geográficos de distribución (Pérez-Tris and Bensch 2005).

Patrones de distribución y beta diversidad de parásitos haemosporidios aviares

Dentro del estudio de los patrones espaciales de la biodiversidad, el estudio de la beta diversidad de especies (i.e., el recambio en la identidad o composición de especies entre ensambles locales o regionales), representa una faceta fundamental para comprender los procesos que intervienen en el ensamblaje y mantenimiento de la biodiversidad (Legendre et al. 2005). Históricamente, la cantidad de estudios que se han enfocado en comprender los procesos asociados a la beta diversidad es mucho menor que los enfocados en comprender los determinantes de la alfa diversidad (i.e., la riqueza o numero total de especies presentes en una comunidad) (Koleff et al 2003). Sin embargo, tanto para organismos de vida libre, como para organismos parásitos, la comprensión de los mecanismos que regulan el recambio de especies en el tiempo y el espacio ha cobrado especial importancia.

Los patrones de distribución y beta diversidad de parásitos haemosporidios aviares se han encontrado influenciados por un gran número de factores. En general, los factores ambientales y características del paisaje (e.g., temperatura, precipitación, altitud, estructura de la vegetación, tipo de uso de suelo) se han considerado como determinantes fundamentales de la diversidad de parásitos haemosporidios. Por ejemplo, la altitud, al estar correlacionada negativamente con la temperatura, puede gobernar la distribución de la diversidad de los haemosporidios por género (van Rooyen et al. 2013; Álvarez-Mendizábal et al. 2021). En general, linajes del género *Plasmodium* tienden a distribuirse en sitios cálidos de menor altitud; linajes del género *Leucocytozoon* se encuentran restringidos en sitios fríos de mayor altitud; y linajes del género *Haemoproteus* pueden distribuirse desde altitudes menores, hasta altitudes intermedias y mayores siendo menos susceptibles a las restricciones climáticas (LaPointe et al. 2010; van Rooyen et al. 2013; Gonzalez et al. 2014). Estos patrones de diversidad y distribución se han asociado a 1) los efectos directos de la temperatura sobre la reproducción y desarrollo de cada género de haemosporidio dentro de sus vectores transmisores, 2) los efectos directos de la temperatura sobre las tasas de reproducción de los vectores, y 3) la estructura de los ensambles de vectores y la coexistencia parásito-vector a través de los sitios (i.e., *Plasmodium* debe coexistir con mosquitos culícidos para su transmisión; *Haemoproteus* con moscas ceratopogónidas e hippobóscidas; y *Leucocytozoon* con moscas simúlidas y/o ceratopogónidas) (Santiago-Alarcon et al. 2012). Por otro

lado, el tipo de uso de suelo y el grado de perturbación de los hábitats también pueden modificar la estructura y composición de las comunidades de haemosporidios aviares y de sus vectores (Hernández-Lara et al. 2017; Abella-Medrano et al. 2015; Hernández-Lara et al. 2020). En general, la perturbación de los hábitats reduce la complejidad de las comunidades, lo que puede favorecer la dominancia por especies generalistas de hábitat y disminuir la riqueza de especialistas (Rubio et al. 2014). Igualmente, la perturbación puede generar sitios aptos para la reproducción de vectores y/o modificar la estructura de la riqueza y la abundancia de las comunidades de vectores (Abella-Medrano et al. 2015). Por ejemplo, Hernández-Lara et al. (2020) encontró un cambio significativo sobre la beta diversidad de linajes de haemosporidios aviares en una población de *Chlorospingus flavopectus* a través de un gradiente de perturbación. Observó una pérdida de la riqueza de linajes de haemosporidios aviares hacia sitios con mayor grado de urbanización; sin embargo, a medida que la perturbación incrementó la población de aves adquirió nuevos linajes de parásitos evidenciando como la urbanización actúa como un filtro para la riqueza de especies y produce un cambio significativo sobre los patrones de composición de las comunidades parasitarias (Hernández-Lara et al. 2020).

Así como las condiciones climáticas y el grado de perturbación de los hábitats influyen significativamente sobre la composición de ensambles de haemosporidios aviares, los factores espaciales (e.g., distancias geográficas, gradientes latitudinales) pueden tener efectos sobre la distribución y la beta diversidad (i.e., el recambio de especies a través de los sitios) de las comunidades parasitarias. Por ejemplo, algunos estudios han demostrado que en ensambles de protozoarios, artrópodos y helmintos la similitud en composición de especies disminuye conforme aumenta la distancia geográfica de sus comunidades (i.e. decaimiento de la similitud con la distancia) (Ishtiaq et al. 2009; Krasnov et al. 2005; Poulin 2003). Así mismo, un estudio de patógenos humanos evidenció la formación de patrones anidados de distribución, en donde los ensambles de patógenos distribuidos en latitudes mayores se encontraron contenidos dentro de los ensambles de patógenos distribuidos en los trópicos; además, los patógenos mostraron gradientes latitudinales en el aumento de la riqueza conforme se acercaron a los trópicos (i.e. gradientes latitudinales de la diversidad) (Guernier et al. 2004). La beta diversidad de los parásitos haemosporidios aviares ha sido explicada por las distancias geográficas entre las comunidades de

hospederos aviares a escalas regionales de estudio (Olsson-Pons et al. 2015; Fecchio et al. 2017). Sin embargo, el efecto del espacio sobre el recambio de los haemosporidios aviares ha sido variable, puesto que la composición de las comunidades parasitarias puede verse afectada no sólo por los factores espaciales, sino también por la distribución y composición de las comunidades de sus hospederos vertebrados y vectores (Stephens et al. 2016).

Algunos factores ecológicos y evolutivos asociados a las especies de hospederos aviares (e.g., rasgos de historias de vida, recambio taxonómico y filogenético de hospederos) también han podido explicar la beta diversidad y distribución de parásitos haemosporidios aviares (Ishtiaq et al. 2010; Scordato and Kardish 2014; Ellis et al. 2015; Ferraguti et al. 2018; Fecchio et al. 2019). Por ejemplo, Scordato y Kardish (2014) evaluaron la composición y beta diversidad de linajes de haemosporidios aviares en poblaciones de *Phylloscopus humei* y *Phylloscopus trochiloides* dentro de tres sitios (localizados en Siberia, Kyrgyzstan e India) a través de un gradiente latitudinal. Encontraron que el recambio de linajes de haemosporidios aviares no aumentó con la distancia geográfica de los sitios estudiados, sino que fue mayor entre las dos especies de aves (pese a encontrarse dentro de los mismos sitios). Esto evidenció un efecto importante de la filogenia de los hospederos sobre el ensamblaje local y composición de las comunidades de haemosporidios aviares (Scordato and Kardish 2014). Así mismo, estudios como el de Williamson et al (2019) han demostrado que el recambio o beta diversidad de parásitos haemosporidios a nivel regional está determinado por el recambio taxonómico de sus hospederos aviares (Williamson et al. 2019).

Pese a toda la información disponible sobre los determinantes de la distribución y beta diversidad de parásitos haemosporidios aviares, no ha sido posible encontrar regularidad en estos patrones de diversidad. De acuerdo con esto, es importante continuar con estudios que ayuden a discernir la importancia de dichos factores para regiones y escalas específicas de estudio. Esta tesis es un intento para contribuir a dicho conocimiento para las regiones Neotropical y Neártica mexicanas, así como para distintas escalas espaciales (i.e., locales a regionales). Mediante la identificación de las estructuras idealizadas de la metacomunidad y el modelado de la beta diversidad, se amplió el conocimiento sobre los factores que delimitan la diversidad, distribución y composición de comunidades de parásitos haemosporidios aviares en sus hospederos y a través de distintos ambientes.

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CAPÍTULO 1.

METACOMMUNITY STRUCTURE REVEALS THAT TEMPERATURE AFFECTS THE LANDSCAPE COMPOSITIONAL PATTERNS OF AVIAN MALARIA AND RELATED HAEMOSPORIDIAN PARASITES ACROSS ELEVATIONS

Metacommunity structure reveals that temperature affects the landscape compositional patterns of avian malaria and related haemosporidian parasites across elevations

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ABSTRACT

Metacommunity ecology studies how species compositional patterns and their distributions vary across local and regional scales and provides insights on processes driving the distribution of communities. Avian haemosporidians comprise a diverse and widely distributed parasite taxon; some studies have analyzed their alpha and beta diversity patterns. Yet, metacommunity structures of avian haemosporidians and thus relevant biotic and abiotic variables explaining such structures at the landscape scale (i.e., 10–200 km) have not been assessed. We studied the metacommunity structure of avian haemosporidian mtDNA cyt *b* lineages and the infected avian host assemblage across four different elevations in Central Veracruz, Mexico. We performed variation-partitioning analyses to evaluate the contribution of host-related traits and climatic variables to the metacommunity. We found a richness of 78 lineages within 38 infected species of birds. At the component community level, we observed that bird species infected with a lower number of parasite lineages (e.g., <3) represented a nested subset of those with a higher number of parasite lineages (e.g., >8) (i.e., nested structure). However, this nested pattern was due to the restricted spatiotemporal co-occurrence of hosts and parasites, given the high degree of turnover across elevations. Host-related traits (functional, transmission-associated, and phylogenetic relationships) only explained a small fraction of the variation (4.4%) in parasite lineage composition across avian hosts. At the habitat level, there was a group turnover by parasite genera across elevation (i.e., quasi-Clementsian structure), which was partly explained by climatic variables (mean annual temperature and annual diurnal range; 27.6%) that may constrain parasite reproduction and vector distribution across the environmental gradient. At the scale of our study, environmental conditions represented a more important driver of avian haemosporidian metacommunity structure than host-related traits, suggesting an important role of environmental filtering structuring parasite assemblages at the landscape level.

1. Introduction

Metacommunity theory has improved our understanding of how patterns of species composition and diversity can arise from processes that occur at both local and regional scales (Leibold and Chase 2018). In general, the metacommunity framework focuses on identifying species distribution patterns across environmental gradients (i.e., pattern-based approach) and on the interacting roles of dispersal and environmental

heterogeneity in producing species' occurrences across space (i.e., process-based approach) (Leibold and Chase 2018). Under this framework, compositional patterns of species distributions have been described as idealized metacommunity structures (Leibold and Mikkelson 2002). These structures have extended from early ecological research on species spatial structures and include random, nested, and anti-nested subsets (Table 1). Additionally, Presley et al. (2010) described three different forms of species loss within nested-subsets (i.e., clumped, random, and hyperdispersed species loss), and defined six quasi-structures related to, but weaker than, any of the six idealized metacommunity structures (i.e., quasi-nested subsets with clumped, random and hyperdispersed species loss, quasi-Clementsian, quasi--Gleasonian and quasi-Evenly spaced structures) (Presley et al., 2010). The development of such conceptual framework has been increasingly applied to the study of free-living taxa communities such as bats, birds, rodents and fish, and through its process-based approach (i.e., the species-sorting, mass-effects, patch-dynamics and neutral archetypes, see Table 2) has been able to disentangle the role of different structuring processes (e.g., dispersal vs. environmental filtering) behind species distribution patterns (Cottenie 2005; Gascón et al., 2016; Heino et al., 2017). Accordingly, the metacommunity framework has been recently proposed as a useful approach for the study of compositional patterns of parasite communities (Mihaljevic 2012; Suzán et al., 2015; Mihaljevic et al., 2018) and thus continuously applied to such antagonistic systems (Dallas and Presley 2014; Costa-Neto et al., 2019; Cardoso et al., 2020).

Applying a metacommunity framework to host-parasite interactions can help identifying factors and inferring ecological processes that shape parasite communities within and among host assemblages (Richgels et al., 2013; Mihaljevic et al., 2018). In theory, groups of species that together exhibit strong associations to the environment (e.g., trophic guilds) might present Clementsian structure, whereas species that exhibit individualistic responses to an environmental gradient (e.g., tolerance to climatic conditions) might present Gleasonian structure (Willig et al., 2011). In a similar way, one could expect that groups of parasites that exhibit strong associations to a type of host (e.g., high host specificity) would present Clementsian structure and that parasites which individualistically infect different hosts (e.g., low host specificity) would present Gleasonian structure (Dallas and Presley 2014).

The variation in species composition behind each parasite metacommunity structure can be determined by several host-related ecological traits (Dallas and Presley 2014). For example, host functional traits such as body mass have been reported to influence the colonization success of parasites over host species (i.e., hosts with a larger body mass could be more easily colonized by a number of different parasites) (Poulin and Valtonen 2001; Korallo et al., 2007). Moreover, a large geographic range size and a high relative abundance

Table 1
Idealized metacommunity structures as defined by Leibold and Mikkelson (2002).

Type of structure	Description	Reference
Random	Species do not show clear patterns in their distributions.	Simberloff (1983)
Checkerboard	Pairs of species present mutually exclusive distributions.	Diamond (1975)
Nested subsets	Species-poor communities are a subset of species contained in species-rich communities, exhibiting species loss between sites.	Patterson and Atmar (1986)
Clementsian	Species are grouped within discrete communities that show turnover between sites.	Clements (1916)
Gleasonian	Species show independent distributions across an environmental gradient.	Gleason (1926)
Evenly spaced	Species show more even distributions across an environmental gradient than expected by chance.	Tilman (1982)

Table 2
The four theoretical archetypes of metacommunity ecology as defined by Leibold and Chase (2018).

Metacommunity archetype	Description
Species sorting	Local environmental conditions determine species coexistence through a heterogenous landscape. Intermediate dispersion rates that allow niche partitioning are assumed.
Mass-effects	Source-sink dynamics determine species coexistence through a heterogenous landscape. High dispersion rates of inferior competitors allow them to persist with superior competitors.
Patch-dynamics	Competition-colonization trade-offs determine species coexistence through a homogenous landscape. Dispersal limitation and stochastic extinctions are assumed.
Neutral	Dispersal limitation and demographic stochasticity determine species coexistence through a homogenous landscape. Ecological equivalence of species is assumed.

are host traits that can also have effects on metacommunity structure by promoting the accumulation of parasite species (Dáttilo et al., 2020), and by increasing the contact rates of infected and susceptible individuals, respectively (Vazquez et al., 2005; Dáttilo et al., 2020). Lastly, a fundamental trait that has been considered to affect the variation in composition of parasite communities is the phylogenetic identity of hosts (Krasnov et al., 2010; Gupta et al., 2020). Phylogenetically related host species are predicted to harbor more similar parasite communities than phylogenetically distant hosts, which will be reflected on parasite community composition (Poulin 2010; Dáttilo et al., 2020).

Besides the important role that host-related traits may have in structuring parasite metacommunities, abiotic factors can also have important effects on parasite community composition (Krasnov et al., 2010). Some studies have shown that both environmental and geographical barriers can govern the assembly and distributional patterns of parasite species across space (Clark et al., 2017; Fecchio et al., 2017). For example, mean annual temperature, precipitation, and fluctuations in diurnal temperature range can directly affect the reproduction rate of some parasites within hosts (i.e., particularly vector-borne parasites) (Paaijmans et al., 2009) and thus limit their colonization and establishment in certain areas (Clark et al., 2017). In addition, the geographical distance among sites has been observed to produce a decay in compositional similarity for some parasite communities (i.e., distance-decay pattern) (Poulin 2003; Ishtiaq et al., 2010). Despite the existing body of literature focusing on the diversity and distribution of parasite communities, most of the factors underlying the assembly and compositional patterns of parasites across local communities seem to be contingent on the host-parasite system and scale under study (Korallo et al., 2007; Krasnov et al., 2008). The compositional similarity of some parasite communities seems not to be exclusively affected by either hosts or the environment, but rather by the direct and indirect effect of both types of factors (Berkhout et al., 2019). Consequently, there is yet much to understand about how different processes at different scales may shape parasite metacommunities.

Avian haemosporidians (Phylum: Apicomplexa, Order: Haemosporida) are globally distributed vector-borne protozoa, mainly represented by the genera *Plasmodium*, *Haemoproteus* and *Leucocytozoon* (Santiago-Alarcon et al., 2012). Their genetic diversity is large as revealed by their mtDNA cytochrome *b* (cyt *b*) gene (currently 4522 lineages; Bensch et al., 2009). Haemosporidian lineages have the ability to infect a broad range of avian families; their host specificities vary from highly specific infecting one bird host species to infecting numerous distantly-related bird host species (particularly parasites of the genus *Plasmodium*, e.g., *Plasmodium relictum* lineages) (Svensson-Coelho et al., 2013; Hellgren et al., 2015; Martínez-de la Puente et al., 2020). Moreover, their level of specialization can change in response to both the environment and the diversity of their hosts (i.e., higher host diversity in the tropics can

decrease host-vector encounter rates and therefore increase host-breath and decrease host specificity) (Svensson-Coelho et al., 2014). Avian haemosporidian parasites can easily switch among hosts (Santiago-Alarcon et al., 2014), which under current changes in environmental conditions could lead to the emergence of novel diseases in native bird assemblages (e.g., Ferreira-Junior et al., 2018).

Recent studies showed that diversity (i.e., alpha and beta diversity) and distributional patterns of avian haemosporidian lineages are influenced by both biotic and abiotic factors. For example, Ferraguti et al. (2018) found that landscape characteristics (e.g., type of habitat, distance to water reservoirs) were major determinants driving avian *Plasmodium* diversity in southwestern Spain. Moreover, van Rooyen et al. (2013) showed that local climatic conditions drive haemosporidian distribution by genera across elevation gradients (e.g., *Haemoproteus* tends to occur from low to intermediate and high elevations, *Plasmodium* from low to intermediate elevations and *Leucocytozoon* occurs at higher elevations). In contrast, Ellis et al. (2015) were not able to observe any direct effects of environmental or spatial variables on the distribution of haemosporidian lineages across eastern North America; instead, they observed a strong effect of host distribution on parasite distributional patterns (Ellis et al., 2015). Also, Scordato & Kardish (2014) and Clark et al. (2018) proposed that host identity and phylogeny were more important drivers of avian haemosporidian regional assembly than environmental and spatial factors. Altogether, these studies suggest that host traits, phylogenetic relationships between hosts, and both environmental and spatial factors can all be major determinants of avian haemosporidian diversity. However, no studies have used a metacommunity ecology framework to evaluate the extent to which host traits and environmental factors might shape haemosporidian lineage composition through idealized metacommunity structures at a local or landscape scale (i.e., 1–200 km). Applying such framework provides a unique approach to understand how local scale patterns and processes can be affected by regional ones, therefore allowing to infer the relative importance of core ecological processes (i.e., neutral vs. species sorting archetypes) that can drive avian haemosporidian spatial distribution patterns. Moreover, it helps to identify potential metacommunity structures where parasite emergence via host switches is more likely (Suzán et al., 2015).

Here, we determined the metacommunity structure of avian haemosporidian cyt *b* lineages across distinct habitat types located at different elevations. Parasite metacommunities were evaluated at two levels, at the 'component community-level' where all haemosporidian lineages detected in one species of bird represented a local community (Bush et al., 1997), and at the 'habitat-level' where all haemosporidian lineages detected in all bird species sampled in one habitat type represented a local community. Also, we evaluated the contribution of host-related traits (e.g., functional, transmission-associated and phylogenetic relationships) and climatic variables (e.g., mean annual temperature, annual diurnal range, annual precipitation and precipitation seasonality), to the variation in haemosporidian lineage composition across metacommunity structures. Lastly, we determined the metacommunity structure of the infected avian assemblage across the different habitat types. At the component community-level, we expected avian haemosporidia lineages to exhibit a Gleasonian or quasi-Gleasonian structure, showing individualistic distributions across bird host species. Also, we predicted that transmission-associated traits would explain a significant amount of variation in lineage community composition across the host metacommunity. At the habitat-level, we expected avian haemosporidian lineages to exhibit a Clementsian structure, where *Plasmodium* lineages would group together in habitats with lower-warmer elevations, *Leucocytozoon* lineages would be restricted to habitats with higher-cooler elevations, and *Haemoproteus* lineages would be distributed across all habitat types. We expected mean annual temperature to be the main variable explaining lineage community composition across the habitat-level metacommunity. Finally, because most biological systems that have been assessed with the

Elements of Metacommunity Structure (i.e., EMS) framework do not appear to exhibit random, checkerboard or nested patterns (Leibold and Chase 2018), we expected avian hosts to present any form of anti-nested metacommunity structure (i.e., Gleasonian, Clementsian or Evenly spaced structure).

2. Methods

2.1. Field work

We conducted two surveys during the avian breeding season (May–July 2017 and 2018) in Central Veracruz, Mexico. To capture regional variation in climatic conditions, we registered and sampled birds in four habitat types located at different elevations: coastal medium deciduous forest 0 m asl (CMDF 19°35′34.3″N, 96°22′52.2″W), tropical deciduous forest 200–800 m asl (TDF 19°20′59.4″N, 96°34′17.7″W), montane cloud forest 1200–1600 m asl (MCF 19°30′56.9″N, 97°00′22.7″W) and pine-oak forest 1800–3000 m asl (POF 19°31′56.4″N, 97° 04′20.5″O) (Fig. 1). Each habitat type was sampled for 5 days using 10 mist nets (12 × 3m) opened daily for 6 h (6am–12pm). Bird species were identified according to the Sibley and Howell & Webb field guides (Howell and Webb 2010; Sibley 2014). We collected 30–75 μl blood samples from each individual by puncturing the brachial vein with sterile needles (Santiago-Alarcon and Carbó-Ramírez 2015). Blood samples were kept under refrigeration (4 °C) until laboratory arrival, where they were stored at −20 °C. All birds were released after sample collection.

3. Laboratory work

3.1. Molecular analyses

DNA extractions from blood samples were performed using the DNeasy Blood and Tissue kit from QIAGEN™. All extractions were visualized in 1% agarose gels containing 0.8 μl of Gel red® (Biotium). Afterwards, we conducted four PCR protocols for the amplification of the mtDNA cytochrome *b* gene of avian haemosporidians.

The amplification of *Plasmodium* and *Haemoproteus* lineages was performed using a nested PCR with primers AE299F-AE974R and AE066F-AE064R, targeting an 1109 bp fragment according to Pacheco et al. (2018). PCRs were carried out with Platinum™ Green Hot Start PCR Master Mix in a final volume of 25 μl. For PCR I, 2 μl of genomic DNA were used with the following amplification conditions: partial denaturation at 94 °C for 4 min, 25 cycles of 30 s at primer melting temperature (56 °C), 2 min extension at 72 °C and 1 min at 94 °C, with a final extension of 10 min. For PCR II, 3 μl of DNA template were used with the following amplification conditions: partial denaturation at 94 °C for 4 min, 35 cycles of 2 min at primer melting temperature (56 °C), 30 s extension at 72 °C and 1 min at 94 °C, with a final extension of 10 min. Negative samples for the Pacheco et al. (2018) protocol were then screened with primers 3760F-4292R, which target a 533 bp fragment following Beadell et al. (2004) and also with a second nested PCR with primers NR1-NR3 and HaemF-HaemR targeting a 479 bp fragment according to Hellgren et al. (2004). For the amplification of *Leucocytozoon* spp., we performed a nested PCR with primers NF1-NR3 and HaemFL-HaemRL (479bp) (Hellgren et al., 2004). Positive (previously bird infected samples from the same area, determined using both microscopy and PCR) and negative controls (ddH₂O) were included in all reactions. All PCR products were visualized in 1.5% agarose gels containing 1.35 μl of Gel red® (Biotium). Subsequently, we purified excised positive gel bands with the MinElute Gel Extraction kit from QIAGEN™. Finally, purified products were sent to Macrogen Inc. (Seoul, Korea) for bi-directional sequencing.

Sequence quality was assessed with the SnapGene® Viewer program (version 4.3.4, from GSL Biotech; available at snapgene.com). Haemosporidian lineage identity was determined based on the percentage of
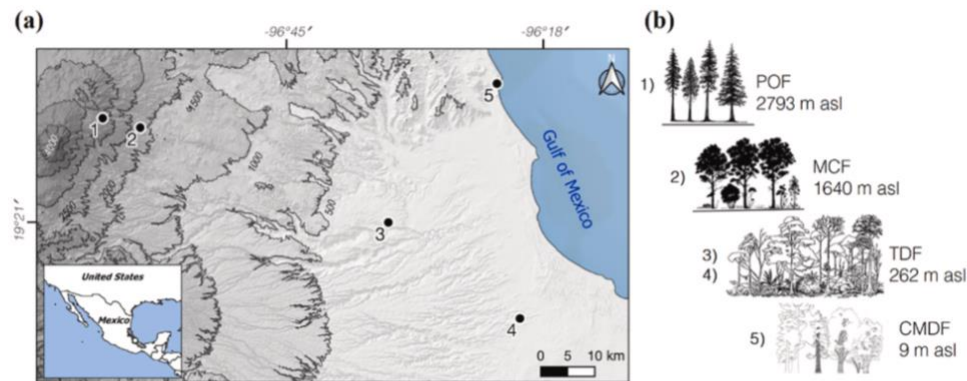
Fig. 1. a) Location of the four sampled habitat types in Central Veracruz, Mexico. b) The elevational distribution of the four sampled habitat types: 1) POF = Pine-oak forest, 2) MCF = Montane cloud forest, 3, 4) TDF = Tropical deciduous forest, and 5) CMDF = Coastal medium deciduous forest.

similarity with other lineages in the MalAvi database (Bensch et al., 2009). DNA sequences that did not match the 479 bp MalAvi fragments were classified as new lineages, named according to Bensch et al. (2009) and deposited in GenBank (see accession numbers in Supporting Information Table 1) and MalAvi databases. Mixed infections were determined when double peaks were observed in the same position in electropherograms. If double peaks were only observed in one position, one of the lineages corresponded to the base of one of the peaks, and the second to the other base. In order to obtain sequences corresponding to each of the infections when double peaks were present in more than one base, we compared the sequence against an already known lineage from MalAvi database (already identified in our samples), or against one of the new lineages from this study (from single infections). Once one of the lineages was confirmed, we inferred the second lineage by observing the alternative base in double peak positions. We also used Poly-PeakParser online software (Hill et al., 2014) as an aid.

4. Host-related traits and climatic variables

4.1. Host-related traits

To explain the variation in haemosporidian lineage composition at the component community-level, we used three sets of explanatory host related traits: functional, transmission-associated and phylogenetic relationships between hosts. Functional traits for each bird species comprised mean adult body mass (g) and trophic guild. These were taken from the Handbook of Avian body masses (Dunning 2008) and from the Cornell Lab of Ornithology Birds of the World website (birdsoftheworld.org). Bird hosts were categorized as 1 = nectarivores, 2 = insectivores/frugivores, 3 = insectivores, 4 = insectivores/granivorous, 5 = insectivores/granivorous/frugivores and 6 = omnivores. Transmission-associated traits comprised host abundance for each bird host species and habitat occurrence, which was used as a proxy for the host's geographic range size. Host abundance was considered as the number of sampled individuals for each host species. Habitat occurrence was categorized as follows: 1 = all birds which exclusively occur in coastal medium deciduous forest, 2 = shared bird species between coastal medium deciduous forest and tropical deciduous forest, 3 = all birds which exclusively occur in tropical deciduous forest, 4 = shared bird species between tropical deciduous forest and montane cloud forest, 5 = all birds which exclusively occur in montane cloud forest, 6 = shared bird species between montane cloud forest and pine-oak forest and 7 = all birds which exclusively occur in pine-oak forest. Phylogenetic relationships between hosts represented their evolutionary relatedness and comprised the first two axes of variation (38.6% and 25.9%) of a Principal Coordinates Analyses (PCoA) performed on a phylogenetic distance matrix of bird hosts (Dallas et al., 2014). To build this matrix,

we obtained a majority rule consensus tree from 10,000 trees generated on BirdTree.org (visited on March 28, 2020) (for details on the phylogenetic reconstruction see Jetz et al., 2012, 2014). Phylogenetic distances were computed using the cophenetic() function from the 'ape' library in R software (Paradis et al., 2004). PCoA was used to reduce the dimension of the phylogenetic distance matrix, capturing most of the variation of phylogenetic dissimilarity in the first two axes, and was performed using the cmdscale() function from the 'stats' package, in R software (version 4.0.2). Moreover, according to Barçante et al. (2017), Boyle (2017), and Ruelas and Aguilar (2010), each infected avian host species was categorized as 1 = altitudinal migrant (i.e., bird species that have supporting data on their migration movements through elevation), 2 = probable altitudinal migrant (i.e., bird species that are probably performing migration movements through elevation according to the Handbook of the Birds of the World) and 3 = no evidence of altitudinal migration (i.e., bird species that were not listed in any of the above mentioned literature).

4.2. Climatic variables

To explain the variation in haemosporidian lineage composition at the habitat-level, we used nine climatic predictor variables for the geographical coordinates of each habitat type extracted from the WorldClim climate surfaces database (worldclim.org) (Fick and Hijmans 2017). Five climatic variables were related to temperature (mean annual temperature, annual diurnal range, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month) and four to precipitation (annual precipitation, precipitation of the wettest month, precipitation of driest month, precipitation seasonality). These temperature- and precipitation-related variables have been often documented to be fundamental factors for haemosporidian and vector development and reproduction (Santiago-Alarcon et al., 2012; Fecchio et al., 2019a) and thus are relevant for parasite transmission (Paaijmans et al., 2009; LaPointe et al., 2010; Beck-Johnson et al., 2017). Since variables showed high collinearity (Pearson correlation≥0.8), we selected two temperature variables (i.e., mean annual temperature and annual diurnal range) and two precipitation variables (annual precipitation and precipitation seasonality). Variable selection was based on both their reported importance in the malaria literature and on a forward selection variance procedure (using function 'ordiR2step' implemented in the vegan library in R software version 4.0.2) (Blanchet et al., 2008).

4.3. Statistical analyses

Bird species that were not infected with at least one haemosporidian cyt *b* lineage were excluded from all analyses. The Elements of

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Metacommunity Structure analysis were also performed for the infected avian host metacommunity. Furthermore, we estimated the molecular prevalence of avian haemosporidians and its 95% confidence intervals using the Quantitative Parasitology Web software (QPWeb) version 1.0.14 (Reiczigel et al., 2019).

4.3.1. Elements of metacommunity structure

The EMS were evaluated according to the metacommunity framework proposed by Leibold and Mikkelson (2002) and extended by Presley et al. (2010). First, for the component community-level, we constructed a lineage-by-bird species incidence matrix (78 haemosporidian linages x 38 infected bird host species). Second, for the habitat-level, we constructed a lineage-by-habitat type incidence matrix (78 haemosporidian lineages x 4 habitat types). These matrices included lineages from all three parasite genera. Finally, for the infected avian host community we constructed a bird species-by-habitat type incidence matrix (38 infected bird host species x 4 habitat types). Incidence matrices were first ordered via reciprocal averaging, where species (i.e., haemosporidian lineages/bird species) with similar distributions, and sites (i.e., bird species/habitat types) with similar parasite compositions were grouped together. Subsequently, we determined the three elements of metacommunity structure (i.e., coherence, turnover and range boundary clumping).

Coherence was evaluated through comparing the number of embedded absences in the ordinated matrix against the estimated mean of absences produced by a null model (1000 iterations) (Leibold and Mikkelson 2002). If a matrix contains significantly fewer embedded absences than the randomized matrix then coherence is considered positive and the next two elements of the framework are assessed. However, significantly more embedded absences than expected by the null model or non-significant results are indicative of Checkerboard and Random structures, respectively. Turnover was assessed by counting the number of times one species/lineage is replaced by another one in the ordinated matrix, and by comparing those replacements against the mean value of replacements generated by 1000 randomizations. When the number of replacements is higher than expected by the null model turnover is considered positive, and depending on the range boundary clumping it can be consistent with Clementsian, Gleasonian or Evenly spaced distributions (Leibold and Mikkelson 2002). When the ordinated matrix contains fewer replacements than expected by the null model, turnover is considered negative and is consistent with Nested subsets. In addition, non-significant results in turnover can be indicative of quasi-structures (Presley et al., 2010). Finally range boundary clumping of species was assessed by using Morisita's Index (I) (Leibold and Mikkelson 2002). This index measures the dispersion of species occurrences among sites (Morisita 1971). Significant values of I were evaluated by using a chi-squared test. Matrices with significant values of I greater than 1 indicate clumped boundaries consistent with Clementsian structure (when values of turnover are positive); however, when values of turnover are negative, they can indicate a pattern of Nested-subsets with clumped species loss (i.e., species-poor sites are contained within species-rich sites and exhibit grouped species loss across an environmental gradient). Similarly, significant I values below 1 indicate hyperdispersed distributions consistent with Evenly spaced structures (when positive turnover occurs) or they can indicate Nested-subsets with hyperdispersed species loss when negative turnover occurs (i.e. species are lost one by one across a nested structure without any clumping between them). Lastly, non-significant chi-squared values can be indicative of Gleasonian structure (when positive turnover occurs) or they can indicate Nested-subsets with random species loss when negative turnover occurs (i.e., species are lost in a stochastic manner across a nested structure without any order). EMS analyses were performed using the 'metacom' library (Dallas 2014) in R software (version 4.0.2).

4.3.2. Variation partitioning

We performed variation partitioning to evaluate which host-related and environmental traits best explained the variation in haemosporidian lineage composition of the two ordinated matrices (i.e., component-community and habitat-level matrices) that resulted from the EMS analyses (Peres-Neto et al., 2006; Meynard et al., 2013). Variation partitioning was based on redundancy analysis (RDA) following the method proposed by Peres-Neto et al. (2006). Furthermore, variation partitioning has been proposed as a complementary statistical analysis to better interpret the pattern-based metacommunity models such as EMS analyses (Meynard et al., 2013). The combination of both statistical analyses has already been applied to study the composition of coccidian, ectoparasite, helminth and viral metacommunities (e.g., Dallas and Presley 2014; Nieto-Rabiela et al., 2018; Cardoso et al., 2020), and it was applied in this study for the first time to avian haemosporidian parasites.

To explain the variation in parasite composition at the component community-level, we used three host-related explanatory matrices, each with two predictor variables previously described. The first one contained 'functional traits' for each bird species (i.e., mean adult body mass in grams and trophic guild). The second one contained 'transmission-associated' traits for each bird species (i.e., host abundance and habitat occurrence). The third one contained the two first axes of variation (38.6% and 25.9%) from a PCoA on a phylogenetic distance matrix of bird hosts. A broken stick model was applied for estimating the number of statistically significant axes of variation needed for the variation partitioning analyses. This was performed using the 'broken-Stick' and 'bsDimension' functions implemented in the PCDimension library in the R software (version 4.0.2).

Finally, to explain the variation in haemosporidian lineage composition at the habitat-level, we first performed a variation partitioning analysis using only temperature-related variables as predictors (i.e., mean annual temperature and annual diurnal range). Second, we conducted this same analysis using only precipitation-related variables as predictors (i.e., annual precipitation and precipitation seasonality). Lastly, to evaluate the joint effect of temperature and precipitation variables on haemosporidian lineage composition, we performed a variation partitioning analysis using two predictor matrices (i.e., a first matrix containing all temperature-related variables and a second matrix containing all precipitation-related variables).

Variation partitioning of both component community- and habitat-level ordinated matrices was performed using the 'varpart' function from the 'vegan' library in R software (version 4.0.2). To determine statistical significance of individual and shared fractions of variation we used function 'anova.cca' implemented in the 'vegan' library (Legendre et al., 2011). The 'varpart' function determines if individual or shared fractions can be expressed as a Redundancy Analysis model (RDA). If so, fractions can be testable to determine statistical significance.

5. Results

We captured a total of 609 individuals comprising 90 bird species. Of these, we obtained 607 blood samples for molecular testing. The total molecular prevalence was 20.5% (125 positive samples for avian Haemosporidia) (Table 3). We detected a total richness of 78 avian haemosporidian lineages in 38 species of bird hosts. In total, we recorded 25 lineages of genus *Plasmodium*, 23 lineages of subgenus *Parahaemoproteus*, 6 lineages of subgenus *Haemoproteus* and 24 lineages of genus *Leucocytozoon* (Supporting Information Table 1). Forty-three of the detected haemosporidian lineages were new (i.e., they have not been reported in the GenBank or MalAvi databases).

5.1. Elements of metacommunity structure

At the component community-level (where all cytb lineages detected in one bird host species represented a local community), the haemosporidian parasite metacommunity exhibited a positive coherence, a negative significant turnover and a significant boundary clumping >1,

Table 3

Summary of captured individuals, positive samples, bird host richness and haemosporidian lineage richness per habitat type.

Habitat type	No. of captured individuals	Prevalence (95% CI)	Bird spp. richness	Haemosporidian lineage richness
Coastal medium decidious forest	89	14.6 (8.3–23.5)	23	7
Tropical decidious forest	206	19.4 (14.5–25.5)	41	34
Montane cloud forest	196	14.8 (10.4–20.6)	34	11
Pine-oak forest	118	35.6 (27.4–44.9)	23	33

consistent with a nested distribution with clumped-species loss (Table 4, Fig. 2). At the habitat-level (where all cytb lineages detected in all sampled bird hosts in one habitat type represented a local community), the haemosporidian metacommunity exhibited a positive coherence, a positive non-significant turnover and a significant boundary clumping >1, consistent with a quasi-Clementsian structure (Table 4, Fig. 3).

5.2. Variation partitioning

Variation in the composition of the haemosporidian parasite metacommunity at the community level was weakly explained by host-related traits. Overall, functional predictors (Adj. $R^2 = 0.031$, $p < 0.05$), transmission-associated predictors (Adj. $R^2 = 0.02$, $p < 0.05$) and phylogenetic distance between hosts (Adj. $R^2 = -0.006$, $p = 0.14$) explained 4.4% of the variation in parasite community composition across bird species ($p < 0.05$) (Table 5). At the habitat level, temperature-related variables explained ~28% of the total variation in lineage community composition across sites ($p < 0.05$). Both mean annual temperature (Adj. $R^2 = 0.093$, $p < 0.05$) and annual diurnal range (Adj. $R^2 = 0.115$, $p < 0.05$) showed statistically significant fractions of variation (Table 5). Precipitation-related variables explained 0.4% of the total variation in lineage community composition across sites ($p > 0.05$). Annual precipitation (Adj. $R^2 = -0.148$, $p > 0.05$) and precipitation seasonality (Adj. $R^2 = -0.115$, $p > 0.05$) did not show statistically significant fractions of variation (Table 5).

5.3. Elements of metacommunity structure of infected avian hosts

The infected avian metacommunity exhibited a positive coherence, a positive non-significant turnover and a non-significant boundary clumping <1, consistent with a Quasi-Gleasonian metacommunity structure (Table 6, Fig. 4, Supporting Information Table 2). Eight of the infected avian host species were categorized as altitudinal migrants, 14 were categorized as probable altitudinal migrants and 16 avian host species do not possess any published information on altitudinal migration.

6. Discussion

Environmental factors have been continuously shown as fundamental drivers of distributional patterns for both free-living and parasitic species (Goetz et al., 2014; Fecchio et al., 2019a). We found that climatic variables are more important drivers of haemosporidian parasite metacommunity structure than host-related traits at a local and landscape scales (i.e., 1–200 km). Moreover, we found a high spatial turnover pattern of the infected avian host assemblage, exhibited in a quasi-Gleasonian metacommunity structure across elevations (i.e., an individualistic turnover of infected bird host species in response to a habitat environmental gradient). These findings suggest that, for both haemosporidian parasites and avian hosts, abiotic factors such as thermal constraints can represent important drivers of their compositional patterns across elevation.

At the component community-level, we expected haemosporidian lineages to individualistically infect bird hosts (i.e., exhibiting a Gleasonian metacommunity structure), but instead we observed that bird species infected by few lineages represented a nested subset of those with many lineages (i.e., exhibiting a nested metacommunity structure). For example, haemosporidian lineage SETCOR06 occurred in *Certhia americana* and was nested within the distribution of JUNPHA01, JUNPHA04-09, TROAED02 and SETGRA02 that occurred in *Junco phaeonotus*. Similarly, *Plasmodium* lineages PADOM11 and GEOTRI02 occurred in *Cyanocompsa parellina* and were nested within the distribution of CYCYA02, GRW06 and PASVER01-05 that occurred in *Passerina versicolor*. Nested species distributions are usually described as patterns in which species-poor sites are contained within species-rich sites (Patterson and Atmar 1986), or in which constrained species distributions are contained within the ranges of more widely distributed species (Leibold and Mikkelson 2002). Explaining the processes that produce this loss or restriction of species' distributions between habitats/sites is not straightforward (Presley et al., 2010) but, in free-living taxa (e.g., bats, ants and butterflies), nested distributions have been associated to mechanisms such as dispersal ability and habitat specialization (Presley et al., 2010; Neves et al., 2020). Since avian haemosporidian parasites exhibit a high degree of host switching (Santiago-Alarcon et al., 2014), we did not expect host specificity or specialization to explain the observed nested distribution of these parasites. We suggest that the apparent constrained distribution of some cytb lineages to occur in particular bird species is likely due to the high degree of turnover of avian infected hosts across the studied environmental gradient, and thus to the restriction of occurrence of both host and parasite lineages to the same habitat type and elevation (i.e., environmental filtering).

Host-related traits can be important in determining the composition of their parasite faunas (Poulin and Valtonen 2001; Gupta et al., 2020). However, we found that bird host traits explained only a small fraction of the variation in haemosporidian lineage composition across the nested metacommunity. Altogether, host ecological traits, representing functional and transmission-related traits, and phylogenetic distances among bird hosts explained merely 4.4% of the total variation in lineage composition across bird species. This lack of association between the nested distribution of haemosporidian lineages and host-related traits agrees with a recent biogeographical study where *Leucocytozoon* lineage diversity was not affected by host phylogenetic relatedness nor by host ecological traits (diet, foraging height and sex) but rather by

Table 4

Results of the Elements of Metacommunity Structure analyses for avian haemosporidian lineages.

Level	Coherence				Turnover				Boundary Clumping		
	Absences	p	Mean	z	Replacements	p	Mean	z	Morisital	p	structure
Component community	32	0.00007	258.4	3.90	5783	0.0004	14028.5	3.40	1.77	0.0001	Nested -clumped species loss
Habitat	10	0.0001	90.75	3.78	2285	0.23	1519.5	−1.15	5.2	0.05	Quasi-Clementsian

Analyses were conducted separately for the component-community and habitat levels.

Fig. 2. Nested metacommunity structure of haemosporidian lineages across bird hosts in central Veracruz, Mexico ordinated by reciprocal averaging (Leibold and Mikkelson 2002). Black boxes indicate two examples of lineage-poor bird host species that appear to be nested within the distribution of lineage-rich bird host species. Complete bird host species names are shown in Supporting Information Table 3.
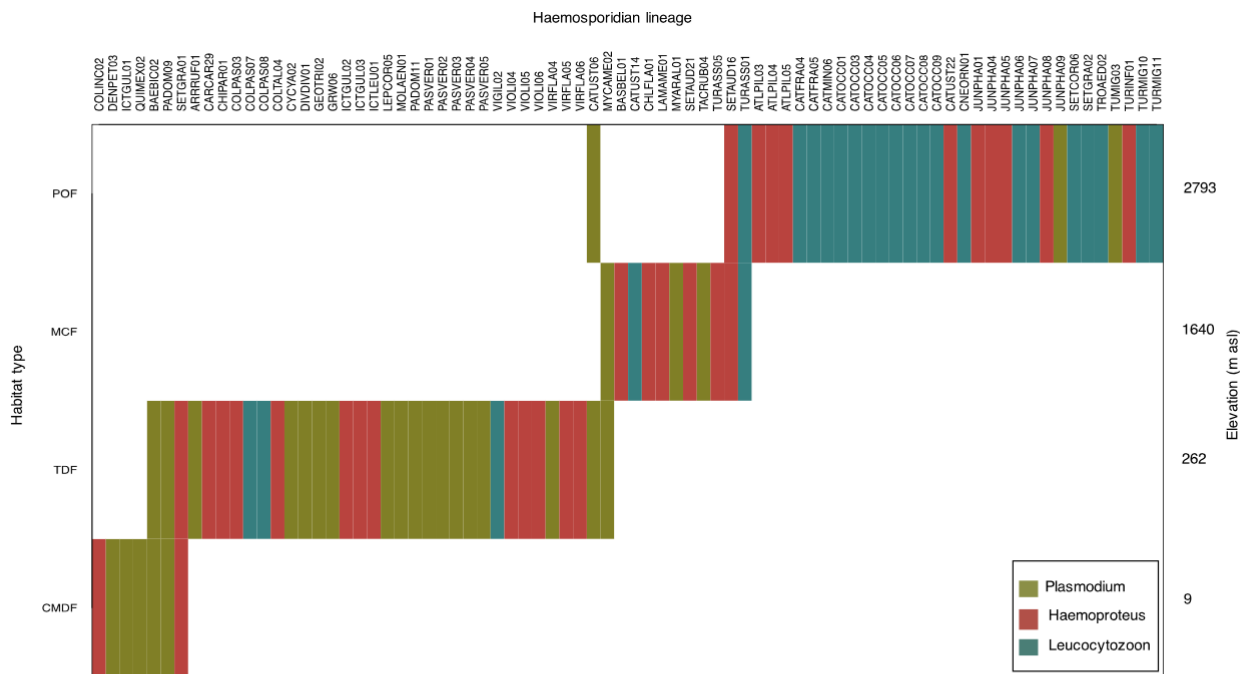

Fig. 3. Quasi-Clementsian metacommunity structure of haemosporidian lineages across habitat types at different elevations in central Veracruz, Mexico ordinated by reciprocal averaging (Leibold and Mikkelson 2002). CMDF = Coastal medium deciduous forest (9 m asl), TDF = Tropical deciduous forest (262 m asl), MCF = Montane cloud forest (1640 m asl), POF = Pine-oak forest (2793 m asl).

Table 5
Variation partitioning analysis based on redundancy analysis to determine the contributions of host-related traits and climatic variables to the variation in haemosporidian lineage communities at the component community and habitat-level, respectively. Statistically significant values of fractions are shown in bold. Negative values of Adjusted $R^2 = 0$ (Borcard et al., 2011).

Level of Assesment	Partition	Df	Adjusted R2	p-value
Component community	Functional [a]	3	0.031	0.001
	Transmission [b]	3	0.002	0.023
	PhyloDist [c]	2	−0.006	0.14
	Functional + Transmission [a+b + d + e + f + g]	6	0.051	0.036
	Functional + PhyloDist [a+c + d + e + f + g]	5	0.042	0.001
	Transmission + PhyloDist [b + c + d + e + f + g]	5	0.013	0.003
	All [a+b + c + d + e + f + g]	8	0.044	0.001
Habitat level	MeanAnnualTemp [a]	1	0.093	0.041
	AnnualDiurnalRange [c]	1	0.115	0.041
	MeanAnnualTemp + AnnualDiurnalRange [a+b + c]	2	0.276	0.041
	AnnualPrecpitation [a]	1	−0.148	0.08
	PrecipitationSeasonality [b]	1	−0.115	0.08
	AnnualPrecipitation + PrecipitationSeasonality [a+b + c]	2	0.004	0.08
	All Temperature [a]	2	0.287	0.04
	All Precipitation [c]	2	0.004	0.16
	All Temperature + All Precipitation [a+b + c]	3	0.291	0.2

temperature and landscape features (Fecchio et al., 2019b). Similarly, for ectoparasitic taxa in rodents, Krasnov et al. (2010) found that environmental variables such as vegetation and climate were more important predictors of parasite community dissimilarity than phylogenetic relatedness of host species. Therefore, as suggested by our findings, host-related traits at a component-community level (i.e., at a host species level; see Bush et al., 1997 for parasitological definitions) may be less important drivers of avian haemosporidian compositional patterns than climate features at the habitat-level.

As we expected, haemosporidian lineage distributions at the habitat-level exhibited a quasi-Clementsian metacommunity structure. This structure suggests that the habitat type represents an environmental filter structuring haemosporidian lineages by genera (i.e., a group turnover by genus is observed across the gradient, in this case elevation). Lower elevation habitats were dominated by *Plasmodium* lineages, whereas higher elevation habitats by *Leucocytozoon* lineages, and *Haemoproteus* lineages were distributed across all habitat types (being more abundant at mid-elevations). These results agree with common observed patterns of avian haemosporidians distributions along elevations (Zamora-Vilchis et al., 2012; van Rooyen et al., 2013; Gonzalez et al., 2014). Also, these results are consistent with a species sorting metacommunity archetype, where differences between local environmental conditions are possibly allowing for niche selection through the elevational gradient (Leibold et al., 2004).

Mean annual temperature and annual diurnal range explained 28% of the variation in haemosporidian lineage community composition through the quasi-Clementsian metacommunity structure. Separately, annual diurnal range explained most of the variation in lineage community composition (11.5%) and mean annual temperature explained a lower percentage of variation (9.3%). Conversely, annual precipitation

and precipitation seasonality did not contribute to explain the variation in lineage community composition through the metacommunity (0.4%, $p > 0.05$). Possibly, the low predictive power of both sets of variables, compared to a higher explanatory power in other avian haemosporidian studies (Clark et al., 2017), relates to their differential effect on species richness and distribution at distinct spatial scales (Rahbek, 2005). Indeed, macroclimatic variables (e.g., broad climatic conditions such as mean annual temperature and precipitation) have been suggested to have an effect on large spatial scales (i.e., continental/regional; Clark et al., 2017), whereas microclimatic variables associated to habitat heterogeneity and structure (e.g., vegetation structure) have been found to have more important effects on smaller spatial scales (i.e., local and landscape scales) (Goetz et al., 2014). Precipitation-associated variables, besides being also considered as broad macroclimatic conditions, might have a greater influence on haemosporidian community prevalence via vector reproduction and abundance, as suggested by REFERENCE?, but not directly on haemosporidian lineage occurrence and community composition (Ferraguti et al., 2018; Fecchio et al., 2019a). Therefore, the macroclimatic variables included at our local and landscape scale (i. e., 1–200 km *sensu* Peterson et al., 2011) of analysis may account for the overall low percentage of explained variation in haemosporidian community composition, then providing an example of how regional macroclimatic processes can sometimes have a minor yet significant effect on local species community patterns.

Despite finding a low percentage of explained variation at the habitat-level, our results imply that temperature has an influence on the metacommunity structure of avian haemosporidians. Temperature has been considered as one of the strongest drivers of avian malaria transmission and distribution (LaPointe et al., 2012). Moreover, diurnal fluctuations in temperature can have a direct effect on vector survival rates and additionally on the incubation period and development of an haemosporidian parasite within them (Beck-Johnson et al., 2017; Ferreira et al., 2020). For example, Paaijmans et al. (2009) demonstrated that both mean monthly temperatures and temperature fluctuations during the diurnal cycle are fundamental variables for explaining malaria epidemics in Africa. They showed how diurnal temperature fluctuations can either slow or speed parasite development within vectors and thus influence malaria transmission rates (Paaijmans et al., 2009). Also, Clark et al. (2017) highlighted the importance of temperature as an environmental barrier that can filter haemosporidian diversity and influence the community composition of avian malaria parasites in Australasia and Oceania. Therefore, the role of temperature as an environmental predictor is clearly important to understand avian haemosporidian communities across spatial scales from local (where parasite transmission occurs, as in this study; see also Santiago-Alarcon et al., 2019) to biogeographic ones (where regional species pools determine community composition; see Clark et al., 2017).

The effect of temperature on haemosporidian lineage composition across the metacommunity can also derive from its effect on vector reproduction rates and distributions. Indeed, the structure of richness, abundance and community composition of vector assemblages can be important for host-vector interactions, and thus, for the probabilities of parasite transmission rates and occurrence across sites (Abella-Medrano et al., 2018). In our studied gradient, cooler running waters in habitats located at higher elevations can provide breeding sites for black flies (Simuliidae) that exclusively transmit *Leucocytozoon* parasites (Santiago-Alarcon et al., 2012). Furthermore, cold temperatures can allow the successful reproduction of *Leucocytozoon* species within vectors

Table 6
Results of the Elements of Metacommunity Structure analyses for the infected avian host assemblage.

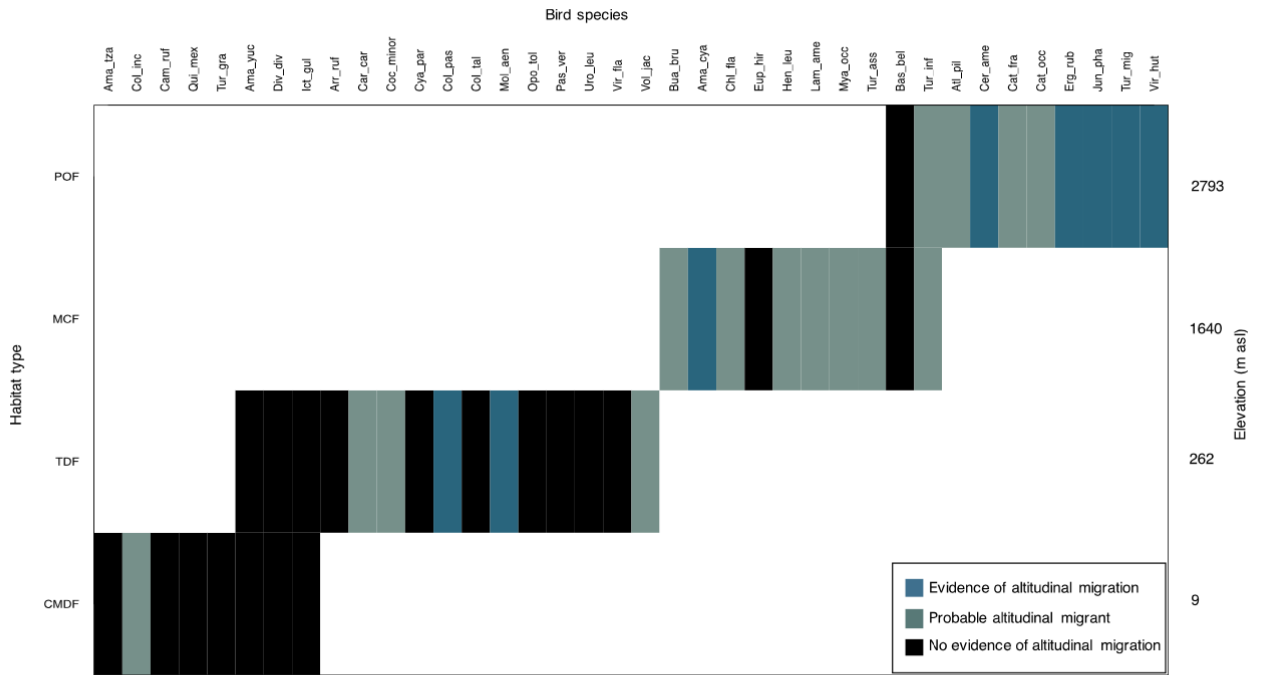| Coherence				Turnover				Boundary Clumping		
Absences	p	Mean	z	Replacements	p	Mean	z	MorisitaI	p	structure
0	0.00001	45.24	5.42	584	0.7	532.87	−0.87	0	0.29	Quasi-Gleasonian

Fig. 4. Quasi-Gleasonian metacommunity structure of infected avian hosts across habitat types at different elevations in central Veracruz, Mexico ordinated by reciprocal averaging (Leibold and Mikkelson 2002). CMDF = Coastal medium deciduous forest (9 m asl), TDF = Tropical deciduous forest (262 m asl), MCF = Montane cloud forest (1640 m asl), POF = Pine-oak forest (2793 m asl). Altitudinal migration status for each bird host species is shown in different colors.

(Valkiūnas 2005) as opposed to *Plasmodium* species which are restricted to warmer temperatures usually associated with lower and intermediate elevations (Reiter and LaPointe, 2009; LaPointe et al., 2010). Moreover, adequate levels of rainfall and relative humidity are necessary for mosquito larval development and survival (LaPointe et al., 2012; Santiago-Alarcon et al., 2012). These abiotic constraints agree with the quasi-Clementsian metacommunity structure of lineages found in the present study. Therefore, mean annual values of temperature and their diurnal fluctuations across habitats might be key factors affecting both vector and parasite reproduction, and consequently determining transmission opportunities and haemosporidian compositional patterns through local host communities (see Fecchio et al., 2019a for the effect of rainfall and seasonality on avian haemosporidian host specificity).

The metacommunity structures found in this study suggest that haemosporidian parasite genera and avian host species are constrained to particular habitat types in response to an environmental gradient (i.e., elevation) associated to climatic conditions. However, we found evidence that more than half of the infected avian hosts (i.e., 22 of 38 avian species) have been registered as either altitudinal migrants or as probable altitudinal migrants (Barçante and Alves 2017; Boyle 2017; Inzunza and Rodríguez, 2010). These results imply that at least one avian species in each habitat type could seasonally perform uphill or downhill movements, and thus could facilitate lineage host switching events and exposure of novel hosts to a wide diversity of haemosporidian parasites. Moreover, under current climate change events, avian hosts and vectors could expand and/or shift their distribution to higher elevations and affect upland avian communities by modifying their structure and increasing their risk of infection (Zamora-Vilchis et al., 2012). Therefore, the dispersion of infected avian hosts across the avian metacommunity could represent a threat to the health and conservation of some native avian species (e.g., the endemic rufous-capped brushfinch, *Atlapetes pileatus*).

A potential limitation of our approach is that both the EMS analysis and the variation partitioning method cannot provide a full account of

the variation of species compositional patterns and their associated ecological processes (Brown et al., 2017; Leibold and Chase 2018). For example, the number of assessed sites and species have been proposed to alter the compositional patterns and assembly processes that are observed in natural systems (Münkemüller et al., 2014). Similarly, metacommunity structure might be driven by different processes at different scales (Dubart et al., 2020). Indeed, species might exhibit a metacommunity structure at local scales that can change at a more regional scale (Leibold and Chase 2018). Also, habitat heterogeneity may affect the way in which an environmental, spatial or in this case a host-related gradient influences metacommunity structure (Garzon-Lopez et al., 2014; Leibold and Chase 2018). Although Leibold and Chase (2018) concluded that the variation partitioning approach can provide some insight into identifying and disentangling some of the factors that might govern the compositional patterns of metacommunity structures, it is apparently only capable of explaining approximately 50% of the variation in metacommunity composition by environmental or spatial gradients, leaving 50% of unexplained residual variation (Cottenie 2005). This could be associated to the fact that this analysis only allows for the inclusion of four explanatory predictor variables, which can lead to biased results by limiting the possibility of including all possible important explanatory variables (Cottenie 2005; Peres-Neto et al., 2006). Because of these limitations, here we have cautiously interpreted the observed EMS analyses and the assessment of the explanatory power of the included predictor variables as suggested by Leibold and Chase (2018); yet, our results are in agreement with the known natural history and biogeography of avian haemosporidians.

7. Conclusion

Taken together, our findings support the hypothesis that environmental conditions, through their direct and indirect effects on parasite and vector ecology, are important factors driving the composition and metacommunity structure of avian haemosporidian parasites. Future

metacommunity studies should incorporate data on vector assemblages to confirm their effects on the spatial compositional patterns of avian haemosporidians. Also, to understand a larger fraction of variation in parasite community composition, studies should incorporate data on other local-scale relevant explanatory environmental variables (e.g., vegetation structure, distance to water reservoirs). We showed that the application of a metacommunity approach to study the EMS and drivers of avian haemosporidians provides insights into the patterns and processes that govern their diversity and distribution at different spatial scales (i.e., component community- and habitat-level), especially in tropical regions where information on the ecology of haemosporidians is limited compared to their temperate counterparts (Santiago-Alarcon and Marzal 2020).

Author contributions

PAM, KRH, CHL and DSA conducted fieldwork. PAM, KRH and CHL performed molecular and sequence analyses. PAM and FV conceived the statistical analyses. DSA and LCV acquired the funds from CONACYT. PAM wrote the first draft of the manuscript, which then received significant contributions from FV, DSA, GSA, ORC, CHL, KRH and LCV. All authors gave final approval for publication.

Data availability

GenBank accession numbers for new haemosporidian lineages are being processed by the National Center for Biotechnology Information.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2021.103789.

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Supplementary Table 1. Haemosporidian cyt b lineage summary per bird host and habitat type.

CMDF = coastal medium deciduous forest (9 m asl), TDF = tropical deciduous forest (262 m asl),

MCF = montane cloud forest (1640 m asl), POF = pine-oak forest (2793 m asl).

* Indicates new genetic lineages detected in this study.

Haemosporidian lineage	Gen Bank accession number	Genus/subgenus or species	Bird host	Habitat type
ARRRUF01*	MZ683438	*Plasmodium*	*Arremonops rufivirgatus*	TDF
ATLPIL03*	MZ683439	*Parahaemoproteus*	*Atlapetes pileatus*	POF
ATLPIL04*	MZ683440	*Parahaemoproteus*	*Atlapetes pileatus*	POF
ATLPIL05*	MZ683441	*Parahaemoproteus*	*Atlapetes pileatus* *Catharus frantzii*	POF
BAEBIC02		*Plasmodium homopolare*	*Arremonops rufivirgatus* *Columbina passerina* *Quiscalus mexicanus*	TDF CMDF
BASBEL01*	MZ683442	*Parahaemoproteus*	*Basileuterus belli*	MCF
CARCAR29*	MZ683443	*Parahaemoproteus*	*Cardinalis cardinalis*	TDF
CATFRA04*	MZ683444	*Leucocytozoon*	*Catharus frantzii*	POF
CATFRA05*	MZ683445	*Leucocytozoon*	*Catharus frantzii*	POF
CATMIN06		*Leucocytozoon*	*Catharus frantzii*	POF
CATOCC01		*Leucocytozoon*	*Catharus frantzii* *Catharus occidentalis*	POF
CATOCC03		*Leucocytozoon*	*Catharus frantzii*	POF
CATOCC04*	MZ683446	*Leucocytozoon*	*Catharus occidentalis*	POF
CATOCC05*	MZ683447	*Leucocytozoon*	*Catharus occidentalis*	POF
CATOCC06*	MZ683448	*Leucocytozoon*	*Catharus occidentalis*	POF
CATOCC07*	MZ683449	*Leucocytozoon*	*Catharus occidentalis*	POF

CATOCC08*	MZ683450	*Leucocytozoon*	*Catharus occidentalis*	POF
CATOCC09*	MZ683451	*Leucocytozoon*	*Catharus occidentalis*	POF
CATUST06		*Plasmodium*	*Catharus frantzii*	POF
CATUST14		*Leucocytozoon*	*Myadestes occidentalis*	MCF
CATUST22		*Parahaemoproteus*	*Catharus occidentalis*	POF
CHIPAR01		*Parahaemoproteus*	*Vireo flavoviridis*	TDF
CHLFLA01		*Parahaemoproteus*	*Arremon brunneinucha* *Chlorospingus* *flavopectus*	MCF
CNEORN01		*Leucocytozoon*	*Atlapetes pileatus* *Basileuterus belli* *Junco phaenotus*	POF
COLINC02*	MZ955363	*Haemoproteus*	*Columbina inca*	CMDF
COLPAS03		*Haemoproteus paramultipigmentatus*	*Cyanocompsa parelllina* *Columbina passerine*	TDF
COLPAS07*	MZ683452	*Leucocytozoon*	*Columbina passerina*	TDF
COLPAS08*	MZ683453	*Leucocytozoon*	*Columbina passerina*	TDF
COLTAL04*	MZ955364	*Haemoproteus*	*Columbina talpacoti*	TDF
CYCYA02		*Plasmodium*	*Passerina versicolor*	TDF
DENPET03		*Plasmodium nucleophilum*	*Dives dives* *Turdus grayi*	CMDF
DIVDIV01*	MZ683454	*Plasmodium*	*Dives dives* *Columbina passerine* *Molothrus aeneus*	TDF
GEOTRI02		*Plasmodium*	*Passerina versicolor* *Cyanocompsa parellina*	TDF
GRW06		*Plasmodium elongatum*	*Passerina versicolor*	TDF
ICTGUL01*	MZ683455	*Plasmodium*	*Icterus gularis*	CMDF
ICTGUL02*	MZ683456	*Parahaemoproteus*	*Icterus gularis*	TDF
ICTGUL03*	MZ683457	*Parahaemoproteus*	*Icterus gularis*	TDF

ICTLEU01		*Parahaemoproteus*	*Icterus gularis*	TDF
JUNPHA01		*Parahaemoproteus*	*Junco phaeonotus*	POF
JUNPHA04*	MZ683458	*Parahaemoproteus*	*Junco phaeonotus*	POF
JUNPHA05*	MZ683459	*Parahaemoproteus*	*Junco phaeonotus*	POF
JUNPHA06*	MZ683474	*Leucocytozoon*	*Junco phaeonotus*	POF
JUNPHA07*	MZ683475	*Leucocytozoon*	*Junco phaeonotus*	POF
JUNPHA08*	MZ683460	*Parahaemoproteus*	*Junco phaeonotus*	POF
JUNPHA09*	MZ683461	*Plasmodium*	*Junco phaeonotus*	POF
LAMAME01*	MZ683462	*Parahaemoproteus*	*Lampornis amethystinus*	MCF
LEPCOR05		*Plasmodium*	*Volatinia jacarina*	TDF
MOLAEN01*	MZ683463	*Plasmodium*	*Molothrus aeneus*	TDF
MYARAL01		*Plasmodium*	*Myadestes occidentalis*	MCF
MYCAME02		*Plasmodium paranucleophilum*	*Coccyzus minor* *Henicorhina leucophrys*	TDF MCF
PADOM09		*Plasmodium*	*Campylorhynchus rufinucha* *Uropsila leucogastra*	CMDF TDF
PADOM11		*Plasmodium*	*Passerina versicolor* *Volatinia jacarina* *Cyanocompsa parellina*	TDF
PASVER01*	MZ955365	*Plasmodium*	*Passerina versicolor*	TDF
PASVER02*	MZ955366	*Plasmodium*	*Passerina versicolor*	TDF
PASVER03*	MZ683464	*Plasmodium*	*Passerina versicolor*	TDF
PASVER04*	MZ683465	*Plasmodium*	*Passerina versicolor*	TDF
PASVER05*	MZ955367	*Plasmodium cathemerium*	*Passerina versicolor*	TDF
QUIMEX02*	MZ683466	*Plasmodium*	*Quiscalus mexicanus*	CMDF
SETAUD16		*Parahaemoproteus*	*Basileuterus belli*	MCF
SETAUD21		*Parahaemoproteus*	*Amazilia cyanocephala* *Basileuterus belli*	MCF

SETCOR06		*Leucocytozoon*	*Certhia Americana* *Junco phaeonotus*	POF
SETGRA01		*Parahaemoproteus*	*Amazilia tzacatl* *Amazilia yucatanensis*	CMDF TDF
SETGRA02		*Leucocytozoon*	*Vireo huttoni*	POF
TACRUB04		*Plasmodium*	*Euphonia hirundinacea*	MCF
TROAED02		*Leucocytozoon*	*Junco phaenotus*	POF
TUMIG03		*Plasmodium unalis*	*Turdus infuscatus*	POF
TURASS01		*Leucocytozoon*	*Turdus infuscatus*	MCF POF
TURASS05*	MZ683467	*Parahaemoproteus*	*Turdus assimilis*	MCF
TURINF01*	MZ683468	*Haemoproteus* *minutus*	*Turdus infuscatus*	POF
TURMIG10*	MZ683469	*Leucocytozoon*	*Turdus migratorius*	POF
TURMIG11*	MZ683470	*Leucocytozoon*	*Turdus migratorius*	POF
VIGIL02		*Leucocytozoon*	*Geothlypis tolmiei*	TDF
VIOLI04		*Parahaemoproteus*	*Vireo flavoviridis*	TDF
VIOLI05		*Haemoproteus* *vireonis*	*Vireo flavoviridis*	TDF
VIOLI06		*Haemoproteus* *vireonis*	*Vireo flavoviridis*	TDF
VIRFLA04*	MZ683471	*Plasmodium*	*Vireo flavoviridis*	TDF
VIRFLA05*	MZ683472	*Parahaemoproteus*	*Vireo flavoviridis*	TDF
VIRFLA06*	MZ683473	*Parahaemoproteus*	*Vireo flavoviridis*	TDF

Supplementary Table 2. Multiple-site partitions of total beta diversity for the infected avian host assemblage, using the Sorensen dissimilarity index across all habitat types (Baselga 2010).

	(beta.multi)	Infected avian hosts
β_{SIM}	turnover component	0.90
β_{SNE}	nestedness component	0.015
β_{SOR}	overall value of beta diversity	0.92

Supplementary Table 3. Names of infected bird host species and abbreviations used in figures

Bird host species name	Abbreviation
Amazilia cyanocephala	Ama cya
Amazilia tzacatl	Ama tza
Amazilia_yucatanensis	Ama yuc
Arremonops_rufivirgatus	Arr ruf
Atlapetes pileatus	Atl pil
Basileuterus_belli	Bas bel
Arremon brunneinucha	Arr bru
Catharus frantzii	Cat fra
Catharus occidentalis	Cat occ
Certhia americana	Cer ame
Chlorospingus flavopectus	Chl fla
Coccyzus minor	Coc min
Columbina passerina	Col pas
Cyanocompsa parellina	Cya par
Dives dives	Div div
Oporornis tolmiei	Opo tol
Henicorhina leucophrys	Hen leu
Icterus gularis	Ict gul
Junco_phaeonotus	Jun pha
Lampornis amethystinus	Lam ame
Myadestes occidentalis	Mya occ
Passerina versicolor	Pas ver
Quiscalus mexicanus	Qui mex
Turdus grayi	Tur gra
Turdus infuscatus	Tur inf
Turdus migratorius	Tur mig
Vireo flavoviridis	Vir fla
Vireo huttoni	Vir hut
Cardinalis cardinalis	Car car
Columbina inca	Col inc
Columbina talpacoti	Col tal
Campylorhynchus rufinucha	Cam ruf
Euphonia hirundinacea	Eup hir
Ergaticus ruber	Erg rub

Molothrus aeneus	Mol aen
Turdus assimilis	Tur ass
Uropsila_leucogastra	Uro leu
Volatinia_jacarina	Vol jac

CAPÍTULO 2.
DRIVERS OF AVIAN HAEMOSPORIDIAN ASSEMBLAGE BETA DIVERSITY ACROSS THE NEARCTIC-NEOTROPICAL TRANSITION

1   Drivers of avian haemosporidian assemblage beta diversity across the Nearctic-Neotropical transition

2

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28   Abstract

29   Understanding the main drivers of parasite beta diversity can provide insights on the processes driving

30   species assembly, and how global environmental changes affect parasite distributional patterns. Studies on

31   avian haemosporidian beta diversity have increased over the last decade, but no general biodiversity

32   patterns have been uncovered since scale- and region-specific drivers seem to govern haemosporidian beta

33   diversity. Here, we assessed the taxonomic and phylogenetic beta diversity of avian haemosporidian

34   assemblages within and between the Nearctic and Neotropical biogeographic regions, and compared

35   whether environmental, spatial, and host taxonomic/phylogenetic dissimilarity gradients could act as

36   drivers of these two components of parasite beta diversity. Within-region key drivers of the taxonomic beta

37   diversity of haemosporidians in the Neotropics included climatic conditions (i.e., mean annual temperature)

38   and geographic distances. In contrast, between-region taxonomic beta diversity of haemosporidians was

39   mainly driven by the taxonomic dissimilarity of avian hosts, and partly by geographic distances between

40   the Nearctic and Neotropical regions. Phylogenetic dissimilarity of avian hosts was the main driver of the

41   phylogenetic beta diversity of haemosporidians, both within and between the Nearctic-Neotropical

42   transition. At both scales of analysis, our results suggest that assemblage-level evolutionary and ecological

43   processes shaped avian haemosporidian diversification and current beta diversity patterns via host

44   biogeographic histories in these two biogeographic regions.

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Introduction

52   Introduction

53   Investigating how ecological, spatial, and evolutionary processes affect the turnover of parasite species

54   composition (i.e., beta diversity) across regions is important to understand their current diversity and

55   distribution patterns, and to assess how these patterns may vary under global environmental changes

56   (Krasnov et al. 2006; Brooks and Hoberg 2007; Scordato and Kardish 2014; Stephens et al. 2016; Fecchio et

57   al. 2021). A major challenge of studying parasite beta diversity is that each host-parasite system (e.g.,

58   vector-borne endoparasites vs. directly transmitted ectoparasites) responds differently to environmental

59   and spatial gradients (Cohen et al. 2020). For example, environmental barriers such as variation in

60   temperature and precipitation can limit parasite species distributions and act as major drivers of turnover

61   of avian haemosporidian parasites (Clark et al. 2017). Also, spatial variation can drive the compositional

62   and functional beta diversity of fleas parasitic on mammals, but not the beta diversity of mite assemblages

63   infecting mammals (Krasnov et al. 2019b), showing that the effect of environment and space in explaining

64   parasites' beta diversity depends on the host-parasite system (Krasnov et al. 2019b). In addition, some

65   studies have shown that many parasite taxa do not follow general biodiversity patterns (i.e., latitudinal

66   diversity gradients, distance-decay of similarity) (Stephens et al. 2016; Clark 2018), whereas others follow

67   them contingent on the region under study (Poulin 2007; Ishtiaq et al. 2010; Cuevas et al. 2020). The

68   relative importance of ecological factors vs historical ones explaining such patterns may also differ

69   depending on the scale of study, with regional scale patterns being better explained by

70   ecological/contemporary processes whereas those at continental scales being better explained by

71   evolutionary/historical ones (Krasnov et al. 2015). As such, uncovering the main drivers of parasite beta

72   diversity for specific host-parasite systems, regions, and scales continues to be central in community

73   infectious disease ecology (Krasnov et al. 2019b).

74   Beyond the differential effect of environmental and spatial gradients, beta diversity of parasite

75   assemblages can be driven by the beta diversity of host species assemblages (i.e., host dissimilarity

76   gradients) (Van Der Mescht et al. 2017; Starkloff et al. 2020; Álvarez-Mendizábal et al. 2021). Host species

77   assemblages represent the habitat and ecological niches that parasites can exploit and occupy, thus

78   parasite richness and composition is closely associated with that of their hosts (e.g., Hechinger and Lafferty

79   2005; Krasnov et al. 2012; Poulin 2014). Hence, taxonomically similar host assemblages are expected to

80   harbour similar parasite assemblages (Krasnov et al. 2005; Poulin 2010), and high rates of host turnover

81   could lead to high rates of parasite turnover (Ellis et al. 2015; Fecchio et al. 2017). In a similar fashion,

82   parasite phylogenetic turnover can be predicted by host phylogenetic turnover (e.g., fleas parasitic on

83   mammals, Krasnov et al. 2012; avian haemosporidians Clark and Clegg 2017; Van Der Mescht et al. 2017),

84   implying that host evolutionary history can be important in determining the presence of parasite species

85   within an assemblage (Williamson et al. 2019). Phylogenetic turnover provides a measure of phylogenetic

86   relatedness between assemblages even when they do not share species (Rosauer et al. 2014), allowing to

87   capture phylogenetic structure and thus evolutionary patterns and processes driving parasite assemblage

88   composition beyond purely taxonomic differences (Krasnov et al. 2012).

89   Avian haemosporidian parasites are a group of vector-borne blood protozoa belonging to the

90   genera *Plasmodium*, *Haemoproteus*, and *Leucocytozoon* (Valkiūnas 2005)*.* Avian haemosporidians are

91   widely distributed across biogeographical regions and only absent from the Antarctic continent (Santiago-

92   Alarcon and Marzal 2020). Their diversity and distribution have been studied across spatial scales revealing

93   contrasting patterns (Barrow et al. 2021). At local and landscape scales (i.e., < 200 km *sensu* Peterson et al.

94   2011 see their fig. 6.2), the distribution of haemosporidians has been mainly explained by ecological and

95   environmental factors such as elevation, temperature variation, and by the potential distribution of their

96   specific vector hosts (Zamora-Vilchis et al. 2012; van Rooyen et al. 2013; Rodríguez-Hernández et al. 2021;

97   Álvarez-Mendizábal et al. 2021). In contrast, at regional scales (200-2,000 km *sensu* Peterson et al. 2011),

98   spatial factors (e.g., geographic distances) have been more important than ecological ones in explaining

99   the beta diversity of avian haemosporidians (Ishtiaq et al. 2010; Olsson-Pons et al. 2015; Fecchio et al.

100   2017). Yet, the decay in species similarity with increasing geographical distance has not been a consistent

101   finding (Scordato and Kardish 2014), and thus, some studies have suggested a greater importance of

102   environmental factors over purely geographical ones in driving haemosporidian assembly (Williamson et

103   al. 2019). Additionally, at regional scales, host turnover has frequently explained haemosporidian turnover

104   at both insular and continental assemblages (Ellis et al. 2015; Clark et al. 2017; Williamson et al. 2019), and

105   one study showed that avian haemosporidian phylogenetic turnover can be mainly explained by host

106   phylogenetic turnover (Clark and Clegg 2017). Avian haemosporidians are thought to have diversified

107   during the radiation of their avian hosts (Pacheco et al. 2018), resulting in strong host-haemosporidian co-

108   phylogenetic associations that are in turn important drivers of haemosporidian phylogenetic turnover

109   (Clark 2018).   Moreover, co-speciation studies have shown that avian haemosporidians possess an

110   evolutionary history of co-divergence at the host-family level (Ricklefs et al. 2004; Santiago-Alarcon et al.

111   2014). Accordingly, the phylogenetic composition of hosts can act as a driver of the phylogenetic

112   composition of avian haemosporidian assemblages. Despite the above-mentioned patterns and drivers of

113   avian haemosporidian richness and composition across spatial scales, no study has jointly assessed the

114   taxonomic and phylogenetic beta diversity of these parasites within and between different biogeographic

115   regions, and evaluated whether environmental, spatial, and/or host taxonomic and phylogenetic

116   dissimilarity gradients can act as drivers of these two different components of parasite beta diversity.

117   Studying the turnover of parasites within and between different biogeographic regions can be

118   interesting for comparing how distinct assemblages of host and parasite species may be driven by distinct

119   ecological, biogeographical, and evolutionary processes (Krasnov et al. 2019a). Biogeographic regions are

120   considered evolutionary arenas and their boundaries have been delimited by different factors such as the

121   turnover of species that occurs between them, climatic heterogeneity, tectonic history, orographic barriers,

122   among others (Vilhena and Antonelli 2015; Ficetola et al. 2017). The boundaries between biogeographic

123   regions sometimes overlap creating complex transition zones where species of different biogeographic

124   origins co-occur (Morrone 2019). This is the case of the Mexican Transition Zone (Morrone 2010), where

125   the Neotropical and Nearctic regions overlap and create a highly diverse hotspot of biological communities

126   (Pinedo-Escatel et al. 2021). Assessing the beta diversity of a highly diverse taxa such as avian

127   haemosporidian parasites within an area of high biotic diversification, such as the transition between the

128   Nearctic and Neotropical regions, can provide insights about the processes driving species assembly across

129   different ecological and evolutionary settings.

130   Here, we aimed to compare the main drivers of taxonomic and phylogenetic beta diversity of avian

131   haemosporidian parasites at two spatial scales: within and between the Neotropical and Nearctic regions.

132   By examining haemosporidian infection data from three surveys performed at different elevations across

133   the Mexican Transition Zone (i.e., the Mexican Plateau, the Sierra Madre Oriental, and the Gulf of Mexico

134   Coastal Plain), we asked whether environmental, geographic, and/or host dissimilarity gradients could

135   explain the taxonomic and phylogenetic beta diversity of avian haemosporidian lineages within and

136   between the two biogeographic regions. Because climatic stratification is higher across the elevation of

137   tropical mountains compared to temperate mountains (Rahbek et al. 2019) and haemosporidian

138   distributions are strongly driven and constrained by temperature variation (LaPointe et al. 2010), we

139   expected to observe a stronger effect (i.e., a steeper slope) of mean annual temperature, annual

140   precipitation, and/or annual diurnal range in temperature on the taxonomic beta diversity of

141   haemosporidian lineages within the Neotropical region compared to the Nearctic region (Fig. 1A). Also,

142   because an important latitudinal gradient exists for temperature and precipitation, we expected to observe

143   a positive relationship between these climatic variables and the beta diversity of haemosporidian lineages

144   between the two biogeographic regions (at the Neotropical-Nearctic transition) (Fig. 1A). Second, because

145   spatial variables have been able to explain the beta diversity of haemosporidian parasites in some regions,

146   we expected that geographic distances would generate a steeper slope on the taxonomic beta diversity of

147   haemosporidian lineages at the Neotropical-Nearctic transition compared to what could be observed

148   within each biogeographic region (Fig 1B). Third, because high values of turnover exist between the

149   Neotropical and Nearctic avian biotas, we expected to observe a strong effect of host taxonomic turnover

150   on the taxonomic turnover of haemosporidian lineages between biogeographic regions (Fig 1C).

151   Furthermore, because avian turnover is also high within each sampled region due to habitat variation, we

152   expected to find a significant effect of host taxonomic turnover on the taxonomic turnover of

153   haemosporidian lineages within each region – albeit minor than that of the environmental effect (Fig.1C vs

154   1A). Lastly, because haemosporidians have a strong history of co-divergence with avian host families, and

155   avian host species of different origins inhabit each biogeographic region, we predicted that the

156   phylogenetic turnover of avian hosts – within and between biogeographic regions – would correlate

157   positively with the phylogenetic beta diversity of haemosporidian lineages (Fig. 1D).

158
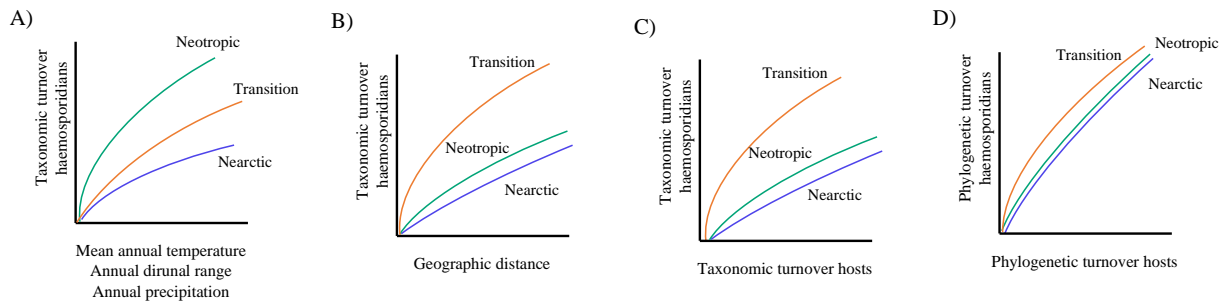
159
160   Figure 1. Predictions on the effect of environmental, geographic and host taxonomic and phylogenetic dissimilarity
161   gradients on the taxonomic and phylogenetic turnover of avian haemosporidian lineages within and between
162   biogeographic regions. A) A steeper slope and positive relationship between temperature/precipitation-related
163   variables and the taxonomic turnover of haemosporidian lineages was expected for the Neotropical region compared
164   to the Nearctic region due to abrupt changes in elevation. Also, a positive relationship between these climatic
165   gradients and the taxonomic turnover of haemosporidian lineages was expected for the Neotropical-Nearctic
166   transition. B) A positive and steeper slope between geographic distance and the taxonomic turnover of
167   haemosporidian lineages was expected for the Neotropical-Nearctic transition compared to the effect of geography
168   on the taxonomic turnover of haemosporidians within each biogeographic region. C) A positive relationship with a
169   shallower slope compared to environmental variables was expected between the taxonomic turnover of avian hosts
170   and the taxonomic turnover of haemosporidian lineages for both biogeographic regions; however, a steeper and
171   positive slope between the taxonomic turnover of avian hosts and the taxonomic turnover of haemosporidian lineages

172   was expected for the Neotropical-Nearctic transition. D) The phylogenetic turnover of avian hosts – within and

173   between biogeographic regions – was expected to correlate positively with the phylogenetic beta diversity

174   of haemosporidian lineages.

175

176   **Methods**

177   **Study areas**

178   We obtained data on a total of 708 avian haemosporidian infections out of 1379 surveyed birds from a

179   total of 20 sites located at the Mexican Plateau, the Sierra Madre Oriental, and the Gulf of Mexico Coastal

180   Plain (Hernández-Lara et al. 2017; Hernández-Lara et al. 2020; Rodríguez-Hernández et al. 2021; Álvarez-

181   Mendizábal et al. 2021) (Ortega-Guzmán et al. unpublished). Of these, 9 sites were located in the state of

182   Veracruz (i.e., Neotropical region and Transition Zone) and 11 sites were located in the state of San Luis

183   Potosí (i.e., Nearctic region and Transition Zone) (Fig. 2).

184   The Neotropical region included the following habitats: coastal medium deciduous forest 9 m asl,

185   tropical deciduous forest 262 m asl, montane cloud forest 1640 m asl, urban forest with fragments of cloud

186   forest and secondary vegetation 1427-1467 m asl, peri-urban forest with second growth vegetation and

187   abandoned coffee plantations 1344-1372 m asl, shade coffee plantation with cloud forest vegetation 1210-

188   1313 m asl, cattle field surrounded by a matrix of cloud forest vegetation1460-1525 m asl, and pine-oak

189   forest 2743 m asl. The Nearctic region included the following habitats: medium deciduous forest 500 m asl,

190   mesquite vegetation 1005-1015 m asl, cattle field with secondary vegetation 2122 m asl, rosetophile

191   shrubland 2140 m asl, izotal shrubland 2152 m asl, mesquite dominated by *Pinus cembroides* 2191 m asl,

192   macrophile shrubland 2241 m asl, pine-oak forest 2250 m asl, and pine forest 2300 m asl.

193
194 Figure 2. Location of the 20 surveyed sites across the Mexican Neotropical/Nearctic regions and transition zone. See

195 Appendix A-Table A1 of supplementary material for geographic coordinates of each sampled site.

196

197

Beta diversity decomposition of haemosporidian lineages and bird host assemblages

199   Before assessing the taxonomic and phylogenetic beta diversity of haemosporidian lineages, we

200 conducted an exploratory analysis of beta and phylo-beta diversity decomposition of haemosporidian

201 lineages and infected bird assemblages within and between our two studied biogeographic regions (i.e.,

202 Neotropic and Nearctic) (Baselga 2010). These analyses were meant to evaluate if haemosporidian lineages

54

203 and bird host assemblage dissimilarity could be interpreted as species replacement between sites (i.e.,

204 turnover component) or as loss of species richness between sites (i.e., nestedness component). Since

205 haemosporidian and bird beta and phylo-beta diversity were mainly interpreted as species replacement

206 between sites (turnover component = $B_{SIM} > 0.5$) (Appendix A Table A2 and A3 of Supplementary Material),

207 we selected the turnover component of both parasites and hosts to perform our statistical analyses (i.e.,

208 general dissimilarity modelling GDM).

209 **Taxonomic and phylogenetic turnover of avian haemosporidian lineages**

210 Taxonomic turnover of haemosporidian lineages between sites for each biogeographic region was

211 estimated using a Bray-Curtis dissimilarity index applied to binary data (Ferrier et al. 2007). This index

212 provided a dissimilarity matrix of values ranging from 0 (when two sites shared all parasite lineages) to 1

213 (when there was no overlap of parasite lineages between pairs of sites) and was computed using the vegdist

214 function of R package 'vegan' (R software version 4.0.2) (Oksanen 2016). Similarly, phylogenetic turnover

215 of haemosporidian lineages between sites for each biogeographic region was estimated using a Sorensen's

216 index of phylogenetic dissimilarity (PhyloSor index) (Ferrier et al. 2007; Bryant et al. 2008). The PhyloSor

217 index represents the fraction of haemosporidian lineage branch lengths shared between pairs of sites and

218 was calculated with the phylosor function of the R package 'picante' (Kembel et al. 2010). Here, the

219 PhyloSor index ranged from values of 0 (when only a small root of the phylogenetic tree was shared

220 between pairs of sites) to 1 (when there were no shared branches between pairs of sites) (Bryant et al

221 2008). To quantify phylogenetic dissimilarity of haemosporidian lineages, we used Bayesian phylogenies

222 built in Mr. Bayes for the set of lineages within each biogeographic region that were then combined to

223 produce a single phylogenetic hypothesis for the whole set of species present in both regions (Appendix A

224 of supplementary material, Figure A1). Partial mtDNA cytochrome *b* gene sequences of approximately 1038

225 bp belonging to 130 Haemosporida lineages were aligned with MUSCLE (Edgar, 2004) in Mesquite 3.61

226 (Maddison and Maddison, 2018). Bayesian inference was used to obtain majority rule consensus trees in

227   MrBayes 3.2.7 (Ronquist et al., 2012) at the CIPRES Science Gateway (Miller et al., 2010) with two runs of

228   four chains each, a 25% burn-in, 10 million generations, saving 10,000 trees, and using *Leucocytozoon* as

229   outgroup. The analyses were performed using a general time reversible model with gamma distribution

230   and a proportion of invariable sites (GTR + G + I) as obtained from jModelTest 2 (Darriba et al., 2012). The

231   taxonomic and phylogenetic turnover of haemosporidian lineages between, rather than within,

232   biogeographic regions (Neotropical-Nearctic transition) was assessed by using the same dissimilarity

233   indexes as mentioned above.

234   **Host, environmental, and geographic predictors**

235   We used three sets of predictor variables to determine the main drivers of taxonomic and

236   phylogenetic turnover of avian haemosporidian lineages within and between biogeographic regions. The

237   first set included the taxonomic and phylogenetic turnover of avian host assemblages. These were

238   estimated using the same dissimilarity indexes as described above for avian haemosporidian lineages. The

239   PhyloSor index for host phylogenetic turnover was calculated using a majority rule consensus tree of avian

240   hosts generated from 10,000 trees as provided by BirdTree.org (Jetz et al. 2012; 2014) (Appendix A of

241   supplementary material, Figure A2). The second set comprised bioclimatic variables extracted from

242   WorldClim (www.worldclim.org) (Fick and Hijmans 2017), which represented environmental gradients

243   within and between biogeographic regions. These included mean annual temperature, annual

244   precipitation, and annual diurnal range in temperature which have been shown to be fundamental

245   predictors of the diversity and assembly of avian haemosporidian communities (Clark et al. 2017; Álvarez-

246   Mendizábal et al. 2021). The third set comprised geographical coordinates for all studied sites. These were

247   used to calculate geographic distances for model fitting within and between sites of both biogeographic

248   regions.

249   **Statistical analyses**

250   We modelled the taxonomic and phylogenetic turnover of parasite assemblages in relation to

251   environmental, spatial, and host-related gradients using the generalized dissimilarity modelling (GDM)

252   approach (Ferrier et al. 2007). This approach allowed us to model a response matrix (e.g., pairwise

253   taxonomic or phylogenetic dissimilarities of parasite assemblages between sites and regions) as a function

254   of several distance matrices (e.g., climate gradients, geographical separation of sites, pairwise taxonomic

255   or phylogenetic dissimilarities of host assemblages between sites and regions) (Ferrier et al. 2007; Van Der

256   Mescht et al. 2017). Also, GDM allows to model a curvilinear relationship between the observed species

257   turnover and the evaluated gradients (Ferrier et al. 2007), which has proven useful to uncover patterns of

258   species turnover (e.g., beta diversity of floras and ectoparasites) (Fitzpatrick et al. 2013; Van Der Mescht et

259   al. 2017) that would not have been revealed by linear regression approaches. We fitted two GDM models

260   to each biogeographic region: the first contained the taxonomic turnover of haemosporidian lineages as a

261   response variable with the taxonomic turnover of host assemblages, climatic gradients, and geographic

262   distances as predictor variables; the second contained the phylogenetic turnover of haemosporidian

263   lineages as response variable with the phylogenetic turnover of host assemblages, climatic gradients, and

264   geographic distances as predictor variables. We also fitted two GDM models (one taxonomic and one

265   phylogenetic) to assess the turnover of avian haemosporidian lineages between biogeographic regions.

266   These contained the same response and predictor variables as explained above for the within-region scale

267   of analysis.

268   Models were fitted using the 'gdm' package in R (version 4.0.2). Three default I-splines were

269   calculated for each predictor variable within each model. I-spline heights provided information on the

270   amount of taxonomic or phylogenetic turnover associated to a given predictor variable while holding all

271   other predictors constant (Ferrier et al. 2007). Because I-splines are partial regression fits, they also provide

272   information on the importance of each predictor variable in explaining patterns of turnover (Ferrier et al.

273   2007). The shape of the slopes fitted by GDMs provided information on the rate and variation of

274 haemosporidian lineages turnover along each gradient. Model significance was quantified through matrix

275 permutation (number of permutations was 100) using the 'gdm.varImp' function of package gdm. To depict

276 the fitted models and I-splines, we used the 'plot' function that plotted all I-spline coefficients that were >

277 0.

278 **Results**

279 Haemosporidian mtDNA cytochrome b lineage recovery was 67% (haemosporidian lineages were

280 determined in 474 samples out of 708 positive samples). Haemosporidian lineage richness was 98 for the

281 Neotropical region (42 lineages belonged to *Plasmodium* genus, 31 to *Haemoproteus*, 25 to *Leucocytozoon*)

282 and 45 for the Nearctic region (25 lineages belonged to *Haemoproteus*, 19 to *Plasmodium*, 1 to

283 *Leucocytozoon*). Of these, 43 lineages were new for the Neotropical region, and 18 lineages were new for

284 the Nearctic region (i.e., they have not been reported in the Malavi data base or in Genbank).

285 Taxonomic and phylogenetic GDMs of the Neotropical region explained 56% and 45% of the

286 variance in haemosporidian turnover, respectively (p<0.01; Table 1). In this region, mean annual

287 temperature and geographic distance were the most important predictor variables of haemosporidian

288 lineage taxonomic turnover (Table 1; Fig. 3), whereas phylogenetic turnover of host communities was the

289 only significant predictor variable explaining phylogenetic turnover of haemosporidian lineages (Table 1;

290 Fig. 4A). The taxonomic GDM of the Nearctic region explained only 6% of the variance in haemosporidian

291 turnover (p=0.4; Table 1). In this region, the taxonomic turnover of host assemblages exhibited a positive

292 yet not significant relationship with the taxonomic turnover of lineages (Fig. 5); none of the other predictor

293 variables were able to significantly explain the taxonomic turnover of haemosporidian lineages. In contrast,

294 the phylogenetic GDM of the Nearctic region was able to explain 44% of variance (p<0.001). Here, the

295 phylogenetic turnover of avian host assemblages was the only significant predictor variable able to explain

296 the phylogenetic turnover of haemosporidian lineages (Table 1; Fig. 4B).
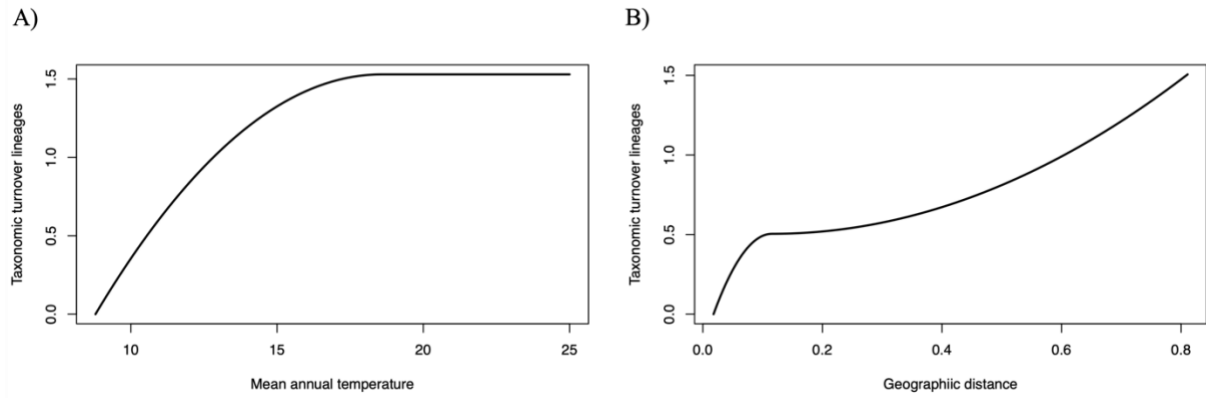
297

298   Figure 3. Generalized dissimilarity model of the Neotropical region for statistically significant predictor variables

299   associated with taxonomic turnover of avian haemosporidian lineages.

300
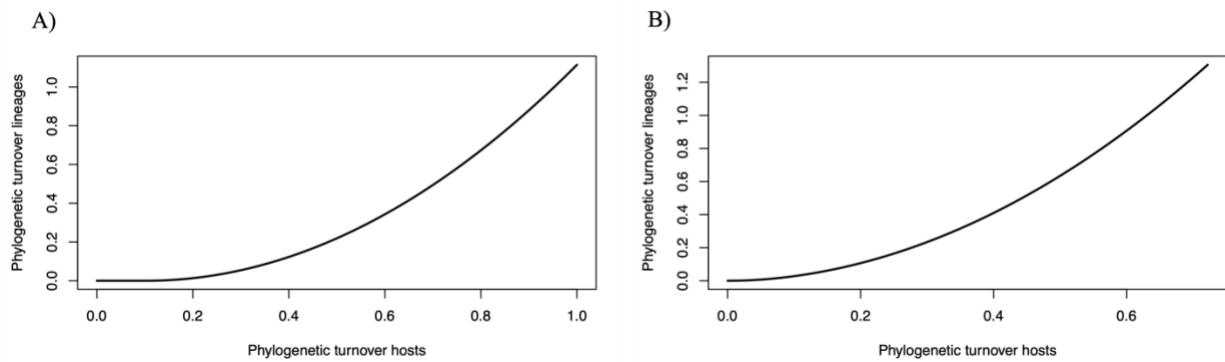
301

302   Figure 4. Generalized dissimilarity model-fitted I-splines of the phylogenetic turnover of avian host assemblages as a

303   predictor of phylogenetic turnover of haemosporidian lineages for A) Neotropical region, and B) Nearctic region.

304

305

306

307
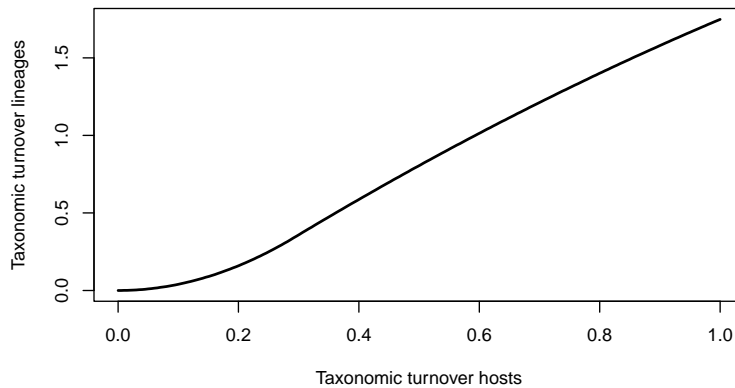
Figure 5. Generalized dissimilarity model-fitted I-spline of the Nearctic region for the positive but not significant relationship between the taxonomic turnover of avian host communities and the taxonomic turnover of haemosporidian lineages.

The plotted I-spline coefficients (Table 1) of GDM models within biogeographic regions showed different relationships between the taxonomic and phylogenetic turnover of avian haemosporidian lineages and predictor variables. Along the temperature gradient in the Neotropics, the rate of taxonomic lineage turnover increased sharply with increasing temperatures until it reached an asymptote at approximately 17-18°C, where it remained constant (Fig. 3A). The rate of taxonomic lineage turnover across geographic distance in the Neotropics also increased sharply at short distances, and then continued to increase gradually and non-linearly as geographic distance increased between sites (Fig. 3B). The rate of phylogenetic lineage turnover at both Neotropic and Nearctic regions increased gradually and non-linearly as the phylogenetic turnover of avian host communities increased (Fig. 4A, 4B), being stronger in the Nearctic region (sum of I-spline coefficients= 1.32) (Table 1).

Table 1. I-spline coefficients of GDM models of the relationship between taxonomic and phylogenetic turnover of haemosporidian lineages and hosts, environmental, and geographic predictors within Neotropical and Nearctic regions. The sum of coefficients shows the partial regression fits for each predictor variable indicating its relative importance in explaining turnover. Most important and statistically significant predictors are shown in bold. Geo

328　distance = geographic distance, mean annual temp= mean annual temperature, Ann diu range= annual diurnal range,

329　Tax turnover hosts= taxonomic turnover of avian hosts, Phylo turnover hosts= phylogenetic turnover of avian hosts.

			I-splines			
Region	Response	Predictor	1	2	3	sum
Neotropic	Taxonomic turnover lineages	Geo Distance	0.5	0	1	**1.5**
		Mean annual temp	1.53	0	0	**1.53**
		Ann Diu Range	0	0	0	0
		Precipitation	0	0	0	0
		Tax turnover hosts	0	0	0	0
	Phylogenetic turnover lineages	Geo Distance	0	0	0	0
		Mean annual temp	0	0	0.041	0.041
		Ann Diu Range	0	0	0	0
		Precipitation	0	0	0	0
		Phylo turnover hosts	0	0	1.12	**1.12**
Nearctic	Taxonomic turnover lineages	Geo Distance	0	0.043	0	0.043
		Mean annual temp	0	0	0.082	0.082
		Ann Diu Range	0	0	0	0
		Precipitation	0	0	0	0
		Tax turnover hosts	0	1.17	0.58	1.75
	Phylogenetic turnover lineages	Geo Distance	0	0	0	0
		Mean annual temp	0.021	0	0	0.021
		Ann Diu Range	0.1	0.52	0	0.62
		Precipitation	0.1	0	0	0.1
		Phylo turnover hosts	0	0.18	1.14	**1.32**

330

331   The taxonomic GDM between the Neotropical-Nearctic transition explained 20.22% of the variance

332   in haemosporidian turnover (p<0.01; Table 2). Here, geographic distance and taxonomic turnover of avian

333   hosts were the only significant predictor variables related to the taxonomic turnover of avian

334   haemosporidian lineages (Table 2, Fig. 6). Mean annual temperature and annual precipitation presented

335   positive but statistically not significant associations with the taxonomic turnover of haemosporidian

336   lineages (Table 2). The phylogenetic GDM between regions explained 17% of the variance in

337   haemosporidian phylogenetic turnover (p<0.01). Phylogenetic turnover of avian hosts was the only

338   significant predictor variable explaining the phylogenetic turnover of haemosporidian lineages (Table 2, Fig.

339   7). Mean annual temperature and annual diurnal range in temperature exhibited positive but non-

340   significant associations with the phylogenetic turnover of haemosporidian lineages (Table 2).

341
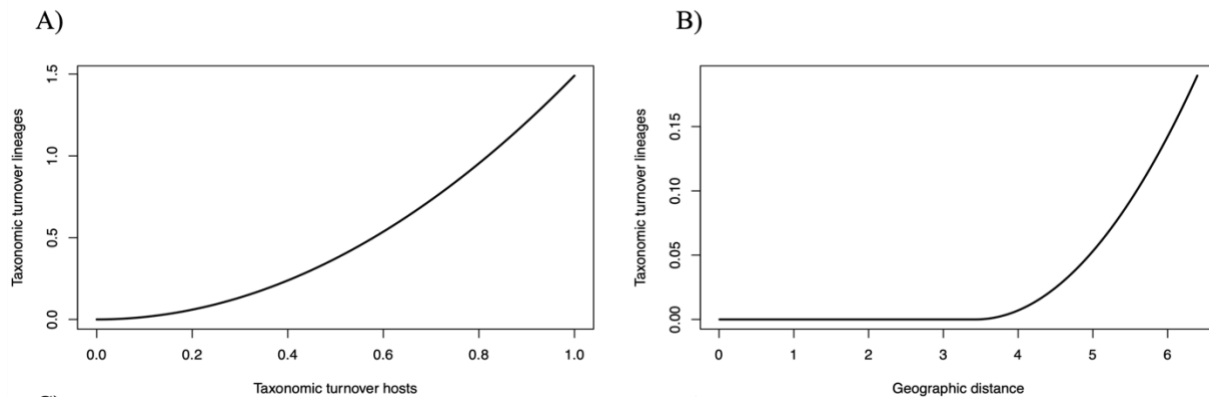
342
343   Figure 6. Taxonomic generalized dissimilarity model between Neotropical and Nearctic regions for statistically

344   significant predictor variables associated with taxonomic turnover of avian haemosporidian lineages.

345
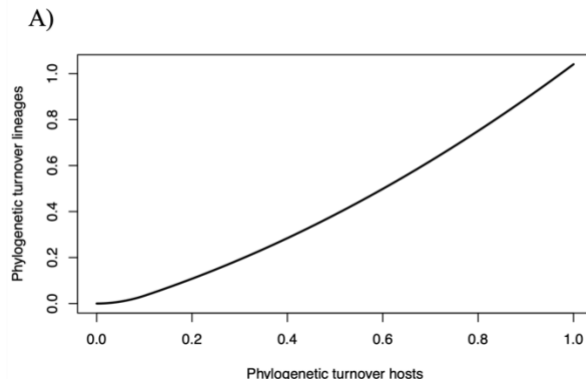
346

347　Figure 7. Generalized dissimilarity model-fitted I-splines of the phylogenetic turnover of avian host assemblages as a

348　significant predictor of the phylogenetic turnover of avian haemosporidian lineages between Neotropical and Nearctic

349　regions

350

351　The taxonomic GDM model between biogeographic regions showed that the rate of haemosporidian

352　lineage turnover increased gradually and non-linearly as the taxonomic turnover of avian hosts increased

353　(Fig. 6A). Also, the rate of haemosporidian lineage taxonomic turnover across geographic distance did not

354　increase at short distances, but then increased sharply at larger distances (Fig. 6B). The rate of phylogenetic

355　lineage turnover between the Nearctic-Neotropic transition increased gradually and almost linearly as the

356　phylogenetic turnover of avian hosts increased (Fig. 7).

357

358　Table 2. I-spline coefficients of GDM models of the relationship between taxonomic and phylogenetic turnover of

359　haemosporidian lineages and hosts, environmental, and geographic predictors between Neotropical and Nearctic

360　regions. The sum of coefficients shows the partial regression fits for each predictor variable indicating its relative

361　importance in explaining turnover. Most important and statistically significant predictors are shown in bold. Geo

362　distance = geographic distance, mean annual temp= mean annual temperature, Ann diu range= annual diurnal range,

363　Tax turnover hosts= taxonomic turnover of avian hosts, Phylo turnover hosts= phylogenetic turnover of avian hosts.

			I-splines			
Region	Response	Predictor	1	2	3	sum
Neotropic-Nearctic	Taxonomic turnover lineages	Geo Distance	0	0	0.19	**0.19**
		Mean annual temp	1.08	0	0.10	1.18

	Ann Diu Range	0	0	0	0
	Precipitation	0	0	0.62	0.62
	Tax turnover hosts	0	0	1.50	**1.50**
Phylogenetic turnover lineages	Geo Distance	0	0	0	0
	Mean annual temp	0.15	0	0	0.15
	Ann Diu Range	0.005	0	0.19	0.195
	Precipitation	0	0	0	0
	Phylo turnover hosts	0	0.34	0.69	**1.03**

364

Discussion

366   Ecological and environmental factors are fundamental drivers of the diversity and distribution of

367 vector-borne parasites (Cable et al. 2017). As revealed by our findings, environmental factors represent

368 major drivers of avian haemosporidian turnover in tropical regions (see also Williamson et al. 2019).

369 Likewise, we found that spatial factors (i.e., geographic distances between sites) were the second most

370 important predictors explaining the taxonomic turnover of haemosporidian lineages in the Mexican

371 Neotropics. Moreover, a strong association between host and parasite phylogenetic turnover was observed

372 for both assemblages within Neotropical and Nearctic regions, and between the Nearctic-Neotropical

373 transition. These results imply that ecological, spatial, and evolutionary drivers contribute – and likely

374 interact – to the turnover of haemosporidian parasites. However, the importance of these drivers can vary

375 for the taxonomic and phylogenetic components of beta diversity, both within and between biogeographic

376 regions (Neotropical and Nearctic in this study).

377   The strong effect of climatic gradients, specifically mean annual temperature, on the taxonomic

378 turnover of haemosporidian parasites was observed in the Neotropical region but was absent in the

379 Nearctic region. This might be explained by the marked temperature variation observed across the

380 Neotropical study sites compared to the Nearctic sites, which is mainly related to the wider elevational

381   span covered by the sites in the Neotropical region. A greater climatic stratification across elevation in

382   tropical regions relative to temperate regions can act as an environmental barrier, driving niche

383   specialization of species with smaller thermal tolerances (e.g., *Plasmodium* and *Leucocytozoon* lineages;

384   Rodríguez-Hernández et al. 2021) and promoting greater beta diversity along tropical mountains (Janzen

385   1976; Rahbek et al. 2019). Particularly, *Plasmodium* and *Leucocytozoon* genera possess strict thermal

386   requirements for sporogonic development (*Plasmodium*: 21-28 C for optimal growth rate, *Leucocytozoon*:

387   15 C for optimal growth rate) (LaPointe et al. 2010; Fecchio et al. 2018). Therefore, it is not surprising that

388   greater temperature variation across our Neotropical sites acted as a climatic barrier for haemosporidian

389   parasites and explains their taxonomic turnover in this biogeographic region. Moreover, these results agree

390   with one of our previous studies (Álvarez-Mendizábal et al. 2021) where mean annual temperature and

391   annual diurnal range in temperature were identified as important drivers of avian haemosporidian

392   compositional turnover across elevations. The lack of a significant effect of temperature and precipitation

393   gradients on the taxonomic turnover of haemosporidians between the Neotropical and Nearctic regions

394   suggests that regional avian haemosporidian turnover is less constrained by environmental characteristics

395   and it is rather driven by the composition and regional turnover of avian host assemblages (e.g., Williamson

396   et al. 2019).

397   Geographic distance between sites was a less important, yet significant predictor of the taxonomic

398   turnover of haemosporidian lineages in the Neotropical region. The decay in species similarity with

399   increasing geographical distance is a well-documented macroecological pattern in free-living species

400   (Nekola and White 1999). However, given that parasite species distributions do not respond solely to spatial

401   factors but also to host and sometimes vector compositions, the decay in species similarity with increasing

402   distance can be weak or absent in parasite faunas (Poulin et al. 2010; Stephens et al. 2016). For avian

403   haemosporidian parasites, Ishtiaq et al. (2010) observed a decay in haemosporidian lineage similarity with

404   increasing geographic distance for *Plasmodium* genus but not for *Haemoproteus* genus between

405 Melanesian islands (Ishtiaq et al. 2010). Similarly, Olsson-Pons et al. (2015) found that *Plasmodium*

406 biogeographic patterns within the same islands studied by Ishtiaq et al. (2010) were mainly driven by

407 geography, whereas *Haemoproteus* biogeographic patterns were driven by avian host species distributions.

408 Moreover, Svensson-Coelho and Ricklefs (2011) failed to observe an overall effect of geographical distance

409 on the beta diversity of haemosporidian assemblages on three avian host species across the Lesser Antilles;

410 they were only able to observe variation in parasite similarity with geographical distance within one avian

411 host (Svensson-Coelho and Ricklefs 2011). Here, we observed an effect of geographic distance on

412 haemosporidian taxonomic composition between the Neotropical and the Nearctic regions, which was also

413 observed for haemosporidian lineages within the Neotropical region. Therefore, a combination of

414 geographical distance decay and environmental dissimilarity between habitat types can be associated to

415 the observed effect on the taxonomic turnover of haemosporidians at both the Neotropical region and the

416 Neotropical-Nearctic transition zone. In turn, the lack of an effect of geography on the Nearctic region is

417 possibly associated to the lower topographic complexity of the Mexican plateau. Topographic complexity

418 derived from tectonic activity has been suggested to promote environmental heterogeneity, intensify

419 climatic gradients, and speciation for some organisms (e.g., birds and mammals) (Qian and Ricklefs 2008;

420 Badgley 2010). In contrast, tectonically inactive areas such as great plains and plateaus present low climatic

421 and environmental heterogeneity between habitats and less probability of speciation events (Badgley

422 2010). In this sense, we suggest that the topography of our Neotropical study sites, by promoting avian

423 species turnover and climatic heterogeneity, promotes a larger effect of geographical distance on

424 haemosporidian lineage turnover, which was not observed across the less heterogeneous Nearctic study

425 sites within the Mexican plateau.

426 Contrary to our expectations, the taxonomic turnover of haemosporidian lineages was not

427 significantly associated to the taxonomic turnover of host assemblages within biogeographic regions.

428 However, a significant association between parasite and host taxonomic turnover was observed between

429 the Neotropical-Nearctic transition. Despite several studies that have identified a positive association

430 between host and haemosporidian turnover (Ellis et al 2015; Clark et al. 2017; Williamson et al. 2019),

431 others have found that haemosporidian lineage turnover does not necessarily depend on host assemblage

432 turnover. For example, Soares, Latta and Ricklefs (2017) found that dissimilarity of haemosporidian parasite

433 assemblages within the Lesser Antilles occurred even when infecting similar and widely distributed avian

434 host assemblages that did not differ in composition between islands (Soares, Latta, and Ricklefs 2017). In

435 our study, a high dissimilarity of avian host species assemblages occurs within and between the Neotropical

436 and Nearctic study sites (see beta diversity analyses for avian hosts in Appendix A Table A4 of

437 Supplementary Material); yet, the differences in the taxonomic species pool within each biogeographic

438 region was not large enough to observe a significant effect of the taxonomic turnover of hosts on the

439 taxonomic turnover of parasites. In contrast, the taxonomic association between haemosporidians and bird

440 hosts was stronger at the Neotropical-Nearctic transition zone, where the size of the taxonomic species

441 pool increased, and region-specific and endemic avian taxa occur (e.g., Emberizidae). Thus, at the within-

442 region scale of analysis, host-parasite taxonomic associations might not be as strong as the evolutionary

443 associations these parasites show with their hosts at the family-level (Ricklefs and Fallon 2002; Santiago-

444 Alarcon et al. 2014).

445 Phylogenetic GDMs revealed an important association between parasite and host phylogenetic

446 turnover for both the Neotropical and the Nearctic regions, and for the Neotropical-Nearctic transition

447 zone. Therefore, we suggest that host-parasite co-divergence between avian hosts and haemosporidians is

448 a fundamental driver of avian haemosporidian beta diversity. This tight association between the

449 phylogenetic turnover of birds and their haemosporidians happens despite the large amount of host

450 switching occurring at shallow phylogenetic levels (Ricklefs et al. 2004; Santiago-Alarcon et al. 2014). By

451 using parasite and avian host mitochondrial genomes, some studies have estimated that the origin and

452 evolution of avian haemosporidian parasites occurred in parallel to the origin and evolution of modern

453   birds (i.e., after the Cretaceous-Paleogene boundary) (Pacheco et al. 2011; Pacheco et al. 2018). However,

454   haemosporidian-avian phylogenies are not congruent below the host family level (Pacheco and Escalante

455   2020), and parasite-host co-speciation is not presumed to entirely explain avian haemosporidian

456   diversification (Pacheco et al. 2018). Evolutionary studies have suggested that the diversification of avian

457   haemosporidians is also associated to assemblage-level evolutionary and ecological processes that shaped

458   host and vector demographic and biogeographic histories (Pacheco et al. 2018). Indeed, studies on other

459   parasite systems (e.g., arthropod ectoparasites, non-human primate malarias) have proposed that parasite

460   assemblage composition can be related to the historical biogeography of host species assemblages

461   (Muehlenbein et al. 2015; Krasnov et al. 2019). For avian haemosporidian parasites, ecological and

462   evolutionary interactions between vertebrate and vector hosts are assumed to have influenced

463   diversification of haemosporidians in specific host assemblages and geographic areas affecting their

464   contemporary spatial distribution patterns (Santiago-Alarcon and Marzal 2020). Possibly, the evolutionary

465   radiation of various endemic avian host species in the studied Neotropical and Nearctic study sites might

466   be related to the diversification of avian haemosporidians in specific host clades and habitat types, and thus

467   explains the strong correlation between parasite and host phylogenetic turnover within and between

468   biogeographic regions.

469   Despite not being able to detect haemosporidian cytochrome b lineages within all positive samples,

470   haemosporidian lineage recovery was 67%, suggesting an adequate representation of parasite assemblages

471   across the studied regions. Moreover, we described 43 and 18 new haemosporidian lineages in the

472   Neotropical and Nearctic regions, respectively, further underscoring the genetic variation these parasites

473   possess and the potential threat that avian haemosporidians could represent to avian health and human

474   economic losses for parasites affecting commercial bird species. Parasite turnover rates were

475   conservatively interpreted, yet we suggest that an increase in lineage recovery could provide further

476   support to our results and improve our understanding on the drivers of avian haemosporidian beta diversity

477   within and between Neotropical and Nearctic regions (e.g., as our study only included resident breeding

478   communities, the role of migratory species in the dispersion of pathogens should be further studied;

479   Ricklefs et al. 2017). Another possible limitation of our study is that data on each parasite genus (i.e.,

480   *Plasmodium, Haemoproteus, Leucocytozoon*) was insufficient to model and comprehend significant drivers

481   of avian haemosporidian beta diversity at the haemosporidian genus-level. We acknowledge that each

482   haemosporidian genus has different environmental requirements for their sporogonic development within

483   mosquito vectors (LaPointe et al. 2010; Fecchio et al. 2018; Ferreira et al. 2020). Moreover, the

484   evolutionary associations haemosporidians have had with avian species may also differ between genera

485   (Clark and Clegg 2017). Accordingly, the taxonomic and phylogenetic turnover of each genus could respond

486   differently to the same environmental, spatial, and host dissimilarity gradients. Yet, our analyses provide

487   insights that help disentangle the general processes driving avian haemosporidian turnover at different

488   scales (within and between biogeographic regions), showing how ecological, spatial, and evolutionary

489   processes contribute to the beta diversity of avian haemosporidian parasites.

490   In conclusion, our study shows that the relative importance of ecological, spatial, and evolutionary

491   processes driving the beta diversity of avian haemosporidian parasites varies contingent on the scale of

492   study (within and between biogeographic regions), as well as for the taxonomic and phylogenetic

493   components of parasite beta diversity. Within-region key drivers of the taxonomic turnover of

494   haemosporidians included environmental and spatial gradients for the Neotropical region, and host

495   phylogenetic dissimilarity gradients for the phylogenetic turnover of haemosporidians at the Nearctic

496   region. Between-region key drivers of the taxonomic turnover of haemosporidians included host taxonomic

497   dissimilarity and spatial gradients, whereas host phylogenetic dissimilarity gradients continued to explain

498   the phylogenetic turnover of haemosporidians at the Neotropical-Nearctic transition zone. The most

499   consistent driver of avian haemosporidian turnover at both scales of analysis was the phylogenetic turnover

500   of bird host assemblages, implying that there is a strong evolutionary association between avian

501   haemosporidians and their bird hosts, highlighting the important role that the historical biogeography of

502   birds have had for the diversification and distribution of haemosporidians. Future studies should explore

503   the relationships between the evolutionary history of vectors, bird hosts, and haemosporidians to reveal

504   the influence that the demography and biogeography of vectors might have had on the current

505   haemosporidians beta diversity patterns.

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Appendix A Supplementary material

Table A1. Geographic coordinates and elevations per habitat type of the 20 surveyed sites at the Mexican Neotropical and Nearctic biogeographic regions. Site numbers indicate the location of each site on the map (Figure 2).

| Biogeographic region	Site No.	Habitat type	Elevation m asl	Geographic coordinate
Neotropical	3	coastal medium deciduous forest	9	19°35'34.3"N, 96°22'52.2"W
	19	tropical deciduous forest	262	19°20'59.4"N, 96°34'17.7"W
	6	montane cloud forest	1640	19°30' 56.9"N, 97°00'22.7"W
	7	montane cloud forest	1200-1600	19°27'15''N, 97°00'28''W
	20	urban forest	1427-1467	19° 33' 07'' N, 96° 56' 18'' W
	10	peri-urban forest	1344-1372	19°30'52''N, 96°56'12''W
	4	shade coffee plantation	1210-1313	19° 27' 32'' N, 96° 59' 26'' W
	2	cattle field	1460-1525	19°31'37''N, 96°59'7''W
	9	pine-oak forest	2743	19°31'56.4"N, 97° 04'20.5"W
Nearctic	17	medium deciduous forest	500	21°55'31.7"N, 99°24'53.9"W
	18	cattle field-medium forest	467	
	12	mesquite vegetation	1005	22° 10' 39.61'' N, 99° 53' 33.46'' W
	15	mesquite vegetation	1015	22° 7' 7.06'' N, 99° 53' 21.44'' W
	8	cattle field	2122	23° 8' 49.48'' N, 101° 8' 50.17'' W
	14	rosetophile shrubland	2140	23° 34' 58.29'' N, 100° 55' 13.58'' W
	5	izotal shrubland	2152	23° 22' 31.72'' N, 101° 10' 20.28'' W
	11	mesquite (*Pinus cembroides)*	2191	21° 57' 52.992'' N, 100° 36' 25.92'' W
	13	macrophile shrubland	2241	21° 54' 2.412'' N, 101° 6' 18.756'' W
	1	pine-oak forest	2250	21° 58' 3.252'' N, 100° 35' 3.12'' W
	16	pine forest	2300	21° 56' 1.78'' N, 101° 5' 47.4'' W
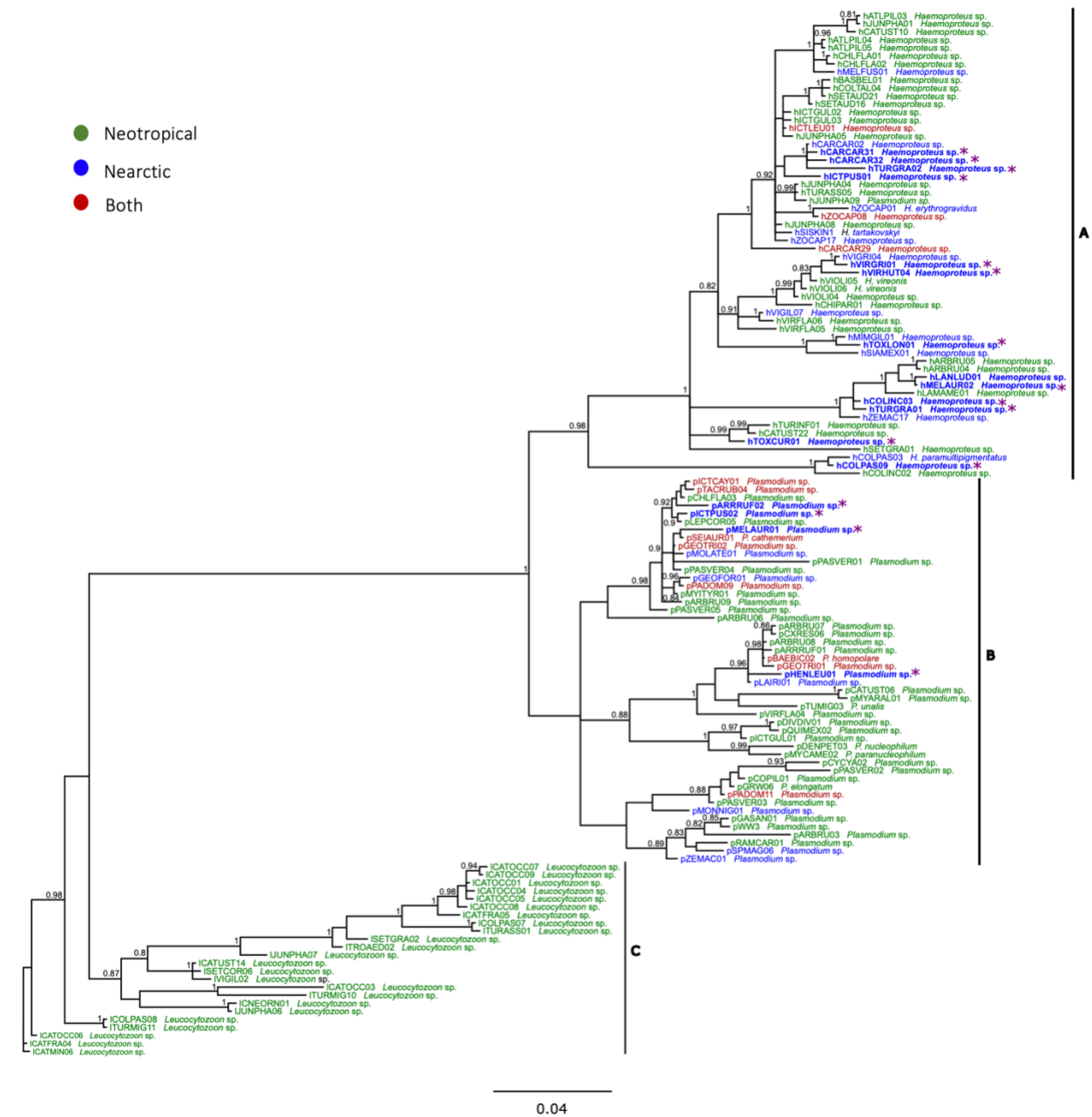
Figure A1. Bayesian phylogeny with 130 Haemosporidan cytochrome *b* lineages found in birds from the Mexican Neotropical (green color) and Nearctic regions (blue color). Haemosporidian lineages that occurred in both biogeographic regions are shown in red color. Clades: A - *Haemoproteus*, B – *Plasmodium* and C - *Leucocytozoon*. MalAvi cyt *b* lineages are followed by the parasite species name. Posterior probabilities are indicated on branch nodes. Bold letters and * indicate new lineages found in this study.
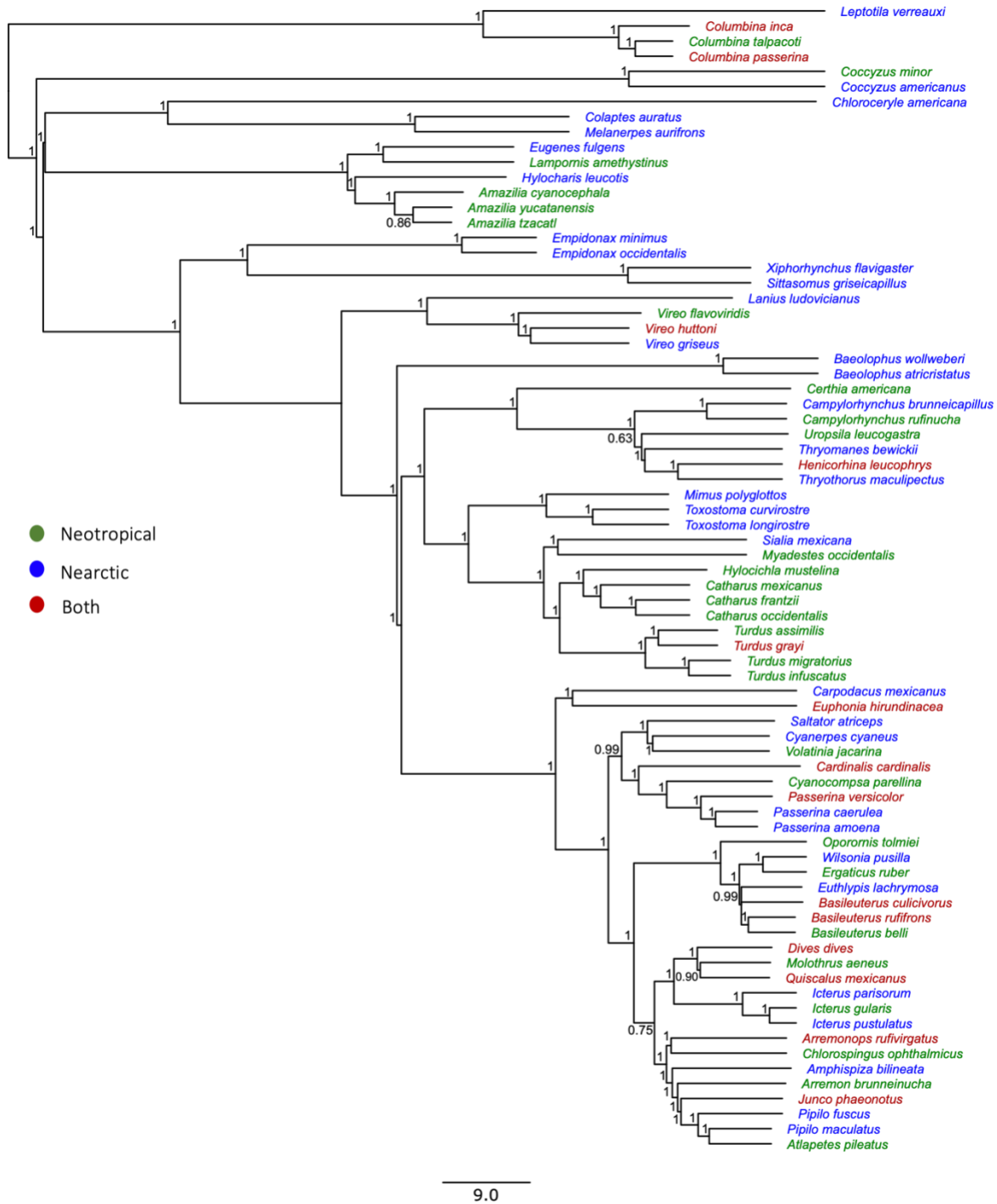
Figure A2. Majority rule consensus phylogeny with 76 bird species from the Mexican Neotropical (green color) and Nearctic (blue color) regions, in which Haemosporidan parasites were identified. Bird species that occurred in bot biogeographic regions are shown in red color. Consensus frequencies are indicated on branch nodes.

Table A2. Beta- and phylo-beta diversity decomposition of haemosporidian lineages, using the Sorensen dissimilarity index (Baselga 2010) across all habitat types within and between biogeographic regions. Bold values indicate that beta- and phylo-beta diversity of haemosporidians was always interpreted as turnover (i.e., species replacement between sites).

Scale of analysis	Type of decomposition		Distance values
within Neotropics	beta diversity decomposition		
	B_{SIM}	turnover component	**0.88**
	B_{SNE}	nestedness component	0.05
	B_{SOR}	overall value of beta diversity	0.93
	phylo beta diversity decomposition		
	B_{SIM}	turnover component	**0.5**
	B_{SNE}	nestedness component	0.2
	B_{SOR}	overall value of beta diversity	0.71
within Nearctic	beta diversity decomposition		
	B_{SIM}	turnover component	**0.75**
	B_{SNE}	nestedness component	0.14
	B_{SOR}	overall value of beta diversity	0.90
	phylo beta diversity decomposition		
	BSIM	turnover component	**0.49**
	BSNE	nestedness component	0.29
	BSOR	overall value of beta diversity	0.78
between Neotropic-Nearctic	beta diversity decomposition		
	BSIM	turnover component	**0.91**
	BSNE	nestedness component	0.04
	BSOR	overall value of beta diversity	0.95

phylo beta diversity decomposition		
BSIM	turnover component	**0.66**
BSNE	nestedness component	0.18
BSOR	overall value of beta diversity	0.85

Table A3. Beta- and phylo-beta diversity decomposition of infected bird host assemblages, using the Sorensen dissimilarity index (Baselga 2010) across all habitat types within and between biogeographic regions. Bold values indicate that beta- and phylo-beta diversity of birds was always interpreted as turnover (i.e., species replacement between sites).

Scale of analysis	Type of decomposition		Distance values
within Neotropics	beta diversity decomposition		
	B_{SIM}	turnover component	**0.84**
	B_{SNE}	nestedness component	0.053
	B_{SOR}	overall value of beta diversity	0.90
	phylo beta diversity decomposition		
	B_{SIM}	turnover component	**0.57**
	B_{SNE}	nestedness component	0.23
	B_{SOR}	overall value of beta diversity	0.80
within Nearctic	beta diversity decomposition		
	B_{SIM}	turnover component	**0.87**
	B_{SNE}	nestedness component	0.054
	B_{SOR}	overall value of beta diversity	0.93
	phylo beta diversity decomposition		
	BSIM	turnover component	**0.68**
	BSNE	nestedness component	0.15

		BSOR	overall value of beta diversity	0.84
between Neotropic-Nearctic	**beta diversity decomposition**			
		BSIM	turnover component	**0.92**
		BSNE	nestedness component	0.02
		BSOR	overall value of beta diversity	0.95
	phylo beta diversity decomposition			
		BSIM	turnover component	**0.79**
		BSNE	nestedness component	0.09
		BSOR	overall value of beta diversity	0.89

Discusión general

Comprender los factores que delimitan la diversidad y distribución de organismos parásitos en sus especies hospederas y a través del tiempo y espacio constituye una tarea fundamental para la ecología de enfermedades infecciosas. Recientemente, y bajo la crisis zoosanitaria producida por la pandemia del SARS-Cov2, han aumentado los estudios que buscan entender la relación entre la prevalencia/diversidad de patógenos, la diversidad de sus hospederos, y el medio ambiente. Los factores antrópicos (e.g., perturbación de los hábitats, cambio de uso de suelo, expansión agrícola y pecuaria, cambio climático) han afectado la distribución e interacciones ecológicas entre especies, teniendo consecuencias sobre el riesgo de emergencia y transmisión de enfermedades infecciosas (Cable et al. 2017). Por esta razón, identificar los patrones y procesos (locales y regionales) que gobiernan de manera natural la distribución y diversidad de los organismos parásitos y de sus hospederos reservorios es fundamental para comprender las consecuencias que las variaciones en la interacción parásito-hospedero pueden ocasionar en un escenario de cambio ambiental global. En este contexto se desarrolló esta tesis, la cual tuvo como objetivo utilizar la teoría ecológica de metacomunidades para estudiar al modelo 'parásitos haemosporidios-aves' a través de distintos tipos de ambientes. La pregunta ecológica central se basó en identificar y entender cuáles son los factores que delimitan la diversidad, distribución y composición de comunidades de haemosporidios a través de comunidades de aves y de gradientes ambientales, geográficos y de disimilitud de hospederos.

Barreras climáticas y la distribución de metacomunidades de haemosporidios aviares

En el primer capítulo se encontró que las barreras ambientales (i.e., la variación climática) representan determinantes fundamentales para la distribución y estructura de la metacomunidad de parásitos haemosporidios aviares a escalas locales y de paisaje (i.e, 1 a 200km). En un gradiente altitudinal, a nivel de hábitat, se identificó una estructura idealizada de la metacomunidad en donde se observó un recambio de parásitos por género a través de la elevación (i.e., estructura quasi-Clementsiana). Esta estructura se asoció a la heterogeneidad ambiental producida por distintos tipos de hábitat (la variación explicada en la composición de linajes de haemosporidios fue del 28%), en donde variables asociadas a temperatura determinaron que los haemosporidios

del género *Plasmodium* dominaran altitudes bajas (dunas costeras y bosque tropical seco), haemosporidios del género *Leucocytozoon* dominaran altitudes elevadas (bosque de pino-encino), y haemosporidios del género *Haemoproteus* se distribuyeran de manera menos restringida a través del gradiente altitudinal (bosque tropical seco, bosque mesófilo de montaña y bosque de pino-encino). La coexistencia de especies de parásitos haemosporidios en este gradiente altitudinal coincide con lo propuesto por el modelo teórico metacomunitario de 'species-sorting' o filtrado ambiental, en donde las condiciones ambientales locales y las tasas intermedias de dispersión de los parásitos determinan la coexistencia local y variación en la composición de especies parasitarias (Cottenie et al. 2003; Leibold and Chase 2018).

Contrario a lo esperado, a nivel de especie de hospedero aviar (i.e., component-community level) (Bush et al. 1997) no se encontró evidencia suficiente para inferir que las características asociadas a los hospederos (e.g., masa corporal, gremio trófico, abundancia relativa, relación evolutiva entre especies de aves, entre otras) pudieran explicar la metacomunidad idealizada de parásitos haemosporidios (estructura anidada). Solamente se pudo explicar el 4.4% del total de la variación en la composición de linajes de haemosporidios a través de sus hospederos aviares. Estos resultados coinciden con estudios recientes en donde las relaciones filogenéticas de los hospederos aviares y sus rasgos ecológicos (i.e. barreras inter-especie) tampoco pudieron explicar la diversidad de haemosporidios aviares del género *Lucocytozoon* (Fecchio et al. 2019). Por lo tanto, se propuso que a nivel de especie de hospedero aviar y en una escala local y de paisaje, los rasgos asociados a los hospederos comprenden determinantes menos importantes que los factores climáticos a nivel de hábitat para explicar los patrones de composición de parásitos haemosporidios aviares.

Determinantes de la beta diversidad de haemosporidios en la transición Neártica-Neotropical

En el segundo capítulo las barreras ambientales continuaron explicando parte de la variación en la composición de linajes de haemosporidios (beta diversidad taxonómica) dentro de una escala regional (específicamente dentro de la región Neotropical). Esto estuvo asociado a una mayor estratificación climática de los hábitats neotropicales (Rahbek et al. 2019) comparada con los hábitats Neárticos que, al igual que en el primer capítulo, promovió la especialización de nicho

por parte de los organismos parásitos y permitió observar un efecto significativo de las variables climáticas asociadas a la temperatura sobre el recambio taxonómico de los ensambles de haemosporidios aviares. Así mismo, la falta de poder explicativo de las barreras climáticas sobre la beta diversidad taxonómica dentro de la región Neártica coincide con estudios previos en donde se observó que el recambio de haemosporidios aviares a nivel regional se encuentra menos influenciado por factores ambientales, más bien se asocia a la composición y al recambio regional de especies de hospederos aviares (Williamson et al. 2019). La asociación entre el recambio taxonómico de hospederos y el recambio taxonómico de haemosporidios tampoco se observó para el modelado de la beta diversidad de los haemosporidios dentro de nuestras regiones de estudio (Neártico y Neotrópico). Sin embargo, la asociación se observó al momento de modelar la beta diversidad taxonómica de parásitos entre las regiones biogeográficas (e.g., en la transición Neártica-Neotropical). Este resultado se asoció al mayor tamaño del pool taxonómico de especies hospederas entre regiones biogeográficas, el cual posee taxones endémicos de hospederos por región, que a su vez permitió observar un efecto del recambio taxonómico de aves sobre el recambio taxonómico de haemosporidios aviares.

Como parte del segundo capítulo, fue posible evaluar el efecto de factores espaciales (i.e., distancias geográficas entre sitios) sobre la beta diversidad taxonómica y filogenética de los haemosporidios aviares, dentro y entre las regiones biogeográficas del Neotrópico y Neártico mexicanos. Se observó un efecto significativo de las distancias geográficas sobre la beta diversidad taxonómica de los haemosporidios dentro de la región Neotropical y entre la transición Neártica-Neotropical. Estos resultados se asociaron a un fenómeno puro de 'distance-decay' (i.e., decremento de la similitud en la composición de especies conforme aumenta la distancia geográfica) particularmente entre la transición Neártica-Neotropical. Sin embargo, dentro de la región Neotropical se propuso que una combinación de factores, por ejemplo 'distance-decay geográfico', exposición a diferentes familias de vectores y heterogeneidad ambiental, se asociaron al patrón observado. La falta de un efecto de las distancias geográficas sobre la beta diversidad de los haemosporidios dentro de la región Neártica se asoció a la baja complejidad topográfica del Altiplano mexicano en donde se encontraron nuestros sitios de estudio Neárticos. La baja complejidad topográfica se asocia frecuentemente a una baja heterogeneidad climática y

ambiental (Badgley 2010), que podría explicar la falta del efecto de la distancia geográfica sobre la beta diversidad taxonómica de los haemosporidios aviares dentro de esta región.

Uno de los resultados con mayor poder estadístico y explicativo del segundo capítulo, fue la fuerte correlación observada entre la beta diversidad filogenética de los haemosporidios aviares y los gradientes de disimilitud filogenéticos de los hospederos aviares. Esta relación se observó dentro de las regiones muestreadas en el Neotrópico y Neártico mexicanos, así como entre ambas regiones biogeográficas. Diversos estudios han sugerido que la diversificación de los haemosporidios aviares está significativamente correlacionada a los procesos ecológicos y evolutivos que determinaron la historia demográfica y biogeográfica de los ensambles de hospederos aviares y de sus vectores (Pacheco et al. 2018). Posiblemente, la radiación evolutiva de aves endémicas dentro de las regiones Neártica y Neotropical esté asociada a la diversificación de los haemosporidios en clados de hospederos y hábitats específicos, lo que podría explicar el fuerte efecto del recambio filogenético de los hospederos aviares sobre el recambio filogenético de los parásitos haemosporidios entre nuestras regiones de estudio.

La importancia de las escalas de estudio y de las aproximaciones estadísticas utilizadas

Los resultados discutidos anteriormente demuestran que la importancia relativa de los factores ecológicos/ambientales, espaciales, y evolutivos sobre la diversidad y distribución de parásitos haemosporidios aviares varía en función de la escala de estudio (local-paisaje, dentro de regiones y entre regiones biogeográficas) y al tipo de diversidad modelada (diversidad taxonómica vs. filogenética). La aproximación de metacomunidades idealizadas utilizada en nuestro primer capítulo nos permitió inferir la importancia de los procesos de filtrado ambiental (modelo metacomunitario de 'Species-sorting') sobre el ensamblaje y distribución de las comunidades de haemosporidios aviares. El capitulo confirmó que a escalas menores de estudio (locales y de paisaje) los procesos determinísticos asociados a la heterogeneidad ambiental y a la disponibilidad y uso de recursos, tienen un mayor peso que las relaciones evolutivas entre los hospederos y parásitos para explicar la distribución de los ensambles de parásitos haemosporidios aviares. Sin embargo, al no haberse considerado algunas variables asociadas a procesos regionales (e.g., proxys para medir dispersión y otros factores espaciales), no fue posible concluir que solamente

estén actuando procesos locales y determinísticos sobre el ensamble de las comunidades de haemosporidios. Sería de importancia incluir predictores que representen tanto procesos locales como regionales, para poder discernir entre la importancia de estos e inferir la combinación de modelos teóricos metacomunitarios que expliquen la distribución y coexistencia de los linajes genéticos de este sistema parasitario.

Aunado a la falta de predictores asociados a procesos regionales, una limitante de los análisis de ecología de metacomunidades radica en la falta de información de las estructuras metacomunitarias a través del tiempo (Guzman et al. 2020). Los análisis de los 'elementos de la estructura de la metacomunidad' (EMS) solamente capturan un momento estático de los patrones de distribución de las especies, lo cual se ha probado insuficiente para discernir confiablemente entre los procesos ecológicos que explican a los patrones de distribución (Guzmán et al. 2020). Así mismo, las aproximaciones multivariadas para medir el efecto de los predictores ambientales, espaciales o asociados a los hospederos (i.e., análisis de partición de la variación) sobre la distribución de las metacomunidades parasitarias debe ser interpretado con cautela debido a los bajos porcentajes de poder explicativo que estos análisis han arrojado durante su aplicación (Cottenie 2005; Soininen 2014).

El modelado de la beta diversidad a través de gradientes ambientales, geográficos y de disimilitud de hospederos representó una aproximación estadística poderosa para identificar los principales factores que delimitan la beta diversidad de los haemosporidios aviares dentro y entre la transición Neártica-Neotropical. Como se esperaba , la importancia relativa de los gradientes varió dentro y entre regiones, siendo importantes los gradientes ambientales dentro de las regiones estudiadas (exclusivamente dentro de la región Neotropical) para la beta diversidad taxonómica; los gradientes espaciales tuvieron una mayor importancia entre regiones biogeográficas para la beta diversidad taxonómica de haemosporidios; y los gradientes de disimilitud filogenética de hospederos fueron predictores significativos de la beta diversidad filogenética de los haemosporidios aviares en ambas escalas de estudio. Esto nos demostró el peso que tienen las relaciones evolutivas entre haemosporidios y sus hospederos aviares sobre el ensamblaje de las comunidades parasitarias, pues la correlación entre el recambio filogenético de hospederos y el recambio filogenético de haemosporidios fue el resultado más fuerte del estudio.

La aproximación estadística utilizada dentro de este segundo capítulo fue el 'generalized dissimilarity modelling' (GDM) (Ferrier et al. 2007). Los modelos GDM han sido utilizados para estudiar la beta diversidad de otros organismos parasitarios (e.g., ectoparásitos) y en teoría son modelos más adecuados que las regresiones lineales para comprender las relaciones entre el recambio de especies y los gradientes deseados (Fitzpatrick et al. 2013; Van Der Mescht et al. 2017). Pese a que no se pudieron recuperar linajes genéticos de haemosporidios en todas las muestras positivas de ambas regiones biogeográficas, se consideró que se obtuvo un porcentaje de recuperación de linajes alto (67%) para que los modelos GDM arrojaran resultados confiables.

Conclusiones y perspectivas futuras de investigación

En este trabajo doctoral se contribuyó al entendimiento de los factores que delimitan la diversidad, distribución y composición de comunidades de parásitos haemosporidios aviares en sus hospederos y a través de distintos ambientes. En términos generales, los efectos de los factores estudiados (i.e., ambientales, geográficos e históricos) sobre los haemosporidios aviares en distintos ambientes y escalas espaciales coinciden con lo que se conoce para otras comunidades biológicas: a escalas menores de organización (i.e., locales y paisaje) la heterogeneidad ambiental, las condiciones micro-climáticas, las interacciones inter-específicas, entre otras, explican de mejor forma la diversidad y distribución de las especies, mientras que a escalas mayores de organización (i.e., regionales/ globales) los procesos históricos y biogeográficos y las asociaciones evolutivas entre especies determinan dichos patrones de distribución (Rahbek 2004; Thomas, Renaud, and Guégan 2006; Goetz et al. 2014).

Para profundizar en el conocimiento que tenemos en la actualidad sobre los patrones y procesos que determinan la diversidad y distribución de parásitos haemosporidios aviares, y sobre las futuras consecuencias que el cambio ambiental global pueda tener sobre estos patrones de distribución y sobre la salud animal, es necesario continuar utilizando teorías ecológicas (por ejemplo teoría de metacomunidades, teoría de redes) y aproximaciones estadísticas robustas (e.g., análisis multivariados) que nos permitan discernir entre la importancia de procesos determinísticos/ neutrales, procesos locales/regionales, y factores bióticos/abióticos sobre las complejas interacciones antagonistas parásito-hospedero y el espacio-tiempo en el que coexisten.

Así mismo, es necesario recabar más información sobre la ecología y evolución de los hospederos invertebrados de estos organismos parásitos. La interacción de la historia evolutiva de los vectores, con la de los haemosporidios y los hospederos aviares, podría ayudarnos a comprender de mejor manera los patrones actuales de diversidad y distribución de parásitos haemosporidios aviares.

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