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## Drivers of distribution patterns of Mesoamerican tropical forest birds

Castillo Chora, Vicente

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# 5

## **Synthesis**

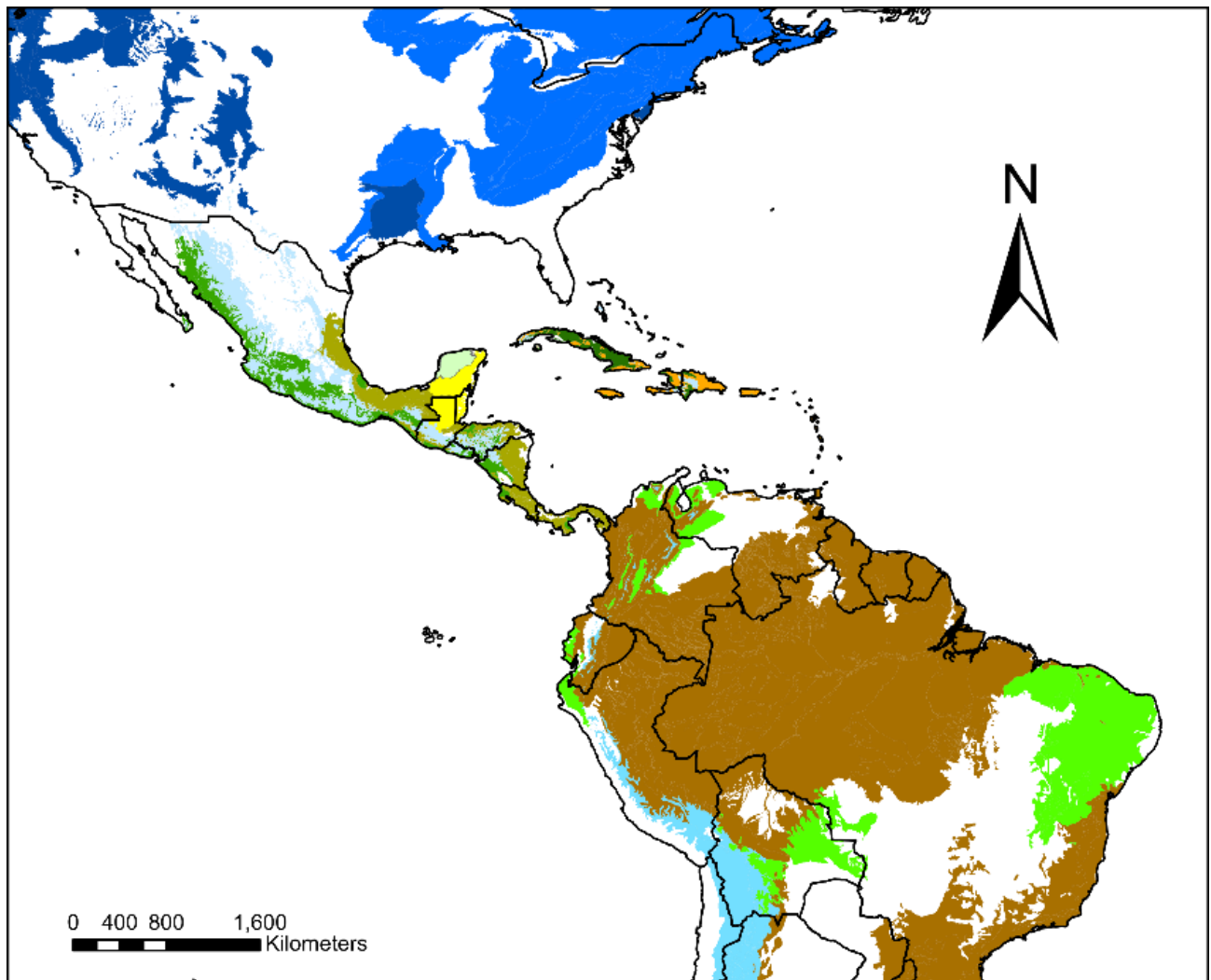
### Summary of the conclusions

An important question in evolutionary biology is how ecological and evolutionary processes predominantly operating at some level of biodiversity grouping (*i.e.*, populations and species) are linked to different diversity scales such as higher taxonomic units or to local and regional community processes and *vice versa* (Vellend & Orrock 2009, Vellend 2010, Miller et al., 2021). The interrelationship between community assembly and niche-based processes has long been recognized and addressed with different approaches to explore how ecological factors (*e.g.*, abiotic factors such as climate, and biotic factors such as competing species) interact with the evolutionary processes of speciation, extinction, and dispersal to create biogeographic patterns (Ricklefs & Schluter 1993, Wiens *et al.*, 2006, Crouch & Tobias 2022, García-Porta et al., 2022). Here I used these complementary frameworks to analyze the relevance of such factors to the avian distribution patterns in the Mesoamerican lowlands.

This thesis aims to provide an integral framework to explain avian distributional patterns in a high-diversity region, where a semi-homogeneous landscape limits proposed causes of species diversification such as environmental heterogeneity (*e.g.*, altitudinal gradients) or conspicuous physical barriers. Hence, other factors are promoting and maintaining the avian diversity in the Mesoamerican tropical forests. Environmental changes through the Pleistocene affected ecosystem distribution and connectivity, and as a consequence the microevolutionary dynamics of populations and species, but also had effects at the macroevolutionary level by shifting immigration, extinction and speciation dynamics (Hewitt 1996, 2000, Weir et al., 2009). In Chapter 2, from an island biogeography approach implemented in DAISIE, I analyzed the assembly pattern of the passerine community of Yucatán Peninsula (YP) based on calibrated phylogenies. I found that the best model to explain the community assembly pattern is based on shifts in macroevolutionary dynamics around 300 ky before the present. In the historical context of YP, the Pleistocene climate shifts are thought to severely affect the biome distribution and metapopulation dynamics by creating routes to dispersal and isolating populations, and then promoting both population and species-based processes of differentiation, adaptation, speciation and extinction.

The putative effects of niche conservatism for species distributions in the geographic and ecological context of the lowland forests are analyzed in Chapter 3. Using as a study model a clade of the New World Jays (Family Corvidae), I found that environmental heterogeneity coupled with different population-based processes (*e.g.*, local adaptation) may be enough to maintain population differentiation despite the semi-continuous distribution of the lowland forests, which may explain some patterns of genetic and morphological differentiation in the clade *Psilorhinus-Calocitta*. Species range shifts affected population demographic dynamics (*e.g.*, bottlenecks or founder events) which are known to have implications for genome evolution due to adaptation or genetic drift and the consequent reduction in genetic diversity (Brandvain & Wright 2016, Wein & Dagan 2019). The geographic structure of the genetic variation may provide valuable information about microevolutionary processes such as gene flow, immigration or local adaptation. In Chapter 4, I discussed how these patterns of genetic structure may be linked to other axes of variation such as

physiological and phenotypic traits or mitochondrial variation. By analyzing variation patterns at these different axes in contact zones it is possible to obtain robust inferences on the population-based evolutionary process driving divergence and speciation, which, ultimately, are related to species niches, distributional patterns and biotic interactions within a community (*e.g.*, the passerine community of the YP).



**Figure 1.** Geographic distribution of some of the American biomes according to Dinerstein et al., 2017. Legend as in Fig. 2.

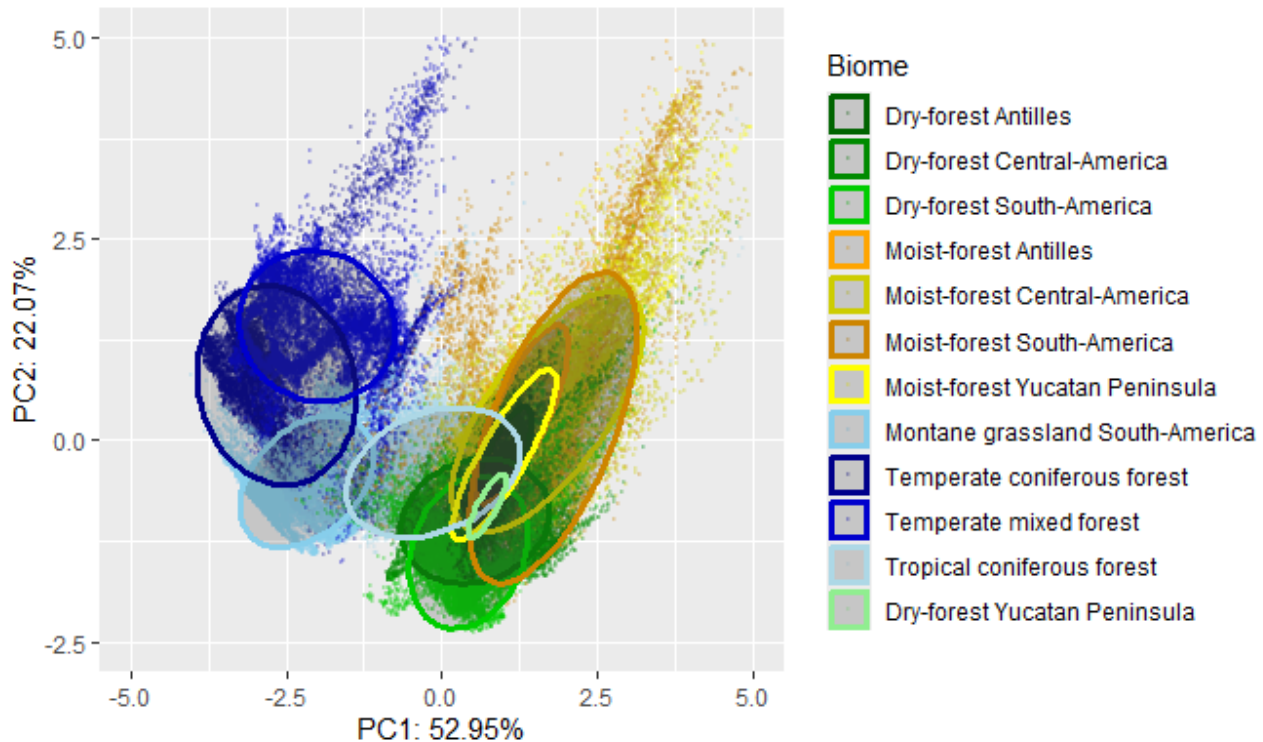
## **Environmental filters and macroevolutionary dynamics in the Mesoamerican Yucatán Peninsula**

Stochastic evolutionary processes (*i.e.*, speciation, extinction and immigration) rely to some degree on species' life history traits, which make them unequally likely to undergo such events. For example, some species may have intrinsic genome-based characteristics that drive expansion and radiation when ecological opportunities exist (*e.g.*, Darwin finches; Valente et al., 2015; Lamichhaney et al., 2018). Likewise, generalist species may show, larger distribution ranges or larger population sizes that make them less susceptible to extinction events, for example as a consequence of direct competition, environmental changes, loss of biotic interactions or loss of genetic diversity (Lynch et al., 1995, Colles et al., 2009). Moreover, immigration rates may be associated to life history traits such as feeding habits or dispersal capabilities, and to speciation rates (Kisel & Barraclough 2010, Smith et al., 2014, Crouch et al. 2019, Miller et al., 2021).

Community assembly theory states that species must pass several hierarchical filters to be part of a community: dispersal constraints determining the geographic species pool, environmental constraints setting the habitat species pool, and internal dynamics acting on the ecological species pool to form the actual species pool (Belya & Lancaster 1999; Booth & Swanton 2002). In the specific case of YP environmental restrictions seem to limit immigration of template-affinity species from geographically near regions such as the highlands of Oaxaca and Chiapas and Central America, mostly dominated by tropical coniferous forest (Fig. 1). By contrast, climate similarity between YP ecosystems (*i.e.*, seasonally dry tropical forest and the moist tropical rainforest) and other ecosystems of lowland regions geographically more distant in Central America or South America (Fig. 2) may facilitate the immigration of different species. The presence of exclusively Neotropical affinity species in YP suggests that geographic distance may be less of a constraint than ecological distance for bird species to immigrate given the historical context of the region.

However, the distribution of climates and ecosystems is dynamic and historical distribution patterns of Neotropical ecosystems are relevant to the understanding of the community assembly pattern on Yucatán Peninsula and its effects on micro- and macroevolutionary dynamics (*e.g.*, Licona-Vera et al 2014, Castillo-Chora et al., 2021b, Chan et al., 2024, Espinosa-Chávez et al., 2024). The YP avian community is in general mostly composed of species that have immigrated from Neotropical ecosystems and it hosts only few endemic species (Weir et al., 2009, Vázquez-Domínguez & Arita 2010). The cyclic formation of routes for dispersal and geographic and ecological barriers limiting gene flow affected immigration rates, and consequently the patterns of genetic and morphologic differentiation in populations. Some populations on YP show both morphological differentiation and different levels of genetic differentiation compared to conspecific populations distributed in other regions in Central America, South America or Western Mexico (Licona-Vera et al 2014, Castillo-Chora et al., 2021b, Chan et al., 2024, Espinosa-Chávez et al., 2024). Such variation across species may be related to species-specific responses because of vagility, feeding patterns and resource distribution (*e.g.*, plant parts, insects or vertebrates), and the intensity of climate effects on demographic size (*e.g.*, bottlenecks or founder events). Changes in abiotic factors could also lead to severe population size reduction resulting in only a small

fraction of the population surviving a selective event or enhancing the effects of genetic drift with great effects on differentiation and extinction (Brandvain & Wright 2016). Moreover, environmental change effects are associated with high extinction and immigration rates, as immigration is also related to both high inter- and intraspecific competence, likely resulting in high species turnover on YP over time. Because of such dynamics of high immigration and high extinction rates, few endemic species are expected.



**Figure 2.** PCA of climate conditions of some biomes of America. PCA values summarize six bioclimatic variables (same as in Chapter 2). Ellipses surround 80% of the points for each ecosystem.

### Functional traits and secondary sympatry and species coexistence

Constraints on species distributions are based to some extent on the inherent characteristic of species to retain and exhibit characteristics of common ancestry (*i.e.*, niche conservatism; Pagel 1999, Peterson et al., 2001). Niche conservatism is based on the high heritability of the traits that allow climate tolerances and biotic interactions, which strongly affect their ability to reach some geographical regions, perform well in determined environments and their probability to survive and reproduce (McGill et al., 2006, Crouch et al., 2019, Barrero et al., 2023). Niche shifts (*i.e.*, niche evolution and niche differentiation) are relevant for species to specialize to a particular environment, increase their distribution ranges or shift of suitable environments (Nosil 2012).

Internal dynamics in the assembly of communities are based on species' functional traits, which can allow or prevent a species from entering a community if they do not perform well in the local environmental conditions (McGill et al. 2006, Menegotto et al., 2019). Examples of functional traits include body mass, beak size, seed size, specific leaf area, wood density, and relative growth rate (McGill et al. 2006, Mittelbach & McGill 2019). This thesis does not explicitly focus on the effects of functional traits on organismal performance, but their relevance is clear because they are the physical characteristics that help organisms interact with the environment.

For birds, bill shape and feeding habits have been considered as indicators of adaptive responses to the environment because of their importance for different activities. In Neotropical resident birds of Central America diet has been suggested to be an important factor with great effects on population distribution patterns, genetic divergence to population and species levels, and in macroevolutionary processes (Smith et al., 2014, Miller et al., 2021). Birds whose diets rely on fruit, seeds, or nectar are known to vary in abundance seasonally and between years relative to birds that eat primarily insects (Boyle 2011). Likewise, species consuming plant products (*e.g.*, fruit, seeds and nectar) show significantly less mitochondrial divergence between allopatric populations than species consuming arthropods (Miller et al., 2021). The foraging stratum also has a significant effect on species diversity with the more dispersal-limited lineages restricted to the forest understory exhibiting significantly higher species diversity than the more dispersive canopy lineages (Burney & Brumfield 2009, Smith et al., 2014). In general, limited dispersal has been identified as an important driver of diversification in Neotropical lowland birds (Wiens et al., 2006, McCain 2009, McCain & Grytnes 2010, Crouch et al. 2019).

Species traits are not static, so the genetic bases and population dynamics underlying their changes may provide valuable information related to some niche-based processes such as adaptation to new environments. Both demographic and adaptive processes can promote genetic and morphological differentiation. Allopatrically distributed populations may diverge or speciate by effects of non-selective processes, and as a result, the two lineages separated by a short evolutionary distance may perform similar ecosystem functions and provide similar ecosystem services as a consequence of niche conservatism (Davies & Buckley 2011). By contrast, different selective pressures on genes whose alternate character states are each better adapted to a particular environment may result in processes of divergent selection or ecological speciation (Nosil & Schluter 2011, Nosil 2012). In such way, niche conservatism and niche divergence are highly relevant to explaining distributional ranges, secondary sympatry and species coexistence.

In the geographic and ecological context of the Mesoamerican lowland forests, alternate episodes of range contraction and range expansion have been proposed as a mechanism to explain the origin of diversity patterns. When neutral divergence in allopatry or broad parapatry does not lead to a sufficient niche separation, then coexistence will not be possible, and if secondary sympatry occurs species may face competitive exclusion (Haffer 1969, Chesson 2000, Barabás *et al.*, 2018). For example, local adaptation during isolation may promote that populations have different average fitness and the small environmental differences along the Mesoamerican lowland forests enhance the isolative effects of subtle environmental barriers (Chapter 3). This simple

mechanism seems to explain both genetic and morphological geographic distribution patterns, and could also explain why populations remain differentiated in the apparently continuous Mesoamerican lowland forests.

However, coexistence in sympatry is essential, because without it every speciation would lead to a subdivision of the existing range and species' ranges would become smaller over time (Payne & Polechová 2020). The geographic structure of the genetic variation suggests that recently diverged bird populations in the lowland forests maintain stretches of sympatric areas where secondary contact may occur (Castillo-Chora et al., 2021a, Sanchez-Gonzalez et al., 2022, 2023, Espinosa-Chávez et al., 2024). Several mechanisms can explain sympatry of closely related species or species with highly similar niche requirements. Spatial co-occurrence is influenced by environmental factors, such as food availability or habitat characteristics and by biotic associations, so species would maintain a stable sympatric coexistence sharing limited resources and partitioning their niches to reduce interspecific competition (Chesson 2000, Chase & Leibold 2003, Barrero et al., 2023). For example, temporally variable selection via environmental fluctuations can lead to stable coexistence of different competing systems under variable controlled temperatures (Descamps-Julien & Gonzalez 2005, Adler et al. 2006). This is because individuals could modify their foraging behavior in response to competition, for example, sympatric species could occupy different microhabitats as a consequence of character displacement (Albrecht & Gotelli 2001, Sanders & Gordon 2004, Sanders et al., 2007, Huang 2010, Colorado 2015).

In the genic view of speciation, the homogenizing effect of gene flow is reduced by diverging selective pressures between two adjacent environments. However, this force opposing genetic homogenization is not operating in sympatry as there is only one shared environment (Abbot 2013, Wu 2001, Wang et al., 2022). When differentiated populations have gene flow, introgression may introduce foreign variation into a population, which may have adaptative effects (*e.g.*, adaptative introgression) expressed in an increase in fitness to previously non-adapted environments (Rheindt & Edwards 2011, Hedrick 2013, Toews *et al.*, 2013, Ferreira et al., 2017, Burgarella et al., 2019). Given the historical context of the Mesoamerican lowland forests, recent climate events may have affected the distributions of the species (*e.g.*, range expansion), resulting in sympatry and secondary contact after allopatric differentiation (Sánchez-González et al., 2022, 2023, Espinosa-Chávez et al., 2024). For example, in the clade *Calocitta*, a gradient in throat plumage coloration between *C. colliei* and *C. formosa* suggests events of secondary contact and introgression (Pizarro et al., 2023). Likewise, secondary contact is inferred by the plumage coloration pattern in *P. morio*, with the brown morph distributed in Northeastern Mexico, the white morph in the Southeastern and the presence of a putative contact zone in between, characterized by the coexistence of the two morphs (Selander 1959). Plumage coloration is also related to geographic distribution, maybe because some phenotypes are better adapted to different environments. Polytypic species showing higher geographical ranges suggest that a higher range of phenotypic traits offers a higher opportunity to fit the biotic and abiotic conditions (Galeotti et al., 2003, Hugall & Stuart-Fox 2012, Flaxman *et al.*, 2014). However, polytypic bird species are

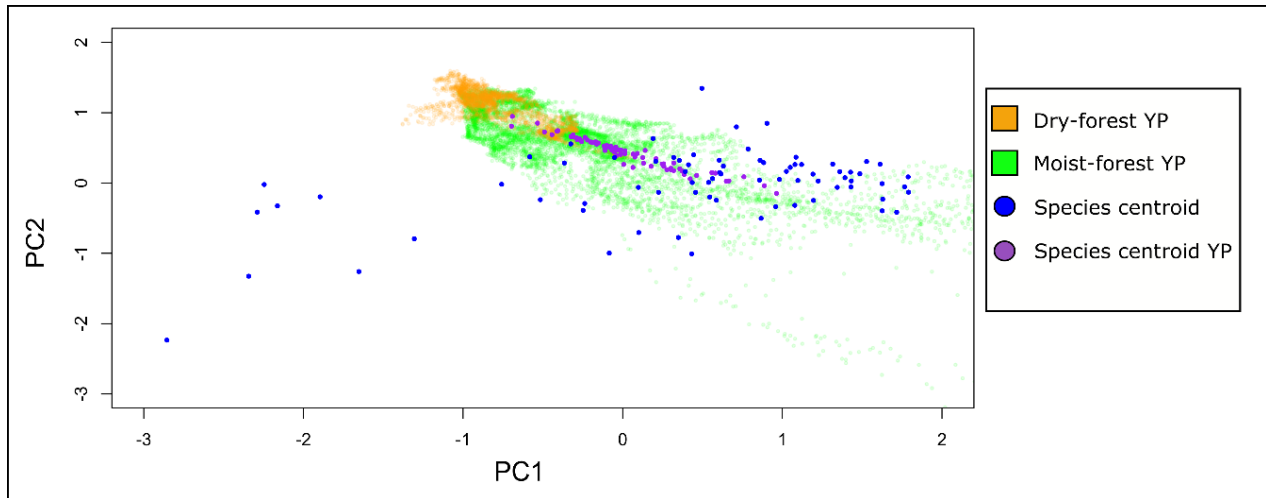


uncommon in nature (Galeotti *et al.*, 2003). One explanation for this pattern is a systemic loss of polymorphism in populations through the fixation of one form through selective or neutral processes and then reestablishing monomorphism (Hugall & Stuart-Fox 2012, Flaxman *et al.*, 2014). Plumage coloration patterns also play an important role in divergence and speciation, for example, because of the role of plumage coloration in the process of mate selection (Galleotti *et al.*, 2003, Galeotti & Rubolini 2004, Gray & McKinnon 2007). The origin and maintenance of coloration patterns could be associated with differences in habitats and different selective pressures, so in each isolated population a different phenotype is favored and fixed in the entire population, although stochastic fixation of a different coloration variant through genetic drift cannot be discarded (Feder *et al.*, 2013). Future investigation could focus on the genomic basis of the adaptation process and its effects on distributional patterns of the avian diversity of the tropical lowland forest (e.g., Ruegg *et al.*, 2018, Bay *et al.*, 2018, Aguirre-Liguori *et al.*, 2021).

### **Integration between climate constraints and macroevolutionary drivers of community assembly**

The island biogeography framework considers that stochasticity in evolutionary processes (*i.e.*, immigration, speciation and extinction) drive community composition without any consideration of species niches or species fitness (MacArthur & Wilson 1963, Chase & Myers 2011). However, as I discussed before, niche-based processes have a clear relationship to species to be able to immigrate, survive and reproduce to successfully form part of a community. The relationship between species' climate-based constraints and their distributional ranges may be expressed in the assembly pattern of communities (*e.g.*, Cortés-Ramírez *et al.*, 2019, Puga-Caballero *et al.*, 2022, Sánchez-Ramos *et al.*, 2022) and species distributions at large scales seem to be based, to some degree, on species tolerances to environmental conditions (Soberón & Peterson 2005, Rissler & Apodaca 2007, Soberón 2007).

A pragmatic way to estimate the climate constraints limiting species distribution is based on ordination approaches or environmental niche models (as in Chapter 3). According to such approaches, the fundamental niche is defined as the climate conditions that species can tolerate, whereas the fundamental realized niche is a part of the fundamental niche that species actually use (Qiao *et al.*, 2018). The niche centroid is represented by climate conditions that allow the better performance of species, so the populations closer to such conditions will show higher fitness. By contrast, populations distributed in geographical regions “further” from these suitable conditions will show lower fitness and smaller population growth rates (Yáñez-Arenas *et al.*, 2012, Osorio-Olvera *et al.*, 2019). The narrow climate conditions of YP may cause some populations to have a different realized niche than their conspecific populations in the rest of their distributional range (Fig. 3). In this way, it may be expected that species with shorter environmental distances between their fundamental niche and the predominant climate conditions in the invaded region (*e.g.*, Yucatán Peninsula) perform better than species with longer environmental distance. This may be expressed, for example, in earlier immigration times and lower extinction rates.



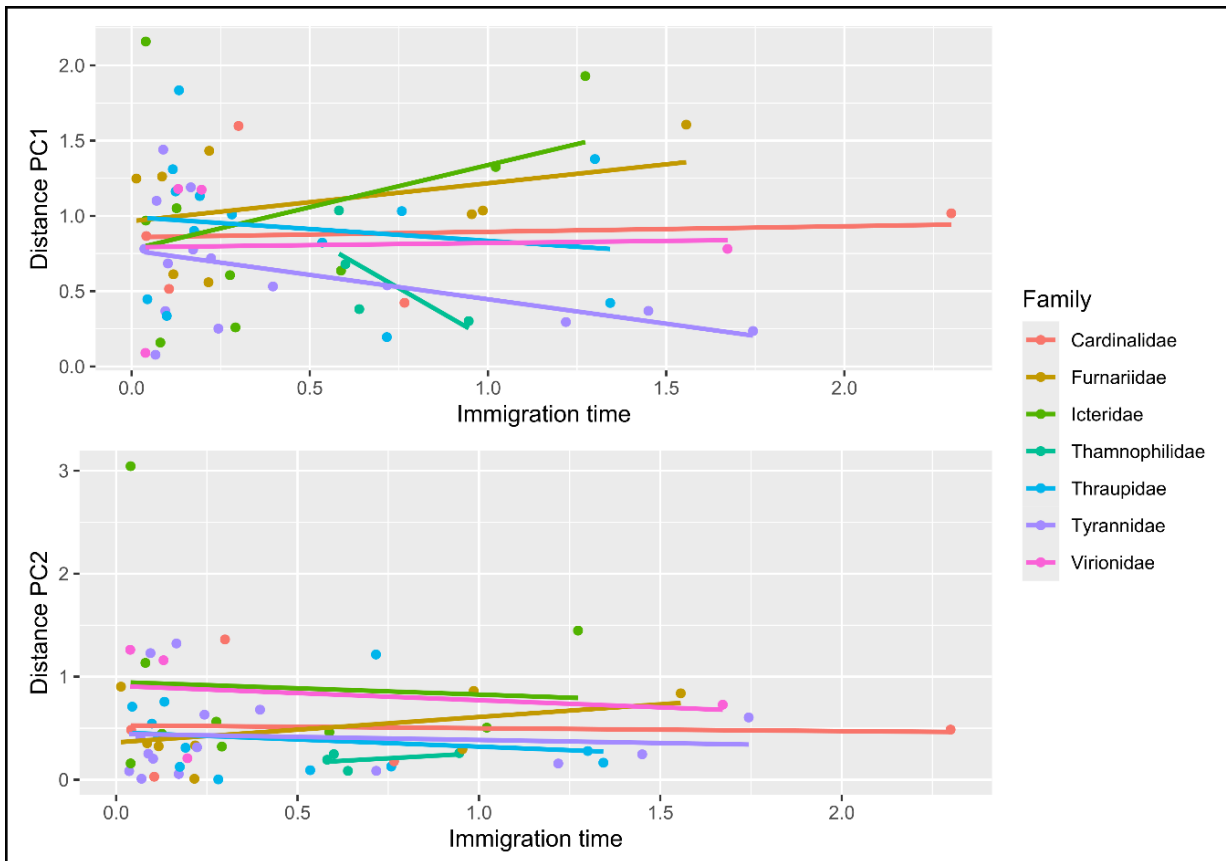
**Figure 3.** PCA summarizing the climate-based condition of YP, using the same bioclimate variables as in Chapter 3. PC1 is mainly associated to temperature variables and PC2 to precipitation variables. Purple circles represent the niche centroid of species in the YP, and blue circles represent the species centroid in the rest of their distributions.

I analyzed this hypothesis of species with fundamental niches closer to the environmental conditions of YP immigrating earlier for seven passerine families (with more than three species) that have immigration times dated using calibrated phylogenies (data from Chapter 2). I used the six bioclimate variables (as in Chapter 3) to define the environmental conditions of the species distribution in YP and in the rest of their distribution. I used data for each species from GBIF and for each species a bioinformatic cleaning was performed. This consisted in removing spatially aggregated records (Aiello-Lammens et al., 2015), and geographic and climate outliers (as in Chapter 3). Finally, I obtained two clean databases for each species, one for individuals distributed in YP and one for the rest of their distribution. Using these databases, I extracted the environmental values for each bioclimate variable for all records. With these extracted values, I performed a PCA analysis and calculated the Euclidean distances between the population realized niche in YP and the realized niche in the rest of their distribution for each species.

For most families, I did not find a correlation between ecological distance and immigration time (Fig. 4). An explanation for such a pattern is that the high extinction and colonization rates operating in YP dominate over any effect of the environmental filters. Another non-exclusive explanation is that climate filters are quite similar for most Neotropical species, and then stochasticity in arrival times, priority effects and biotic filters exert major pressures for community assembly. Stochastic factors in immigration may have different effects on community composition (Fukami 2015). For example, alternative community structures could arise if more than one invasion sequence is possible, and if early invaders are involved in interactions that promote or prevent the subsequent establishment of other species; that is, the order in which species arrive in

a locality can have lasting impacts on the diversity, composition and function of ecological communities (Belyea & Lancaster 1999, Chase 2003, Fukami 2015).

However, for the Tyrannidae family, I found for PC1 distances (aligned with temperature variables) a weak pattern of species with niche centroids closer to existing conditions of YP to immigrate earlier, whereas species with larger niche distances immigrated later. This pattern may be explained by low extinction rates in this family in YP (Tyrannidae species are characterized by having wide geographic ranges and high vagility), in addition to early colonizing species exerting strong interspecific competition, so only highly niche-differentiated species are more likely to immigrate later. By contrast, the Icteridae and Furnariidae families show the opposite pattern with species with larger niche distances immigrating before species with smaller niche distances. This may be explained by stochasticity in immigration and priority effects, for example, because after the first immigration event, then only better pre-adapted species were able to immigrate and coexist successfully or because of higher intraspecific competence compared to interspecific competence and high extinction rates.



**Figure 4.** Birds in YP do not show a clear correlation between species niche distance (between their range in the American continent and the conditions used in the Yucatán Peninsula) and immigration time. PC1 is mainly associated to temperature variables and PC2 to precipitation variables. Immigration time indicates the time between immigration and the present.

The flexibility of the DAISIE framework allows testing whether two species groups have different evolutionary dynamics. An easy way to integrate the DAISIE model with climate envelopes or ENM is by clustering species according to niche distances. Using the DAISIE Two-Type model one can test the relevance of such niche-based differences not just for immigration rates, but also for extinction and speciation rates, similar to what I did for testing different macroevolutionary dynamics for tropical dry-forest and moist-forest species and for Tyrannidae and Non-Tyrannidae species. Another way may be by weighting the different macroevolutionary events according to such environmental distance. For example, for each clade, species could be more or less likely to go through immigration, speciation or extinction depending on the climate distance between the invaded area and the current range area.

### **Conclusion**

Painting a unified picture that incorporates the most important processes driving species diversity and distribution is an exciting task in evolutionary biology. In this thesis, I made use of several specialized software and genetic and distributional available data to weave a link along different complementary axes of the study of Mesoamerican avian diversity. I moved from macroevolutionary drivers of community assembly in YP, to niche-based process and its effects on species and populations distributional patterns in the Mesoamerican lowland tropical forests, and a glance at the study and effects of the genetic basis on distributional patterns. I hope that the analysis and results provided here have increased our knowledge about such processes and may advance our understanding of both macroevolutionary dynamics and niche-based processes in avian diversity and their relationship to environmental factors.

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