

University of Groningen

Drivers of distribution patterns of Mesoamerican tropical forest birds

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DOI:

[10.33612/diss.1144835955](https://doi.org/10.33612/diss.1144835955)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version

Publisher's PDF, also known as Version of record

Publication date:

2024

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Castillo Chora, V. (2024). *Drivers of distribution patterns of Mesoamerican tropical forest birds*. [Thesis fully internal (DIV), University of Groningen]. University of Groningen. <https://doi.org/10.33612/diss.1144835955>

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**Drivers of distribution patterns:
from communities to populations**

Introduction

The study of the spatial and temporal patterns of biological diversity at all its levels (from genetics at the population level to species richness at the community level and in higher taxonomic units), is a cornerstone in biogeography, aimed at understanding and reconstructing the evolutionary history of the biota on Earth.

Different processes operating simultaneously on several spatio-temporal scales have diverse effects on biodiversity patterns. For example, to understand the composition of local communities, we must consider colonization from the regional species pool, which is ultimately determined by long-term speciation and extinction processes (Ricklefs 2004, Belmaker & Jetz 2012, Carstensen *et al.*, 2013). But short-term effects of demographic stochasticity and niche-based processes that define species distributions and range limits must also be considered (*e.g.*, environmental drivers generating large-scale biogeographic diversity patterns; Chase & Myers 2011, Tilman 2004).

This array of factors that promote diversity patterns is embedded in different theories. Island biogeography theory (MacArthur & Wilson 1963) describes patterns of compositional turnover and diversity as a result of stochastic colonization and extinction processes whereas niche theory (*e.g.*, Grinnell 1917, Hutchinson 1959, Chesson 2000, Schoener 2009) describes patterns of species ecological distributions and geographic range limits, coexistence of species at local scales, as well as patterns of species diversity along environmental and biogeographic gradients (Schluter & Pennell 2017) as a result of deterministic ecological interactions.

The fact that different theories placed a distinct emphasis on the relative importance of niche-based processes to community assembly has been called MacArthur's paradox (Loreau & Mouquet 1999, Chase & Myers 2011). Whereas MacArthur's work on island biogeography theory ignored differences among species traits when predicting species diversity on islands (MacArthur & Wilson 1963), MacArthur's work on limiting similarity, competition and coexistence (*e.g.*, MacArthur & Levins 1967) viewed species trait-environment relations as key factors determining species coexistence and diversity at local spatial scales.

Hubbell's (2001) neutral theory, based on island biogeography theory, suggests that dispersal limitation, ecological drift and a balance between random extinction and speciation could explain a wide variety of ecological patterns. Niche-based theories (*e.g.*, Chesson's coexistence theory) argue that similarity and coexistence are based on explicit consumer-resource interactions and trade-offs in the way that organisms use different resources and other factors that influence their birth and death rates. Connections between these contrasting approaches are important to understand how real communities are assembled, such as incorporating larger spatial processes into local community interactions, as well as aspects of species trait differences at regional scales (Chase & Myers 2011).

Macroevolutionary drivers of diversity

Regional species pools are ultimately shaped by major processes that act on an evolutionary scale (*e.g.*, speciation, immigration, and extinction), coupled with factors that influence such evolution, as regional age, diversification rates, and ecological limits (Cornell & Harrison 2014). Assuming that there are no intrinsic limits to regional diversity (*e.g.*, carrying capacity; K), the number of species is expected to be higher in older regions, because there is more time for diversification (Meseguer *et al.*, 2021). Evolutionary processes lead to the accumulation of species over a time span that may be defined by the origin of major geographic features or by major climatic and biotic changes (Cornell & Harrison 2014, Meseguer *et al.*, 2021). However, temporal variation in evolutionary rates (immigration, speciation and extinction) due to external factors (*e.g.*, climate shifts) may cause diversification rates to shift drastically over the lifetime of a clade (*e.g.*, Rabosky 2009). Hence, we would expect higher species richness in regions where immigration and net diversification are high because of the combination of intrinsic and extrinsic factors (*e.g.*, Crouch & Tobias 2022.).

From a simplified island biogeography perspective, species are equivalent in the sense that stochastic factors determine community structure, (*i.e.*, immigration and extinction are strongly influenced by the size and isolation of the island from the mainland (MacArthur & Wilson 1963). Likewise, neutral theory (Hubbell 2001) sees local communities as the result of stochastic dispersal, speciation, ecological drift and extinction dynamics. Local communities are sampled from the regional species pools, in which the probability of dispersal to the community is related to the distance and abundance of a species in the pool rather than its identity (Chase & Myers 2011).

Some authors have pointed out that neutral theory makes predictions of biodiversity on speciation rate and species longevity that are unrealistic (Hubbell 2001; Rosindell *et al.*, 2010). The protracted speciation model (*i.e.*, speciation is assumed not to take place instantaneously but is allowed to take time) has been shown to resolve these problems. With this simple consideration, protracted speciation implies more realistic numbers of rare species, speciation rates and species lifetimes in neutral theories (Rosindell *et al.*, 2010).

Speciation and extinction rates may also depend on organismal traits (Maddison 2006, Paradis 2008). In many cases, shifting environments and dispersal barriers among localities and/or the evolution of key innovations allow populations to expand their distributions and become part of the species pool for other localities, otherwise, communities would comprise exclusively endemic species (Agosta & Klemens 2008). Additionally, organismal traits may influence species distribution and species coexistence. Positive correlations between divergence time and range overlap suggest that species tend to arise in allopatry and subsequently spread into sympatry with their relatives and other species (*e.g.*, Fitzpatrick & Turelli 2006, Pigot & Tobias 2013).

Diversity itself may also have a strong role in affecting diversification rates to change over time. Ecological factors exert feedback on speciation and extinction rates, possibly as increasing species richness saturates available niches (Etienne & Haegeman 2012, Burbrink & Pyron 2010, Phillimore & Price 2008). Then, when niche space fills as a region accumulates species,

immigration or net diversification will decrease as diversity increases, and regional diversity becomes independent of regional age (Ricklefs 2012, Cornell 2013). Diversity-dependent dynamics appear to be a common feature of empirical phylogenies (Etienne *et al.*, 2012), supporting ecological theories of adaptive radiation that rapid saturation of available niche space reduces rates of diversification (Heaney 2000, Burbrink *et al.*, 2012).

Niche-based processes of community assembly

Niche concepts were fundamental in the development of the ‘local perspective’ of ecological communities, which views communities as limited membership assemblages in which interspecific biotic interactions and abiotic conditions are the primary factors influencing community composition (Chase & Myers 2011). Assembly rules explain why only a limited subset of the species found in the regional pool (which includes all the species that could colonize a local site or community over ecological time) are present in a local community (Kraft *et al.*, 2007, Mittelbach & Schemske 2015, Mittelbach & McGill 2019). Niche-based theories postulate that from the potential colonists, some species are limited in their ability to disperse, some are limited by their ability to survive the abiotic environment, and some are limited by their interactions with other species (Cadotte & Tucker 2017, Mittelbach & McGill 2019).

Niche selection is considered a more deterministic process in which environmental factors interact with species traits to determine which and how many species are found in different areas (Chase & Myers 2011). Niche-based processes associated with species niches and their responses to environmental conditions can be critical in community assembly, especially under conditions imposed by strong abiotic and biotic filters (Chase 2010). When conditions are relatively benign (*e.g.*, high productivity, low disturbance and absence of predators), this niche effect has reduced impact as filters, stochastic factors (*e.g.*, colonization and species drift) gain relevance affecting community composition. Alternatively, under harsher environmental conditions (*e.g.*, low productivity, drought and predators), niche selection is expected to have stronger effects preventing species from persisting in local communities (Chase 2010, Chase & Myers 2011).

Environmental and biotic filters act individually or in concert, and the functional traits of species determine their success in passing through these filters to colonize a local site (Mittelbach & McGill 2019). At the local community level, coexistence depends upon both stabilizing niche differences that facilitate coexistence and relative fitness differences driving competitive exclusion (Chesson 2000, Barabás *et al.*, 2018). Niche differences driving frequency-dependent population growth can arise from differences among species in their response to limiting factors (*e.g.*, shared resources), whereas fitness differences can arise through different mechanisms *e.g.*, differences in the ability to take up resources or biotic interactions. Such relative fitness differences are what stabilizing niche differences (*i.e.*, niche differences that underlie stable coexistence) must overcome to generate coexistence (Chesson 2000, Barabás *et al.*, 2018).

Different evolutionary processes occur during allopatric speciation, such as divergent adaptation, accumulation of reproductive isolation, and the evolution of locally adapted populations (Nosil 2012, Edelaar 2018). Because phylogenetically closely related species are more

likely to share traits (i.e., phylogenetic niche conservatism; Pagel 1999), the ancestral niche can determine the regions and habitats to which the clade can spread, and those in which it will persist in the face of environmental change (Wiens 2004, Wiens & Donoghue 2004). As geographically isolated populations evolve, both reproductive isolation and niche divergence increase, and together these factors should promote coexistence if secondary sympatry is achieved (Mittelbach & McGill 2019). Niche evolution (i.e., the expansion of niche breadth or specialization for new conditions) should enable the invasion of new habitats or climatic regimes that had previously limited the distribution of a clade (Wiens & Donoghue 2004). Knowing how these niche shifts occurred along the phylogeny and their relationship to ecological factors, distributional ranges and biotic interactions (e.g., competence between recently diverged species/populations) is important for understanding the community assembly process (e.g., Cortés-Ramírez *et al.*, 2019, Moreno-Contreras *et al.*, 2020, Garcia-Porta *et al.*, 2022).

Geographic and genomic view of the speciation

Understanding community assembly process and the importance of dynamic species pools should include information related to the geography of speciation, formation of secondary sympatry and feedback between local and regional processes (Mittelbach & Schemske 2015). Hence, assessing the role of geographical barriers in speciation and its contribution to community assembly becomes relevant.

Speciation models are usually defined based on geography, and the main difference between them is the assumed *a priori* amount of gene flow between populations. In allopatric speciation, a geographical barrier prevents gene flow between populations and reproductive isolation may evolve as a byproduct of divergent natural selection or genetic drift. In sympatric speciation, there is no geographical isolation and barriers to gene flow evolve in sympatry. In parapatric speciation, strong divergent selection between neighboring populations leads to the accumulation of reproductive isolation despite gene flow (Wiens 2004, Butlin *et al.*, 2008, Fitzpatrick *et al.*, 2009, Nosil 2012).

The genic view of the speciation process was an important step in the transition from searching for geographic patterns to divergence processes, in addition to offering a genetic perspective in both the differentiation processes and in the mechanisms involved in defining range limits (Wu 2001, Wiens 2004). The genic view of speciation considers that a purely geographic distinction could be an oversimplification that makes assumptions about previously poorly quantified processes, such as gene flow, genetic drift, and divergent adaptation (Feder *et al.*, 2012).

From this geographic view of speciation, when allopatric populations come into secondary sympatry, three main results are expected: 1) In individuals with long-distance dispersal competitive exclusion or strong local adaptation may limit coexistence. 2) As allopatric populations become adapted to their local environments, they are also less likely to successfully colonize the geographical range of their sister species. 3) Stable secondary sympatry arises as a consequence of range expansion and coexistence through diminished local adaptation and niche divergence (e.g., large-scale environmental change may cause range shifts that erase local

adaptation to ancestral habitats; Haffer 1969, Abbot *et al.*, 2010, 2013, Mittelbach & Schemske 2015). Secondary sympatry may originate in a contact zone, where populations of the two species coexist and exchange genetic material (Abbot *et al.*, 2010, 2013). Various results could be expected from this encounter: reinforcement, hybridization, or maintenance of a stable hybrid zone, depending on the genomic and ecological context of the populations. Particularly, in hybrid zones where secondary sympatry results in coexistence, subsequent adaptation to reduce niche overlap (competitive displacement) or hybridization (reinforcement) is possible (Wielstra 2021).

Avian diversity of the Mesoamerican lowland forests

High-diversity regions with complex biogeographic histories offer the opportunity to analyze distribution and diversity patterns, test different hypotheses and assess the importance of multi-scale processes in the formation and maintenance of biodiversity patterns. Tropical forests have been identified as the most diverse and productive forests on the planet (Pennington *et al.*, 2006). They are considered ecosystems of interest because they are an important part of the biosphere and harbor several natural resources, but also because of their biogeographic and evolutionary history (Díaz-Gallegos *et al.*, 2010).

The neotropical realm (*sensu* Olson *et al.*, 2001) possesses an exceptional physiographic heterogeneity and harbors some of the most diverse and extensive neotropical ecosystems such as tropical lowland forests, savannas, deserts, montane forests and grasslands (Hughes *et al.*, 2013). Particularly, in the Mesoamerican portion of the Neotropical realm, two major lowland biogeographic regions are distinguished: the lowlands of the Pacific slope and the lowlands of the Gulf of Mexico and the Caribbean (Stotz *et al.*, 1996; Enríquez *et al.*, 2012, Llanes-Quevedo *et al.* 2024*). The most predominant ecosystems there are the seasonally dry tropical forest (SDTF) and the humid tropical forest (HTF; Gentry 1992; Villaseñor & Ortíz 2013; Fig. 1).

These two types of lowland tropical forests are among the most extensive and diverse ecosystems, which host a high number of endemic vertebrate and plant species (Gentry 1992). The lowlands of Mesoamerica are isolated by the effect of the main mountain ranges of North and Central America. The SDTF characterizes the province of the Pacific lowlands, although they also contain humid tropical forests. This province does not exceed 400 m in altitude (Dinerstein *et al.*, 1995, Linares-Palomino *et al.*, 2011). The distribution of SDTF is along the Pacific coast from Sonora, Mexico to Guanacaste, in northern Costa Rica. In Mexico, small patches of tropical forest are also distributed in the lowlands of the Gulf of Mexico and the Caribbean, particularly northern Yucatán Peninsula, and in the states of Veracruz and Tamaulipas (Dinerstein *et al.*, 1995; Pennington *et al.*, 2009; Villaseñor & Ortíz, 2013; Prieto-Torres *et al.*, 2016, 2018; Guerra-Martínez 2020; Fig. 1). The HTF is distributed in the lowlands of the Gulf of Mexico and the Caribbean from the Northeast and Southern part of Mexico to Central America (Costa Rica and Panama). It is found at altitudes of 0 to 1,000 m, although occasionally it can be located up to 1,500 m (Asner *et al.*, 2009; Villaseñor & Ortíz, 2013; Guerra-Martínez 2020; Fig. 1).

The SDTF is characterized by a short period of rainfall and prolonged dry season as a result of its climatic seasonality, which is associated with its location, latitude and elevation (Rzedowski

1978; Gentry 1995; Ceballos *et al.*, 2010). The Sierra Madre Occidental and the Trans-Mexican Volcanic Belt are the main orogenic features that allow the establishment of the Mexican lowland forest because they maintain favorable climatic conditions blocking the cold fronts of the North (Becerra 2005). The contrasting precipitation regime between the dry season and the rainy season plays an important role in the physiognomy of the dry tropical forest, which presents leaf loss during the 5–8 dry months and is leafy and green during the rainy months (Rzedowski 1978; Gentry 1995; Ceballos *et al.*, 2010). By contrast, the HTF is distributed in regions with abundant precipitation (> 1500 mm) and their plant community is dominated by trees.

There is a strong association between SDTF and THF, because the last allows refuge for different species during the dry season; this promotes the coexistence of species typical of humid environments with species adapted to dry conditions (Vega Rivera *et al.*, 2010; Pérez-García *et al.*, 2012). Vertebrate communities in dry forests are generally represented by groups of species typical of dry forests and a subset of species of fauna from nearby humid forests (Ceballos & Valenzuela 2010). Some of the areas with the greatest species richness in Mexico are areas bordering the SDTF and other ecosystems, for example, in the Isthmus of Tehuantepec and central Veracruz with THF and in Jalisco-Colima with the pine-oak forest (Ríos-Muñoz & Navarro-Sigüenza 2012).

The Pacific lowlands are among the main areas of endemism of neotropical bird species (Stotz *et al.*, 1996). Just in Mexico more than 200 species are present in the SDTF and more than 220 species in the HTF (Vega Rivera *et al.*, 2010). In addition, Escalante *et al.*, (1998) indicated that the SDTF is home to more than 40 endemic bird species, making it the third ecosystem on the list of most bird endemism in Mexico, after the Tropical rain forest and the semideciduous tropical forest (Escalante *et al.*, 1993). Complex vegetation responses and changes in bird activity (*e.g.*, changes in feeding patterns in response to drastic changes in water availability) as well as being host to the diversity of Nearctic-affinity migratory birds may explain the great diversity that characterizes the SDTF (Vega Rivera *et al.*, 2010).

Effects of Pleistocene climate shifts on bird diversification in the Mesoamerican lowland forests

Avian evolution and the mechanisms that promoted its diversification and distribution are among the most fruitful and exciting fields of biology. Birds represent one of the best-known groups, with information available for most of the around 10,000 living species. Neotropical regions are host to an important percentage of this diversity.

To explain the species richness of the lowland tropical forests of South America, Haffer (1969) suggested that during the dry periods of the Pleistocene and post-Pleistocene the forests were isolated in multiple small patches, which served as refuge areas, whereas during the wet periods they were reconnected, which gave rise to a dynamic of metapopulations. This hypothesis was generalized by Hewitt (1996, 2000) who suggested that climate changes had produced changes in the distribution patterns of most living beings. Hewitt (2000) also integrates a genetic perspective of the effects of Pleistocene climate shifts, including analysis with several genetic

markers to estimate the divergence times of differentiation or speciation, which support an important role of the Pleistocene period.

Allopatric differentiation has received high empirical support (Prado & Gibbs 1993; Gentry 1995; Pennington *et al.*, 2000). However, this hypothesis of climatic changes as the main trigger for the diversification of Neotropical biota has been challenged with the hypothesis of paleographic reorganizations during the Miocene linked to the Continental drift (*e.g.*, such as the closure of the isthmus of Panama), which seems to fit better to lineages whose diversification precedes the Quaternary (Nores 2004; Rull 2008).

Both the hypothesis of Quaternary climatic changes and the hypothesis of paleographic reorganizations during the Miocene have received empirical support from genetic, geological and palaeoecological data (Rull 2008). Due to these contrasting results, an attempt has been made to reconcile the two hypotheses. For example, Weir (2006) analyzing data from 27 bird taxa found that lowland species have greater diversification during the Miocene, while highland birds exhibit higher rates of diversification during the Quaternary. An alternative hypothesis was proposed by Noonan & Gaucher (2006). The perturbation-vicariance hypothesis suggests that cold periods during the Pleistocene allowed altitudinal migrations to the lowlands of species adapted to temperate climates, followed by fragmentation and isolation of their populations during warm periods, which could result in adaptive radiation and allopatric speciation.

Genetic approaches have been used to understand the timing and mode of speciation in the region. By comparing the patterns of genetic divergence between multiple taxa that are distributed in the same geographical area, inferences can be made about the processes and patterns common to those lineages, and thus the influence of historical geographical or ecological events, which similarly affected different populations of different groups (*e.g.*, vicariance; Avise *et al.*, 1987; Bermingham & Moritz 1998; Arbogast & Kenagy 2001; Avise 2009; Hickerson *et al.*, 2010), can be recognized. Avian phylogeographic comparative analysis has shown that there is a population genetic structure within the lowland forests of Mesoamerica, which occurs in areas without conspicuous physical barriers limiting dispersal or gene flow (Arbeláez-Cortés & Navarro-Sigüenza, 2013, Ortiz-Ramírez *et al.*, 2018, Castillo-Chora *et al.*, 2021). This is a pattern that has been described for mammals (Arcangeli *et al.*, 2017), reptiles (Devitt 2006) and plants (Hughes *et al.*, 2013).

Additional evidence about the evolutionary history of bird lineages associated with the lowlands of Mesoamerica, based on genetic markers, showed patterns that allow inferring similar biogeographic processes affected the evolutionary of different species of birds with no close phylogenetic relationship, but that present sympatric or partially sympatric distributions in the STDF of Mesoamerica (Arbeláez-Cortés & Navarro-Sigüenza, 2013; Arbeláez-Cortés *et al.*, 2013; Ortiz-Ramírez *et al.*, 2018, Castillo-Chora *et al.*, 2021; Sánchez-González *et al.*, 2021, Espinosa-Chávez *et al.*, 2024). Results of such analyses studying the biological and genetic diversity of STDF suggest some generalities in bird species as niche conservatism, high phylogeographic structure, predominance of allopatric differentiation, and Pleistocene divergences at the population level.

Objectives and outline of the thesis

Throughout this thesis, I focus on different aspects of biological diversity that operate at different spatial and temporal scales, but that act jointly to create the bird distributional patterns that we currently observe in the Mesoamerican lowland forests.

In **Chapter 2**, I analyze the stochastic macroevolutionary processes that drove the passerine diversity of Yucatán Peninsula (YP) from a community assembly perspective, using an island biogeography approach to explain the species diversity of the system in terms of the processes of immigration, speciation and extinction. YP, in the lowlands of Mesoamerica, is host to a high diversity of avian species that stem from clades that evolved in South America and immigrated to the peninsula, since the beginning of the Pleistocene (~2.6 MYA). YP has a complex geological and bioclimatic history which make it likely that these macroevolutionary processes did not occur at constant rates and were not equal for all clades. In line with this, I test four different models to explain the diversity patterns of the passerine community of YP: 1) a null model, which assumes constant rates over time and no variation in rates across species; 2) a shifting rates model, which allows for a shift in one or more rate parameters at some point in time. 3) a relaxed rate model, which accounts for overall inter-species variation in rates and 4) a two-type model, which allows to test if a particular group of species shows differences in at least one rate. The results show that the community assembly of passerine species of YP is best explained by a shift in macroevolutionary rates. The best fitting scenario suggests that extinction rate was constant over time, but the immigration rate increased drastically around 0.3 MY before the present. Glacial-interglacial periods varied in their intensity and geographic expression, so we suggest that our estimated increase in immigration rates is a consequence of the fact that during 243 ky–337 ky changes in immigration and extinction rates highly impacted passerine community assembly in the YP.

For the Mesoamerican lowland forests, there is strong evidence for the effects of Pleistocene climate shifts in modifying range distribution and promoting differentiation. Although species responded differently to past climatic and environmental changes, some patterns have been described. In general, species modified their distribution ranges in response to climate shifts, through latitudinal or/and altitudinal movements or contraction of the area of distribution (Mastretta-Yanes *et al.*, 2015, Castillo-Chora *et al.*, 2021). In **Chapter 3**, I analyze from a climate-based approach what are the consequences of niche conservatism at the species and subspecies level, and their putative explanatory power for geographic patterns of morphological and genetic differentiation. I test a hypothesis of niche differentiation between the different species and lineages of the *Psilorhinus* – *Calocitta* clade. I perform a paleo-reconstruction of the distribution range of the different lineages to evaluate the possible effects of the Pleistocene climate changes on the current patterns of subspecies distribution, and test whether lineages have been influenced by similar processes in different regions of the lowland tropical forests. Finally, I assess the importance of areas that could act as environmental barriers at the infra-species level. Our results show that at the species level, the effects are associated with responses to climate shifts, because past geographic transferences seem to have good explanatory power for the current distribution

and variation of subspecies. At the subspecies level effects are associated with ecological barriers limiting the connection between populations with similar niche requirements. In particular, the Isthmus of Tehuantepec and the Wetlands of Tabasco may act as current biogeographic barriers. A possible consequence of these Pleistocene climate shifts is the formation of contact zones between recently diverged taxa.

The presence of such contact zones can provide information regarding Pleistocene distributions, postglacial recolonization routes, as well as information related to isolation and speciation mechanisms (Hewitt 2001). In **Chapter 4**, I discuss and integrate what information could be obtained by analyzing contact zones, focusing on the genetic consequences of secondary contact at the mitochondrial, genomic, and phenotypic levels, in addition to analyzing the ecological factors that determine the potential for sister species to coexist. This chapter is motivated by recent empirical evidence based on genomic data suggesting that secondary contact and genetic exchange between separate lineages is a recurrent process. Given this rethinking of the evolutionary process and with the increasing availability of data the different lines of evidence must be properly analyzed and integrated into evolutionary studies. Throughout this review, I briefly discuss some of the main patterns found in contact zones, some of the consequences of hybridization and introgression, such as the genomic patterns of nuclear introgression and their relationship to the phenotype, and how different lines of evidence could be integrated and complemented to address specific questions into evolutionary studies. Finally, in **Chapter 5**, I synthesize the main findings from the previous chapters and discuss how the analysis presented here may contribute to increasing the knowledge of different evolutionary aspects and to a better understanding of the evolutionary history of the Mesoamerican birds.

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