Influence of phylogenetic structure and climate gradients on geographical variation in the morphology of Mexican flycatcher forests assemblages (Aves: Tyrannidae)

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Abstract

Morphological variation is strongly related to variation in the ecological characteristics and evolutionary history of each taxon. To explore how geographical variation in morphology is related to different climatic gradients and phylogenetic structure, we analyzed the variation of morphological traits (body size, bill, and wing) of 64 species of tyrant flycatchers (Tyrannidae) distributed in Mexico. We measured these morphological traits in specimens from biological collections and related them to the climatic and topographic data of each collection locality. We also calculated the phylogenetic structure of flycatcher assemblages of each locality in order to explore the influence of climatic variables and the phylogenetic structure ~~over~~ on the morphological variation of tyrant flycatchers, by means of linear mixed-effects models. We mapped the spatial distribution of the variation of morphological traits in relation to environmental gradients taking into account the phylogenetic structure. The climatic variables that better explained the morphological variation were those of temperature ranges (seasonality) and the results suggest that the phylogenetic clustering increases towards the highlands of Sierra Madre Oriental and Sierra Madre del Sur, and the lowlands of Balsas Depression. ~~At~~ For the regional assemblage, the spatial distribution of body size show~~s~~ed a pattern coincident with ~~the ecogeographical~~ Bergmann's rule, with ~~an~~ increasing~~e~~ in size from south to north. In the tropical lowland forests assemblage, body size tend to increase in seasonally dry forests (western Mexico) and decrease in the humid ones (eastern Mexico). ~~At~~ In the assemblage of highland forests and other types of vegetation, morphological trait values increased. Phylogenetic structure helped~~s~~ to explain the variation of morphology at ~~lower assemblages~~the assemblage level but not at the regional ~~assemblage~~level. The patterns of trait variation ~~along~~ in the lowland~~s~~ and highland~~s~~ assemblages~~,~~ suggest that parts of morphological variation ~~is~~ are explained ~~in~~ both by the

Kommentiert [CH1]: Confusing.
Maybe rephrase in either of these two ways, depending on what you mean:
1) the spatial variation of morphological…
2) the spatial variation of the relationship between morphological traits and environmental gradients, taking into account…

Kommentiert [CH2]: better than what?
Maybe rephrase like this
Important climatic variables explaining the morphological variation were those of temperature ranges (seasonality)…

Kommentiert [CH3]: You need to briefly mention that you do the analyses separately for different assemblages (1 regional, 2 habitat-specific).
In addition to that, the current terminology is quite confusing. Could it be a solution to redefine the levels of analysis as (1) the regional level and (2) the assemblage level, which are split into (2a) lowland forests and (2b) highland forests and other vegetation types?
I think this would make it much easier to follow - here and throughout the text.

Kommentiert [CH4]: …with…? / …compared to…?

Kommentiert [CH5]: Following my suggestion regarding the terminology (see above).

Kommentiert [CH6]: It's not clear to me what you mean with "along" here – maybe my edits helped to improve this; if not, please modify in a sensible way.

climatic gradients and by the lineage relatedness of communities. Overall, our results suggest that ~~M~~morphological variation is best explained by a varied set of variables, and that regression models representing this variation ~~and~~ as well as integrating phylogenetic patterns at different community levels provide a new understanding ~~into~~ of the mechanisms underlying the links ~~between~~ among biodiversity, its geographical setting, and ~~the~~ environmental change.

Introduction

A long-standing goal in ecology and evolutionary biology is to understand the relationships among morphological diversity, evolutionary history, environment and geographic distribution. Environmental drivers of morphological diversity across geography have been extensively studied in many regions with different taxonomic groups, at different geographic, taxonomic and functional scales (Losos & Miles, 1994; Cavender-Bares et al., 2009; Kluge & Kessler, 2011; Violle et al., 2014; Jarzyna et al., 2015; Jarzyna & Jetz, 2016; Lawing et al., 2017; Schneider et al., 2017; Seeholzer et al., 2017; Phillips et al. 2018; Mazel et al., 2018). As a result of previous studies that analyze the role of environment and geography as promoters of morphological diversity, patterns of gradual variation of traits have been detected for many groups. Climate seems to be one of the main environmental promoters of morphological variation, strongly influencing the distribution and variation of morphological traits across species and regions (e.g. James, 1970; Graves, 1991; Kivelä et al., 2011; Maestri et al., 2016; Xu et al., 2017). However, the role of climate and other environmental variables is poorly understood. Even though many studies have demonstrated its associations with morphological traits, the question remains to what extent and by which mechanisms such associations are maintained and may influence

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distribution patterns (Violle et al., 2014). It has been suggested that several variables may act simultaneously, promoting morphological variation at many taxonomic and geographic scales.

Morphological diversity across species is driven by several ecological and evolutionary processes and is usually studied as the evolution of form and function, or ecomorphology (Losos & Miles, 1994; Ricklefs, 2012; Dehling et al. 2014; Seeholzer et al. 2017; Phillips et al. 2018). Also, variation in morphological diversity within communities can have effects in structuring broad-scale biogeographical patterns of species richness along climatic and geographical gradients (Deutsch et al., 2008; Cicero & Koo, 2012). Morphological variation is related to ecology and reflects a response to biotic and abiotic environmental factors, and it may determine species' responses to climate change (Wainwright and Reilly, 1994; Pontarotti, 2010; Cicero & Koo, 2012). Climatic variables, such as temperature and precipitation, are recognized as major factors determining geographical patterns of morphological variation (Hawkins et al., 2007). For instance, bill size increases with higher temperatures, supporting the hypothesis that larger bills are an adaptation to release heat while minimizing evaporative water loss in hot, dry environments (Greenberg et al., 2012). In this way, overall bill size may be related to physiological responses to regional climates, and the season of critical thermal stress may vary geographically, even on relatively small spatial scales (Campbell-Tennant, Gardner & Kearney, 2015; Danner and Greenberg, 2015).

Other factors such as evolutionary history also have been found to determine geographical gradients in species variation (Jetz & Rahbek, 2002, Kissling et al., 2007). For instance, habitat filtering is an ecological process by which species are eliminated from a community because of morphological or ecological similarity with other established members of the community (Wainwright and Reilly, 1994). Under this interpretation, the variation of morphological

Kommentiert [CH8]: I suggest starting a new paragraph here variables across communities and geography is proportional to the amount of phylogenetic dissimilarity among communities (Pillar and Duarte 2010), taking into account that morphology is structured by phylogeny at the species level if there is phylogenetic signal. Morphological variation occurs within and across species, so the complex interaction of evolutionary history and environment makes it difficult to identify the underlying causes of broad scale patterns of variation (Endler, 1977; Ricklefs & Miles, 1994; Violle et al., 2014; Forister et al., 2015).

The recognition of the promoters of broad scale patterns of morphological variation is challenging due to the differential response of organisms' traits to environmental variation and geographical settings (Violle et al. 2014). This limits our ability to elucidate the causes and consequences of the patterns of species’ morphological diversity. For instance, the geographical patterns of community structure and morphological variation in response to climatic gradients has shown contrasting effects of the same environmental variables (e.g. Forister et al., 2015; van de Pol et al., 2016; Lawing et al., 2017). To understand how morphological diversity arises, it is necessary to explore and quantify how species’ morphological traits are related to their ecology, how they vary geographically along environmental gradients, consider both large and small spatial scales in the same region, and account for the historical contingencies limiting the distribution of species assemblages and their traits (Cavender-Bares et al., 2009). In this sense, phylogenetic structure and distributional data provide the historical framework to quantify ecological, geographical and evolutionary patterns, in order to infer the processes that established them (Saito et al. 2016; Sobral & Cianciaruso 2016, Phillips 2018). Also, quantifying the geographical distribution of morphological variation may help disentangle trade-offs found in the relationship between morphology and environmental and phylogenetic variables. Then, analyses of the distribution of morphological variation are necessary for improving regional and global predictions of morphological and functional change (Diniz-Filho, 2004; Rodríguez & Ojeda, 2014).

To evaluate broad scale patterns of morphological variation and the underlying processes which promote them, it is necessary to quantify the distribution of morphological traits in relation to the ecology of related functional groups of species. In that sense, some authors have found that the global patterns of functional richness are associated with environmental variables (Kissling et al., 2009; Brum et al., 2012). To describe how morphology varies geographically with environment, we explored the spatial distribution of a set of morphological variables in relation to climatic gradients of a mainly insectivorous assemblage of birds, the tyrant flycatchers (Tyrannidae). The tyrant flycatchers constitute a functional group of species that use insects and arthropods as their main food resource (Hespenheide 1971; Sherry 1984). This taxon includes more than 400 species distributed across the Americas (IOU, 2018) occurring in almost every habitat. They are adapted to different elevations and occupy all vertical forest strata (Fitzpatrick et al., 2004, Ridgely and Tudor, 2009). We chose the Tyrannidae of Mexico as a model system because: (1) they are widely distributed in the country (Ridgely et al., 2005; Berlanga et al., 2008); (2) the natural history, phylogenetic structure, and functional significance of their morphological traits is relatively well known (Ohlson, Fjeldså & Ericson, 2008; Tello et al., 2009); (3) their morphology can be related to their ecology (e. g., Fitzpatrick 1980, 1981, 1985); and (4) their morphology varies across environmental and geographical gradients (Brum et al., 2012).

Our main goal was to investigate the variation of morphology across geography and to determine the relationship of environmental climatic gradients as explanatory factors of morphological function-related traits. We have considered the phylogenetic structure of Mexican flycatchers as a factor that may help to explain how broad scale patterns in species variation are established and how historical contingencies influence the response of morphological variation to the environment. Our specific objectives were to test (1) whether climate conditions (temperature, precipitation, and their seasonality), are associated with the observed variation in morphology across tyrant flycatchers assemblages; (2) the influence of the phylogenetic structure of assemblages on the geographic distribution of morphological variation and its response to climate; and (3) to map the spatial distribution of morphological variation along climatic gradients. Because traits are related to the ecology of the organism, for instance foraging behavior or habitat use (Fitzpatrick, 1985), morphological variation is expected to reflect species' responses to environmental gradients. Then, the approach we used takes into account varied ranges in climate and seasonality within a lineage, abiotic variables influencing the geographic distribution of species, and the phylogenetic relationships among the tyrant flycatchers. Taking into account phylogenetic relationships within a community by accounting for phylogenetic structuring~~,~~ may help to understand the influence of the composition of a community on the response of traits to environmental variation (Bonetti & Wiens, 2014; Maestri et al., 2016).

Hypothesis and assumptions

Given that climatic gradients and phylogenetic structure of an area potentially play a role as promoters or constrainers of morphological variation, and because this role may vary in strength and direction, we analyzed the morphological data by constructing regression models in order to explain the relationship between morphology, environment and phylogenetic structure. We hypothesized that, once historical and geographic factors are accounted for: Hypothesis 1) climate gradients explain morphological change across geography; and hypothesis 2) phylogenetic structure of a community ~~should~~ influence morphological variation of the co-occurring species. To support~~For~~ hypothesis 1, ~~we assumed that~~ morphology ~~would~~ should show

Kommentiert [CH9]: To be concordant with hyp 1, you should delete "should" here. Or add it in hyp 1 clinal variation related to one or more climatic variables, ~~then~~ and a latitudinal pattern when the model is translated into a map. Conversely, to support ~~for~~ hypothesis 2, we would expect that ~~we assumed that~~ morphological change cannot solely be explained by climatic variables, but that ~~also~~ phylogenetic structure ~~would~~ is also ~~be~~ significantly associated to variation in morphology ~~(evidence for hypothesis 2)~~. Latitudinal variation in morphology is likely to be affected by the phylogenetic composition of the area, that is, the variation of morphological traits across geography is expected to be proportional to the amount of phylogenetic dissimilarity among communities (Duarte, 2011). Phylogenetically clustered areas are expected to show different patterns of morphological variation than areas that are phylogenetically overdispersed. Because of the tendency of species to remain in an environmental space similar to that of their ancestors (Wiens & Graham, 2005) we expect that morphological variation within assemblages will be constrained. Phy~~l~~logenetically clustered assemblages are more likely to be restricted in their climatic ranges, whereas phy~~l~~logenetically overdispersed assemblages are more likely to be found in the transition zones where there is a high species turnover (Graham et al., 2009) s~~e~~pecies competition influences the local trait composition of a community (Wainwright~~h~~ & Reilly, 1994). Phylogenetic structure alone is unlikely to explain the variation of morphology; instead it is expected to influence morphology along with climatic variables, meaning that the response of the trait could be driven by either environmental filtering (species are filtered from a community due to morphological or ecological similarity with other co-occurring species), other biotic interactions (e.g. competition), or random factors (Cavender-Bares et al., 2009; Lawing et al., 2017).

Kommentiert [CH10]: Not sure where this belongs – do you want it to be a new sentence or be connected to the previous one?

Kommentiert [CH11]: This section should be moved in front of the specific hypotheses and predictions.

METHODS

Morphological traits data and data treatment

Morphological data. In order to construct regression models of environmentally-related morphological variation, the morphological traits were associated to locality-specific climate, topographic and phylogenetic structure data. We obtained morphological data from a sample of 296 skin specimens from 60 species of Tyrannidae distributed in Mexico (Table S1). We measured five traits (Claramunt, 2010, following recommendations by Eck et al., 2011): body size (using mass data as a proxy), bill length, bill width, and bill depth (the last two taken at the anterior border of the nostrils), and wing chord (wing length from the carpal joint to the tip of the longest primary feather without flattening the wing). We selected these traits because they have been associated use of environmental space in birds (Miles & Ricklefs, 1984). Size is a significant attribute at all levels of organization, as it predicts and explains the variation of many organismal and species traits, from the proportion of parts to metabolic rates to the distribution patterns (Schmidt-Nielsen, 1975; Brown, 1995; Diniz-Filho, 2004; Bonner, 2011). Bill size can be positively correlated with temperature in avian taxa (Allen's rule), and the common explanation for this pattern is that larger surface area of the appendage functions to dissipate excess heat in warm climates and small area to retain heat in cold climates (Symonds & Tattersall, 2010; Greenberg, 2012). The bill is also the functional trait by which birds obtain food, so it can be related to habitat and ecomorphological variation (Mazer & Wheelwright, 1993; Jones; 2012). The relative variation of bill measures represents its variation in size and shape. Finally, wing chord plays a role in determining the aerodynamics and mechanical aspects of the avian wing, thus it interacts with the effective exploitation of habitat; so it is strongly related with ecology and behavior (Hamilton, 1961; Lockwood, 1998, Swaddle & Lockwood, 1998, Gatesy & Dial; 1996). Together, body size, bill size and wing chord represent morphological traits that are related to the flycatcher ecology.

In general, we only measured adult male specimens to homogenize the data set and to avoid morphological variations associated with sexual dimorphism. In some cases, we had to measure female specimens (~8% specimens) to complete the sample, and used these data based on a previous test (Cortés-Ramírez, Ríos-Muñoz & Navarro-Sigüenza, 2012) that showed that the variation between sexes is smaller than interspecific variation (*sensu* Claramunt, 2010). We took all the measurements with digital or analog Mitutoyo calipers, with a precision of 0.01 mm. For statistical analysis we used *natural log*-transformed measures in order to normalize the dataset, and because all morphological measurements may scale with overall body size, we made bill and wing size measurements relative to body size by dividing each measurement by body mass. Relative variation of the three bill measurements was obtained by performing a principal component analysis (PCA) to reduce the dimensionality of bill variation (Table S2), retaining the first principal component as representative of bill variation and size. The first principal component represented 86% of bill variation and overall size of the bill. Each morphological variable was evaluated independently from the other variables.

Environmental and geographic data.

Climatic variables. We considered the geographic location of each specimen to obtain locality-specific climate data based on a set of 19 bioclimatic variables (Hijmans et al., 2005). To reduce the dimensionality without eliminating bioclimatic variables, we constructed four climatic indexes by applying a PCA on climatic variables following Alvarado-Cárdenas et al. (2013, Table 1). These four indexes represent annual temperature variation, temperature range or seasonality, variation of precipitation in the most humid season, and variation of precipitation in the driest season. We decided to use the first principal component of each climatic index, as they account for most of the climatic variation in the study area (Table S3). For each specimen we extracted locality-specific climate index data using a geographic information system. We used the climatic index data for each individual as a fixed explanatory variable in the regression models.

Topographic variables. In order to separate the effects of the geographical setting, we used the USGS Digital Elevation Model (altitude, USGS, 2015, https://lta.cr.usgs.gov/GTOPO30) and aspect as predictor variables in all regression models. To facilitate the use of aspect as a variable that describes topographic orientation, we transformed it using the cosine to express northness and the sine for eastness following Kobelkowsky-Vidrio, Ríos-Muñoz, & Navarro-Sigüenza (2014).

Historical distribution and relatedness data

Assemblages of the tyrant flycatchers. In order to discriminate the effects of the evolutionary/historical distributional of the tyrant flycatchers, we divided the data into three separate sets taking into account characteristics of three constructed assemblages of tyrant flycatchers distributed across Mexico. We defined an assemblage as a temporal and spatial arrangement in which species potentially occur and interact; i.e., the pool of species in a geographic area (Halffter & Moreno, 2005, Lessard et al., 2016). We defined three assemblages on the basis of environmental factors delimited by elevation and vegetation type (Fig. 1, Table S1): Type I- Assemblage of the lowland forests (species distributed only below 1500 m), Type II- Assemblage of the highland forests (species present mainly above 1500 masl) and other types of vegetation, and the Regional assemblage (species distributed in both assemblages, which represent the species distributed in all Mexico). We assigned the species to each assemblage and carried out statistical analysis independently for each data set. We focused on the type I assemblage data because Mexican lowland forests are characterized by high levels of species

Kommentiert [CH12]: Not clear. Maybe “evolutionary and distribution history”?

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I suggest to talk about a regional and an assemblage level – the latter could be specified as “assemblage I” and “assemblage II” instead of “type I” and “type II”, which would make it simpler.

richness, endemism, and habitat specialization, and patterns of biogeographic distribution define them as areas with a particular evolutionary history (Ríos-Muñoz & Navarro-Sigüenza, 2012; Olguín-Monroy et al., 2013). The Type II and Regional assemblage datasets were used to contrast the response of morphological variation to environmental gradients at different spatial scales and community levels. It is known that the influence of different variables on the morphological variation change at different scales of analysis (Lawing et al., 2017).

Phylogenetic signal and phylogenetic structure. We reconstructed a phylogenetic tree for the species of Tyrannidae distributed in Mexico using Jetz et al.'s (2012) bird tree with the Hackett et al. (2008) backbone (Fig. S1), in order to calculate the phylogenetic signal of traits and the phylogenetic structure of the localities. The phylogenetic signal was calculated for each morphological variable using the generalized K statistics (Adams, 2014). Phylogenetic signal indicates the tendency of related species to resemble each other more than species drawn at random from the same tree (Blomberg & Garland, 2002). Generalized K statistics tests a null model of evolution of a trait by Brownian motion (drawn at random from the tree), $K = 1$ indicates that trait evolution is consistent with Brownian motion model, while $K<1$ indicates less similarity in the trait than expected under Brownian motion model, and $K>1$ indicates greater similarity in the trait than expected under Brownian motion model (Blomberg et al., 2003). Phylogenetic signal tests were conducted using the *geomorph* package (Adams & Otarola-Castillo, 2013) in R version 3.4.1 (R Core Team, 2017).

To determine if the species in a particular area were more closely related than expected by chance, we measured the phylogenetic structure of the Tyrannidae distributed at each locality. To calculate the metric, we used the Net Relatedness Index (NRI, Webb et al., 2002) in the R-package *PhyloMeasures* (Tsirogiannis & Sandel, 2016). Values of NRI greater than zero indicate phylogenetic clustering and values lower than zero indicate phylogenetic evenness or overdispersion. Phylogenetic clustering is found when the co-occurring species of an area are more closely related than expected by chance. Phylogenetic evenness or overdispersion is found when the coexisting species of an area are less related than expected by chance (Webb et al., 2002). To calculate the NRI for each locality, we used the reconstructed phylogenetic hypothesis and we established which species likely co-occur by extracting presence data from distributional hypotheses for Mexican Tyrannidae, generated elsewhere using ecological niche models (Navarro-Sigüenza et al., unpubl. data).

Statistical analyses

The regression models

We evaluated the effects of environmental gradients and phylogenetic structure on morphological variation in the tyrant flycatchers of Mexico using regression models. We constructed trait maps (see below) and obtained our inferences based on the fitting of linear mixed-effects models predicting morphological variation in body size, bill and wing length. We used linear mixed-effects modeling because our data are nested in the sense that samples derive from multiple species, and from each species we have various specimens.

To find the best fitting models for each morphological variable (and assemblage dataset), we followed the protocol recommended by Zuur et al. (2009). In the first step, we started with a model for each morphological variable that contained all the predictor variables and their interaction in the fixed part of the model. There are seven fixed predictor variables (temperature variation index, temperature range or seasonality index, variation of precipitation in humid season, variation of precipitation in the dry season, topographic setting, altitude, and phylogenetic structure) and four interactions (relationships between altitude and the temperature and precipitation indexes, Table 2, Table S4 model 1). After obtaining the more complex linear model, we made a new model allowing random intercepts for the nested structure of individuals of a species within a subfamily (Table 2, Table S4 model 2). The random intercept implies that the basal value of the response is influenced by the nested structure of the data, so measures within a species are more likely to be correlated just because they belong to the same phylogenetic group (Militino et al., 2010). Next, we allowed random slopes and intercepts for individuals of a species within a subfamily (random intercept), influenced by the phylogenetic structure of the communities (random slope, Table 2, Table S4 model 3). Letting the slope to change implies that morphological traits can change between communities in function of how closely related are the species distributed on it. Then, we included the optimal variance structure to the optimal model for the random terms (Table 2, Table S4 model 4). We considered that different variance exist for the observations that have distinct phylogenetic membership. Next, we selected the best fitting model structure for the fixed terms by sequentially adding each predictor variable and their interactions (Table 2) to the optimal random and variance structure model (Table S4 models 5-16). We tested if phylogenetic structure influenced morphological variation (Evidence for hypothesis 2, Table S4 model 12) by including it to the best fitting model for the fixed terms. Finally, we included the interaction term between phylogenetic structure and the climatic variables that best explained the morphological variation (temperature seasonality, model 17). The interaction between phylogenetic structure and temperature seasonality implies that phylogenetic structure modifies the effect of temperature seasonality on the morphological variation within assemblages. The final products of the procedure described were nine best fitting models predicting each morphological variable, at each assemblage, in relation to climatic variables, phylogenetic structure and phylogenetic membership (Table S4, Table 3). We considered the best-fitting model for each variable the one with the highest maximum likelihood

(ML), the Akaike information criterion (AIC), and Bayesian informative criterion (BIC, Burnham & Anderson, 2002). We performed all statistical analyses using the *nlme* (Pinheiro et al., 2013) package in R version 3.4.1 (R Core Team, 2017).

Mapping the spatial variation of morphological traits

To map the spatial variation of the morphological traits, we extrapolated the best-fitting models into GIS layers. First, we extracted the value of the predictor climatic variable in each pixel (30 seconds ~~per side~~resolution) of Mexico within each assemblage. Then, we translated the best-fitting model formula for the climatic index value at each pixel. For instance, if the model was: "*Size expected at pixel X = slope*value of climatic index at pixel X + intercept*", we obtained a different value for the morphological variable at each pixel according to the model and the variation of the predictor variable, generating a map of the measurements of the functional traits (Moles et al., 2011). We performed all analyses using the Maptools (Lewin et al., 2011) package in R version 3.4.1 (R Core Team, 2017). Trait maps were visualized using ArcGIS 10 (ESRI, 2011).

RESULTS

Relationship between climatic gradients and morphological variation

Climatic gradients were positively associated ~~positively~~ with morphological variation of the three measured traits in all three assemblages (Table 3). All best fitting models included at least one climate variable among the fixed terms, specifically, temperature seasonality (temperature range) or mean variation. Temperature appeareds~~s~~ to explain variation in morphology at all levels analyzed. At the regional assemblage, for body size, bill and wing length, temperature ~~is~~ was related positively and significantly to morphological change, ~~and~~ which reflects an increase in the

Kommentiert [CH14]: Confusing term which does not appear before or in Table S3.
Either explain or remove.

Kommentiert [CH15]: See above: Replace by "regional level"?

Kommentiert [CH16]: Please carefully correct the tense of the results throughout. Results should be reported in past tense, interpretation in present tense.

morphological variable~~s~~ values as temperature seasonality increases. The magnitude of the response is higher for body and bill sizes (slopes 0.42 and 0.65, respectively), whereas for wing length it is close to zero (slope = 0.091); that means that although it is positive and reflects an increase in the morphological variable values, this change is small. In other words, ~~while the climatic seasonality increases,~~ wing length ~~will~~ does not ~~tend to~~ increase as much as body and bill size with increasing climatic seasonality, ~~it~~which reflects a poor association between wing length and temperature range index.

For type I and type II assemblages, the relationship between morphological variables and temperature range ~~is~~ was also positive but not significant for some variables (*p-value*>0.05). For instance, the regression models for bill size and temperature range, and wing length and temperature range, ~~in~~ for ~~the~~ assemblage II (highland forests and other types of vegetation) ~~assemblage~~ indicates that the relationship is not significantly different from 0 (there is no relationship between the morphological variable and temperature range). ~~Also, f~~For assemblage I ~~the~~ (lowland forests~~) assemblage~~, ~~regression model for~~the relationship between wing and temperature range ~~is~~ was not significant either. Only the relationship between body size and temperature range ~~is~~ was significantly positive in all assemblages. The relationship between bill variation and temperature range ~~is~~ was significant in ~~lowland forests~~ assemblage I, but the magnitude of the response was~~is~~ less steep (slope=0.43).

Influence of phylogenetic structure on morphological variation

Linear mixed-effects model~~s~~ results indicate~~d~~ that phylogenetic relatedness also helped to explain morphological variation in type I and type II assemblages, for body size, bill and wing variables (Table 3). ~~At~~ In assemblage II (highland forests and other types of vegetation) ~~assemblage~~, models for bill and wing were not significant (*p-value*>0.05), whereas the model for body size ~~is~~

Kommentiert [CH17]: I find this obvious, so it could be deleted.

Kommentiert [CH18]: Not needed, either.

Kommentiert [CH19]: See above

Kommentiert [CH20]: Try to be more consistent with the climatic variable terminology. You defined "temperature seasonality" as "temperature range" further above (line 354). After that, you should stick to "temperature seasonality".

Kommentiert [CH21]: See suggestion above

Kommentiert [CH22]: Simplify: "there is no significant relationship between…"

Kommentiert [CH23]: If you add ", either" in the end, you don't need "also" here.

Kommentiert [CH24]: wing length? Or, more general, wing characteristics?

Kommentiert [CH25]: Less steep than… ?

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Kommentiert [CH27]: Can be deleted

was significant and positively related to phylogenetic structure (slope= 0.60). A positive correlation between body size and phylogenetic structure means that body size values increase ~~at~~ in areas ~~with~~ where more phylogenetically related species co-occur~~ring~~ ~~at the community~~ (phylogenetic clustering), and decreases in areas with less phylogenetically related species (phylogenetic overdispersion). For assemblage I (lowland forests), phylogenetic structure was positively correlated ~~to~~ with bill variation, and negatively ~~correlated to~~with bo~~s~~dy size. The relationship between wing and phylogenetic structure was not significant. The results indicate that there is a tendency of decreasing~~e in~~ body size ~~while~~ when communities bec~~a~~ome more phylogenetically clustered.

Our results indicate that phylogenetic structure exhibits a geographical pattern (Fig. 2). Both ~~highland and lowland forests~~ assemblages ~~presented~~ comprised areas with phylogenetic overdispersion and phylogenetic clustering (Table S5). Areas of higher phylogenetic clustering appeared to be distributed along the lowland areas of the Balsas Depression, and the highlands of Sierra Madre del Sur (mountain range in the southern Mexico) and Sierra Madre Oriental (mountain range in eastern Mexico). Areas with high phylogenetic overdispersion are mainly distributed in southeastern Mexico (i.e. southeastern Yucatan Peninsula, Tehuantepec Isthmus).

We also measured the phylogenetic signal of the morphological traits, ~~in order to explore the tendency of the traits to resemble each other taking into account phylogenetic relatedness.~~ ~~Phylogenetic signal analysis~~ which returned ~~a~~ values of K = 0.85 for body size, K = 0.88 for bill variation, and K = 0. 87 for wing chord. All values were statistically significant at α = 0.05. These values indicate that although the phylogenetic signal for each morphological variable at the species level is lower than 1, values are close to a Brownian motion model (no tendency of traits to resemble each other due to phylogenetic relatedness), which means that they are slightly less similar than expected due to phylogenetic relatedness.

Kommentiert [CH28]: Specify: more species or species that are more closely related or both?

Kommentiert [CH29]: See above: less related or fewer species?

Kommentiert [CH30]: Was explained in the methods section, so could be deleted here.

Kommentiert [CH31]: See above: wing length? Characteristics?...

Kommentiert [CH32]: This is confusing – maybe just delete.

Spatial variation of morphological traits in relation to environmental gradients

Overall, trait variation was explained by temperature gradients and phylogenetic structure at assemblages other than the regional level. Mapping the predictions of the best fitting models (Table 3) yielded different patterns of spatial distribution for morphological variation (Figures 3-5), across the geography at different scales. Maps represent the gradient of change of the morphological traits with respect to the environmental variable that better explain their variation. We only mapped the statistically significant models. At the regional assemblage (Fig. 3), for the three morphological variables, morphological trait values increased with increasing latitude. Phylogenetic structure does not help to explain morphological variation in the regional assemblage. Lowland forests assemblage showed a morphological trait variation from northeast to southwest (Fig. 4), in which body size and bill size increases towards the southwest. In the lowland forests assemblage, bill size increases with increasing phylogenetic structure. Conversely, body size increases in areas with low phylogenetic structure (overdispersion) and decreases in areas with phylogenetically clustereingd (Fig. 2A). Geographically, thisat means that phylogenetic structure decreases body size in areas where temperature gradients predict an increase in body size, and it increases in body size where temperature gradients predict a decrease. For the type II assemblage (Fig. 5), we mapped body size and bill variation, which are explained by temperature seasonality. Increases in body size and bill variation were predicted in areas of higher phylogenetic clustering and in southwestern Mexico (Fig. 2B).

Kommentiert [CH33]: See above

Kommentiert [CH34]: Better than… ?

Kommentiert [CH35]: See above

Kommentiert [CH36]: Unspecific term. Maybe better: phylogenetic relatedness

Kommentiert [CH37]: See above: relatedness ?

Kommentiert [CH38]: See above: please modify/s

Kommentiert [CH39]: See above

DISCUSSION

Our results suggest that both climatic variables and phylogenetic structure influence the morphological variation of Mexican tyrants, but the influence of the phylogenetic structure varies between different assemblages and morphological traits. When we focused on how climatic gradients explain the variation in morphology, our results suggest that temperature seasonality is the most influential climatic variable, but the magnitude of the influence varies across different assemblages. This variable assumedly represents tolerance limits of species to variation in temperature, likely influencing morphological variation through maintaining habitat use through time (Wiens & Graham, 2005). Our results showed a latitudinal pattern that is consistent with ~~the~~ Bergmann's rule for birds: as temperature increases, body mass is likely to decrease (McNab, 1971). This is a common finding in many studies, because the total surface area of an animal is a proxy for heat dissipation, and predicts that a larger size can be reached in colder climates than in warmer ones, which is linked to the temperature economy of the animal (Salewski and Watt, 2017). Due to the distribution of temperature at the regional assemblage, the latitudinal pattern is likely to show an increase in body size from south to north (Fig. 3), but some studies found exceptions ~~at another~~in other regions (e.g. James, 1970).

Patterns of morphological variation in western Mexico type I and II assemblages showed a pattern in which the tendency to increase in size was predicted in direction to both highlands and lowlands of western Mexico (Fig. 4 and Fig. 5), which also contain areas with the highest values of phylogenetic structure. A larger body size in less vegetated or highly seasonal areas may be an adaptation to live in these types of isolated environments, and higher phylogenetic structuring agrees with the fact that western areas have been identified as a complex biogeographical and ecological setting in which a highly endemic and phylogeographically structured bird fauna occurs (e.g. García-Trejo & Navarro-Sigüenza, 2004; Navarro-Sigüenza et al., 2004; Ríos-Muñoz & Navarro-Sigüenza, 2012; Arbeláez-Cortés et al., 2014). For~~-~~ patterns of morphological variation in the eastern lowlands, like the phylogenetically overdispersed Yucatan Peninsula or the Tehuantepec Isthmus, relatively constant (i.e., less seasonal) temperatures in the

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Kommentiert [CH41]: Or "different"?

Kommentiert [CH42]: See above

Kommentiert [CH43]: Do you mean body size?

Kommentiert [CH44]: Very complicated phrasing, with redundancies ("patterns showed a pattern") and confusing terminologies (highlands and lowlands refer to type I and II assemblages, right?)

Kommentiert [CH45]: See above: "structure" is a general, unspecific term. Please specifiy – highest signal or relatedness or other phylogenetic structure characteristics. – I have indicated this in a few places, but please specify throughout the manuscript!

east~~,~~ may have influenced the distribution of lineages and the variation of ~~its~~ their morphological traits, and consequently the particular phylogenetic community structure in those regions (Martin et al., 2018).

The results of several studies support the idea that environmental gradients influence the phylogenetic structure of the communities and therefore, phylogenetic clustering increases with decreasing temperature, meaning that closely related species tend to have a strong phylogenetic signal, and more similar traits and geographic distributions than expected by chance (Helmus et al., 2007; Donoghue, 2008; Graham et al., 2009; Flynn et al., 2011; Tedersoo et al., 2012; Miller et al., 2013). For instance, Miller et al. (2013) found that the tendency of species to remain in an environmental space similar to that of their ancestors (niche conservatism, Wiens & Graham, 2005) constrains honeyeater assemblages in arid regions, along a gradient of decreasing precipitation. Instead, we found that tyrant's assemblages became more phylogenetically clustered along a gradient of increasing temperature seasonality, but with low phylogenetic signal. Our findings might reflect that variation in morphological traits of phyl~~l~~ogenetically clustered assemblages is more restricted in their climatic ranges. Moreover, on another study, Graham et al. (2009) found that ~~phylogenetic diversity of~~ hummingbird communities of the Andean region tend to be phylogenetically clustered at higher elevations and colder areas, and to be overdispersed at lower elevations, whereas in the transition zone between lowlands and highlands there is a species turnover of relatively distant related species that can be associated to the environmental gradient. We found similar results in which phylogenetically clustered communities are found in the western areas (Fig. 2) which includes mountainous ranges above 1500 masl (southern Sierra Madre Oriental, and the Sierra Madre del Sur), although lowland areas like the Balsas Depression also show high values of phylogenetic clustering.

Phylogenetic clustering at higher elevations supports the idea of environmental filtering, a pattern where similar traits are selected above other variations because they have an advantage within the community and the environment, also allowing the coexistence of close relatives (Webb et al., 2002). Phylogenetic clustering in lowlands like the Balsas Depression supports the idea of the effect of dispersal barriers over community structuring, where communities are phylogenetically similar despite their large differences in species composition, a pattern reflecting the influence biogeographic barriers (Graham et al., 2009) that promote regions with a set of related species with a common and isolated history, like areas of endemism (Harold & Mooi, 1994).

The phylogenetic overdispersion patterns we found could be more related to the expectation that competition influences the local trait composition of a community by promoting the filling of the morphological and ecological space exploited (Wainwright & Reilly, 1994); but it ~~can~~ could also be associated with the distribution of a lineage along a transition zone, that is, an area where a mixed set of distinct biotic elements overlap (Morrone 2004). Areas found with higher phylogenetic overdispersion have been recognized by other authors as areas where different biotic elements overlap, e.g parts of the Mexican Transition Zone (Sierra Madre Oriental), Yucatan Peninsula and the limits of the Tehuantepec Isthmus (Morrone, 2006, 2014).

Kommentiert [CH46]: More than…?

Kommentiert [CH47]: To be consistent with the “could” of the 1st half of the sentence

Contradictory to the expectations of patterns of phylogenetic structuring, our data show low phylogenetic signal, so traits are less similar than expected due to phylogenetic relatedness. We would have expected a strong phylogenetic signal, as closely related species of a community tend to occupy similar morphological space due to common ancestry, especially in phylogenetically clustered areas. Overdispersion of traits driven by competitive interactions and divergent trait evolution, as well as the taxonomic and spatial scale, may have influenced the results by masking phylogenetic signal patterns at different assemblages (Webb et al., 2002;

Cavender-Bares et al., 2006; Lawing et al., 2017). The latter seems to be the case for tyrant flycatchers, as many closely related clades that supposedly have a similar distribution of traits, are concentrated in the same areas of high phylogenetic structure. For example, closely related and morphologically similar *Empidonax* and *Contopus* are concentrated southeastward, while another set of closely related *Empidonax* are found concentrated westward (i.e. *E. difficilis, E. occidentalis, E. fulvifrons* and *C. cooperi*, *C. pertinax and C. sordidulus*). On the other hand, the areas that have more phylogenetically diverse communities (phylogenetic overdispersion) are found in southeastern tropical region, for example the Yucatan Peninsula.

Another contradicting pattern revealed by our analyses was defined by the discordant response of variation in body size in relation to temperature seasonality and phylogenetic structure (Fig. 4). Our results indicate that body size increases as temperature seasonality increases, but as communities became more phylogenetically clustered, body size decreases, resulting in a trade-off between the influences of temperature seasonality and phylogenetic structure over variation in body size. An evolutionary trade-off suggests that the functional trait of body size is limited by the action of another trait of evolutionary and ecological importance, like the relatedness of the species occurring within the community. Trade-offs can occur at different hierarchical levels, and situations can even occur in which the selection on traits of individual organisms is opposed to the selection on an emergent characteristic at the species level (Jablonski, 2007), establishing variation patterns that cannot be fully explained by analyzing a single level. Then, the variation of a characteristic of the individual like body size could be opposed to the selection of a property at the species level (Diniz-Filho, 2004), like the structuring of communities.

Kommentiert [CH48]: Contradicting to…?

Kommentiert [CH49]: Correct?

CONCLUSIONS

Our analyses demonstrate that the environment has an effect on morphological variation that is mediated by the phylogenetic structure of communities across geography. The use of different environmental variables to elucidate patterns of morphological change in lineages, with distinct levels of phylogenetic signal, and varied patterns of lineage composition across space provides greater explanatory power than only taking into account species richness or abundance, or simply presence/absence distributional data (Olson et al., 2009; Maestri et al., 2016; Lawing et al., 2017). Several authors have noticed that morphological variation is best explained by a varied set of variables, given that the effect of a single climatic variable, most of the time explains variation only at one scale (taxonomic or geographic, James 1970; Dial 2008; Olson et al. 2009; Martínez-Monzón et al. 2017). Assessing the distribution of ecomorphological traits of organisms is the best way to predict change over an environmental gradient (Olson et al. 2009; Santos et al. 2016) and consequently, regression models representing variation of functional traits provide new insights into elucidating the general mechanisms that relate biodiversity across environmental and geographical changes (Violle et al. 2014). A spatial visualization of the predicted response of trait variation in relation to environmental factors can integrate individual and interspecific level responses to evaluate the importance of morphological adaptation in the explanation of broader scale processes. Finally, our results highlight that to allow a better understanding of the spatial distribution patterns of morphological traits, and the processes that promote them in different assemblages, it is necessary to consider the relationship of different ecomorphological traits of the species in conjunction with the phylogenetic composition of the communities.

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References

Adams D, and Otárola-Castillo E. 2013. geomorph: an r package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution* 4:393-399. doi:10.1111/2041-210X.12035

Adams DC. 2014. A Generalized K Statistic for Estimating Phylogenetic Signal from Shape and Other High-Dimensional Multivariate Data. *Systematic Biology* 63:685-697. 10.1093/sysbio/syu030

Alvarado-Cárdenas LO, Martínez-Meyer E, Feria TP, Eguiarte LE, Hernández HM, Midgley G, and Olson ME. 2013. To converge or not to converge in environmental space: testing for similar environments between analogous succulent plants of North America and Africa. *Annals of Botany* 111:1125-1138. 10.1093/aob/mct078

Arbeláez-Cortés E, Milá B, and Navarro-Sigüenza AG. 2014. Multilocus analysis of intraspecific differentiation in three endemic bird species from the northern Neotropical dry forest. *Molecular Phylogenetics and Evolution* 70:362-377.

Formatiert: Englisch (Vereinigtes Königreich)

Berlanga H, Rodríguez-Contreras, V., Oliveras de Ita, A., Escobar, M., Rodríguez, L., Vieyra, J., Vargas, V. 2008. Red de Conocimientos sobre las Aves de México (AVESMX). CONABIO.

Blamires D, De Oliveira G, de Souza Barreto B, and Diniz-Filho JAF. 2008. Habitat use and deconstruction of richness patterns in Cerrado birds. *Acta Ecologica* 33:9 7 – 1 0 4.

Blomberg SP, Garland Jr T, and Ives AR. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717-745.

Blomberg SP, and Garland T. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology* 15:899-910.

Bonetti MF, and Wiens JJ. 2014. Evolution of climatic niche specialization: a phylogenetic analysis in amphibians. *Proceedings of the Royal Society of London B: Biological Sciences* 281:20133229.

Bonner JT. 2011. *Why size matters: from bacteria to blue whales*: Princeton University Press.

Bowlin MS, and Wikelski M. 2008. Pointed Wings, Low Wingloading and Calm Air Reduce Migratory Flight Costs in Songbirds. *PLoS ONE* 3:e2154.

Brown JH. 1995. *Macroecology*. Chicago: The University of chicago Press.

Brum FT, Kindel A, Hartz SM, and Duarte LDS. 2012. Spatial and phylogenetic structure drive frugivory in Tyrannidae birds across the range of Brazilian Araucaria forests. *Oikos*:no-no. 10.1111/j.1600-0706.2011.19978.x

Campbell-Tennant DJE, Gardner JL, Kearney MR, and Symonds MRE. 2015. Climate-related spatial and temporal variation in bill morphology over the past century in Australian parrots. *Journal of Biogeography* 42:1163-1175. doi:10.1111/jbi.12499

Cavender-Bares J, Keen A, and Miles B. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87.

Cavender-Bares J, Kozak KH, Fine PVA, and Kembel SW. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12:693-715. 10.1111/j.1461-0248.2009.01314.x

Cicero C, and Koo MS. 2012. The role of niche divergence and phenotypic adaptation in promoting lineage diversification in the Sage Sparrow (Artemisiospiza belli, Aves: Emberizidae). *Biological Journal Of the Linnean Society* 107:332-354. 10.1111/j.1095-8312.2012.01942.x

Claramunt S. 2010. Discovering exceptional diversification at continental scales: the case of the endemic families of neotropical suboscine passerines. *Evolution* 64:2004–2019.

Cortés-Ramírez G, Ríos-Muñoz CA, and Navarro-Sigüenza AG. 2012. Ecomorphological distribution of the Tyrannides in Mexico. North American Ornithological Conference V. Vancouver, Canada. p 359

Dawideit BA, Phillimore AB, Laube I, Leisler B, and Böhning-Gaese K. 2009. Ecomorphological predictors of natal dispersal distances in birds. Journal of Animal Ecology 78:388-395

Dehling DM, Fritz SA, Töpfer T, Päckert M, Estler P, Böhning-Gaese K, and Schleuning M. 2014. Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. Ecography 37:1047-1055.

Formatiert: Deutsch (Deutschland)

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, and Martin PR. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences* 105:6668-6672.

Dial KP, Greene E, and Irschick DJ. 2008. Allometry of behavior. *Trends in Ecology & Evolution* 23:394-401.

Formatiert: Deutsch (Deutschland)

Diniz-Filho JAF. 2004. Macroecology and the hierarchical expansion of evolutionary theory. *Global Ecology and Biogeography* 13:1-15.

Donoghue MJ. 2008. A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences* 105:11549-11555.

Duarte LdS. 2011. Phylogenetic habitat filtering influences forest nucleation in grasslands. *Oikos* 120:208-215.

Eck S, Fiebig J, Fiedler W, Heynen I, Nicolai B, Töpfer T, Van den Elzen R, Winkler R, and Woog F. 2011. Measuring Birds – Vögel Vermessen.

Endler JA. 1977. *Geographic variation, speciation, and clines*: Princeton University Press.

Faaborg J, Holmes RT, Anders AD, Bildstein KL, Dugger KM, Gauthreaux SA, Helglund P, Hobson KA, Jahn AE, Johnson DH, Latta SC, Levey DJ, Marra PP, Merkprd CL, Nol E, Rothstein SI, Sherry TW, Sillet ST, Thompson FR, and Warnock N. 2010. Recent advances in understanding migration systems of New World land birds. *Ecological Monographs* 80:3-48.

Felice RN, and Goswami A. 2017. Developmental origins of mosaic evolution in the avian cranium. Proceedings of the National Academy of Sciences:201716437.

Fitzpatrick JW. 1980. Foraging Behavior of Neotropical Tyrant Flycatchers. *Condor* 82:43-57.

Fitzpatrick JW. 1981. Search strategies of tyrant flycatchers. *Animal Behaviour* 29:810-821.

Fitzpatrick JW. 1985. Form, Foraging Behavior, and Adaptive Radiation in the Tyrannidae. *Ornithological Monographs* 36:447-470.

Flynn DF, Mirotchnick N, Jain M, Palmer MI, and Naeem S. 2011. Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. *Ecology* 92:1573-1581.

Forister ML, Novotny V, Panorska AK, Baje L, Basset Y, Butterill PT, Cizek L, Coley PD, Dem F, and Diniz IR. 2015. The global distribution of diet breadth in insect herbivores. *Proceedings of the National Academy of Sciences* 112:442-447.

Förschler MI, and Barlein F. 2011. Morphological shifts of the external flight apparatus across the range of a passerine (Northern Wheatear) with diverging migratory behaviour. PLoS ONE 6:e18732

García-Trejo EA, and Navarro-Sigüenza AG. 2004. Patrones biogoegráficos de la riqueza de especies y el endemismo de la avifauna en el oeste de México. *Acta Zoologica Mexicana* 20:167-185.

Gatesy SM, and Dial KP. 1996. Locomotor Modules and the Evolution of Avian Flight. *Evolution* 50:331-340.

Graham CH, Parra JL, Rahbek C, and McGuire JA. 2009. Phylogenetic structure in tropical hummingbird communities. *Proceedings of the National Academy of Sciences* 106:19673-19678.

Graves GR. 1991. Bergmann's rule near the equator: latitudinal clines in body size of an Andean passerine bird. *Proceedings of the National Academy of Sciences* 88:2322-2325. 10.1073/pnas.88.6.2322

Greenberg R, Danner R, Olsen B, and Luther D. 2012. High summer temperature explains bill size variation in salt marsh sparrows. *Ecography* 35:146-152. 10.1111/j.1600-0587.2011.07002.x

Hackett SJ, Kimball RT, Reddy S, Bowie RCK, Braun EL, Braun MJ, Chojnowski JL, Cox WA, Han K-L, Harshman J, Huddleston CJ, Marks BD, Miglia KJ, Moore WS, Sheldon FH, Steadman DW, Witt CC, and Yuri T. 2008. A Phylogenomic Study of Birds Reveals Their Evolutionary History. *Science* 320:1763-1768. 10.1126/science.1157704

Halffter G, Moreno, C. E. 2005. Significado biológico de las diversidades alfa, beta y gamma In: Halffter G, Soberón J., Koleff, P. & Melic, A., ed. *Sobre el significado biológico de las diversidades alfa, beta y gamma* México: CONABIO, 1-18.

Hamilton TH. 1961. The Adaptive Significances of Intraspecific Trends of Variation in Wing Length and Body Size Among Bird Species. *Evolution* 15:180-195.

Harold AS, and Mooi RD. 1994. Areas of endemism: definition and recognition criteria. *systematic Biology* 43:261-266.

Hawkins BA, Diniz-Filho JAF, Jaramillo C, and Soeller SA. 2007. Climate, Niche Conservatism, and the Global Bird Diversity Gradient. *The american Naturalist* 170:516-529.

Helmus MR, Savage K, Diebel MW, Maxted JT, and Ives AR. 2007. Separating the determinants of phylogenetic community structure. *Ecology Letters* 10:917-925.

Hespenheide HA. 1971. Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. *Ibis* 113:59-72.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, and Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965-1978.

IOU. 2018. IOC World Bird List, v8.1. Checklist dataset https://doi.org/10.15468/anfqn6 accessed via GBIF.org.

Jablonski D. 2007. Scale and hierarchy in macroevolution. *Palaeontology* 50:87-109.

James FC. 1970. Geographic Size Variation in Birds and Its Relationship to Climate. *Ecology* 51:365-390. doi:10.2307/1935374

Jarzyna MA, and Jetz W. 2016. Detecting the multiple facets of biodiversity. *Trends in Ecology & Evolution* 31:527-538.

Jarzyna MA, Zuckerberg B, Porter WF, Finley AO, and Maurer BA. 2015. Spatial scaling of temporal changes in avian communities. *Global Ecology and Biogeography* 24:1236-1248. 10.1111/geb.12361

Jetz W, and Rahbek C. 2002. Geographic range size and determinants of avian species richness. *Science* 297:1548-1551.

Jetz W, Thomas GH, Joy JB, Hartmann K, and Mooers AO. 2012. The global diversity of birds in space and time. *Nature* advance online publication.

Jones OR, Purvis A, and Quicke DLJ. 2012. Latitudinal gradients in taxonomic overdescription rate affect macroecological inferences using species list data. *Ecography* 35:333-340. 10.1111/j.1600-0587.2011.06956.x

Formatiert: Englisch (Vereinigtes Königreich)

Kissling WD. 2007. Macroecology of avian frugivore diversity Doktor der Naturwissenschaften. Johannes Gutenberg-Universität in Mainz.

Kissling WD, Böhning-Gaese K, and Jetz W. 2009. The global distribution of frugivory in birds. *Global Ecology and Biogeography* 18:150–162.

Kivelä SM, Välimäki P, Carrasco D, Mäenpää MI, and Oksanen J. 2011. Latitudinal insect body size clines revisited: a critical evaluation of the saw-tooth model. *Journal of Animal Ecology* 80:1184-1195. 10.1111/j.1365-2656.2011.01864.x

Kluge J, and Kessler M. 2011. Phylogenetic diversity, trait diversity and niches: species assembly of ferns along a tropical elevational gradient. *Journal of Biogeography* 38:394-405. 10.1111/j.1365-2699.2010.02433.x

Kobelkowsky-Vidrio T, Ríos-Muñoz CA, and Navarro-Sigüenza AG. 2014. Biodiversity and biogeography of the avifauna of the Sierra Madre Occidental, Mexico. *Biodiversity and Conservation* 23:2087-2105.

Lawing AM, Eronen JT, Blois JL, Graham CH, and Polly PD. 2017. Community functional trait composition at the continental scale: the effects of non-ecological processes. *Ecography* 40:651-663. 10.1111/ecog.01986

Lewin-Koh NJ, Bivand R, Pebesma E, Archer E, Baddeley A, Bibiko H, Dray S, Forrest D, Friendly M, and Giraudoux P. 2011. maptools: Tools for reading and handling spatial objects. *R package version 08-10, URL http://CRAN R-project org/package= maptools*.

Lockwood R, Swaddle JP, and Rayner JMV. 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *Journal of Avian Biology* 29:273.

Formatiert: Englisch (Vereinigtes Königreich)

Formatiert: Deutsch (Deutschland)

Formatiert: Englisch (Vereinigtes Königreich)

Losos JB, and Miles DB. 1994. Adaptation, constraint, and the comparative method: phylogenetic issues and methods. *Ecological morphology: Integrative organismal biology*:60-98.

MacArthur R, and Levins R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* 101:377-385.

Maestri R, Luza AL, Barros LD, Hartz SM, Ferrari A, Freitas TRO, and Duarte LD. 2016. Geographical variation of body size in sigmodontine rodents depends on both environment and phylogenetic composition of communities. *Journal of Biogeography* 43:1192-1202.

Martin JM, I MJ, and S BP. 2018. Bison body size and climate change. *Ecology and Evolution* 8:4564-4574. doi:10.1002/ece3.4019

Martínez-Monzón A, Blain H-A, Cuenca-Bescós G, and Rodríguez MÁ. 2017. Climate and amphibian body size: a new perspective gained from the fossil record. *Ecography*:n/a-n/a. 10.1111/ecog.03440

Mazel F, Pennell M, Cadotte M, Diaz S, Dalla Riva G, Grenyer R, Leprieur F, Mooers A, Mouillot D, Tucker C, and Pearse W. 2018. Is phylogenetic diversity a surrogate for functional diversity across clades and space? *bioRxiv*. 10.1101/243923

Mazer SJ, and Wheelwright NT. 1993. Fruit size and shape: Allometry at different taxonomic levels in bird-dispersed plants. *Evolutionary Ecology* 7:556-575. 10.1007/bf01237821

McNab BK. 1971. On the Ecological Significance of Bergmann's Rule. *Ecology* 52:845-854. 10.2307/1936032

Miles DB, and Ricklefs RE. 1984. The Correlation Between Ecology and Morphology in Deciduous Forest Passerine Birds. *Ecology* 65:1629-1640.

Militino AF. 2010. Mixed Effects Models and Extensions in Ecology with R. *Journal of the Royal Statistical Society: Series A (Statistics in Society)* 173:938-939.

Miller E, Zanne A, and Ricklefs R. 2013. Niche conservatism constrains Australian honeyeater assemblages in stressful environments. *Ecology Letters* 16:1186-1194.

Moles AT, Wallis IR, Foley WJ, Warton DI, Stegen JC, Bisigato AJ, Cella-Pizarro L, Clark CJ, Cohen PS, and Cornwell WK. 2011. Putting plant resistance traits on the map: a test of the idea that plants are better defended at lower latitudes. *New Phytologist* 191:777-788.

Morrone JJ. 2004. Panbiogeografía, componentes bióticos y zonas de transición. *Revista Brasileira de Entomologia* 48:149-162.

Morrone JJ. 2006. Biogeographic areas and transition zones of latin america and the Caribbean Islands basen on panbiogeographic and cladistic analyses of the Entomofauna. *Annual Review of Entomolgoy* 51:467-494.

Morrone JJ. 2014. Biogeographical regionalisation of the Neotropical region. *Zootaxa* 3782:1-110.

Navarro A, Garza-Torres H, De Aquino SL, Rojas-Soto O, and Sánchez-González L. 2004. Patrones biogeográficos de la avifauna. In: Luna I, Morrone JJ, and Espinosa D, eds. *Biodiversidad de la Sierra Madre Oriental*. Mexico: Las Prensas de Ciencias, UNAM, México, DF, 439-467.

O'Donnel MS, and Ignizio DA. 2012. Bioclimatic predictors for supporting ecological applications in the conterminous United States. US Geological Survey.

Ohlson J, Fjeldså J, and Ericson P. 2008. Tyrant flycatchers coming out in the open: phylogeny and ecological radiation of Tyrannidae (Aves: Passeriformes). *Zoologica Scripta* 37:315-335.

Olguín-Monroy HC, Gutiérrez-Blando C, Ríos-Muñoz CA, León-Paniagua L, and Navarro-Sigüenza AG. 2013. Regionalización biogeográfica de la mastofauna de los bosques tropicales perennifolios de Mesoamérica. *Revista de Biología Tropical* 61:937-969.

Olson VA, Davies RG, Orme DL, Thomas GH, Meiri S, Blackburn TM, Gaston KJ, Owens IPF, and Bennet PM. 2009. Global biogeography and ecology of body size in birds. *Ecology Letters* 12:249-259.

Peters RH, and Peters RH. 1986. *The ecological implications of body size*: Cambridge University Press.

Phillips AG, Töpfer T, Rahbek C, Böhning-Gaese K, and Fritz SA. 2018. Effects of phylogeny and geography on ecomorphological traits in passerine bird clades. Journal of Biogeography 00:1-11. https://doi.org/10.1111/jbi.13383

Pol M, Bailey LD, McLean N, Rijsdijk L, Lawson CR, and Brouwer L. 2016. Identifying the best climatic predictors in ecology and evolution. *Methods in Ecology and Evolution* 7:1246-1257.

Pontarotti P. 2010. *Evolutionary Biology. Concepts, Molecular and Morphological Evolution*: Springer.

R-Core-Team. 2017. R: A language and environment for statistical computing.

Ricklefs RE, and Miles DB. 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. *Ecological morphology: integrative organismal biology University of Chicago Press, Chicago* 101:13-41.

Ricklefs RE. 2012. Species richness and morphological diversity of passerine birds. Proceedings of the National Academy of Sciences. 10.1073/pnas.1212079109

Ridgely RS, T. F. Allnutt, T. Brooks, D. K. McNicol, D. W. Mehlman, B. E. Young, and J. R. Zook. 2005. Digital Distribution Maps of the Birds of the Western Hemisphere, version 2.1. NatureServe, Arlington, Virginia, USA.

Ridgely RS, and Tudor G. 2009. *Field guide to the songbirds of South America: the passerines*: University of Texas Press.

Ríos-Muñoz CA, and Navarro-Sigüenza AG. 2012. Patterns of species richness and biogeographic regionalization of the avifaunas of the seasonally dry tropical forest in Mesoamerica. *Studies on Neotropical Fauna and Environment* 47:171-182. 10.1080/01650521.2012.734175

Rodríguez D, and Ojeda RA. 2014. Scaling functional diversity of small mammals in desert systems. *Journal of Zoology* 293:262-270.

Ruggiero A, and Werenkraut V. 2007. One-dimensional analyses of Rapoport's rule reviewed through meta-analysis. *Global Ecology and Biogeography* 16:401-414.

Saito VS, Cianciaruso MV, Siqueira T, Fonseca-Gessner AA, and Pavoine S. 2016. Phylogenies and traits provide distinct insights about the historical and contemporary assembly of aquatic insect communities. *Ecology and Evolution* 6:2925-2937.

Salewski V, and Watt C. 2017. Bergmann's rule: a biophysiological rule examined in birds. *Oikos* 126(2). 10.1111/oik.03698

Santos AMC, Cianciaruso MV, and De Marco P. 2016. Global patterns of functional diversity and assemblage structure of island parasitoid faunas. *Global Ecology and Biogeography* 25:869-879. 10.1111/geb.12340

Schmidt-Nielsen K. 1984. *Scaling: why is animal size so important?*: Cambridge University Press.

Schneider FD, Morsdorf F, Schmid B, Petchey OL, Hueni A, Schimel DS, and Schaepman ME. 2017. Mapping functional diversity from remotely sensed morphological and physiological forest traits. *Nature Communications* 8:1441. 10.1038/s41467-017-01530-3

Seeholzer G, Claramunt S, and Brumfield, R. 2017. Niche evolution and diversification in a Neotropical radiation of birds (Aves: Furnariidae). Evolution 71:702-715.

Seoane J, Bustamante J, and Dıaz-Delgado R. 2004. Competing roles for landscape, vegetation, topography and climate in predictive models of bird distribution. *Ecological Modelling* 171:209-222.

Sherry TW. 1984. Comparative dietary ecology of sympatric, insectivorous Neotropical flycatchers (Tyrannidae). *Ecological Monographs* 54:313-338.

Sobral FL, and Cianciaruso MV. 2016. Functional and phylogenetic structure of forest and savanna bird assemblages across spatial scales. *Ecography* 39:533-541.

Swaddle JP, and Lockwood R. 1998. Morphological adaptations to predation risk in passerines. *Journal of Avian Biology* 29:172.

Symonds M, and GJ Tattersall. 2010. Geographical Variation in Bill Size across Bird Species Provides Evidence for Allen’s Rule. *The american Naturalist* 176:188-197. 10.1086/653666

Team RC, Pinheiro J, Bates D, DebRoy S, and Sarkar D. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-113.

Tedersoo L, Bahram M, Toots M, Diedhiou AG, Henkel TW, Kjøller R, Morris MH, Nara K, Nouhra E, and Peay KG. 2012. Towards global patterns in the diversity and community structure of ectomycorrhizal fungi. *Molecular Ecology* 21:4160-4170.

Tello JG, Moyle RG, Marchese DJ, and Cracraft J. 2009. Phylogeny and phylogenetic classification of the tyrant flycatchers, cotingas, manakins, and their allies (Aves: Tyrannides). *Cladistics* 25:1-39.

Tsirogiannis C, and Sandel B. 2016. PhyloMeasures: a package for computing phylogenetic biodiversity measures and their statistical moments. *Ecography* 39:709-714. doi:10.1111/ecog.01814

Violle C, Reich PB, Pacala SW, Enquist BJ, and Kattge J. 2014. The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences* 111:13690-13696.

Wainwright PC, and Reilly SM. 1994. *Ecological morphology: integrative organismal biology*: University of Chicago Press.

Webb CO, Ackerly DD, McPeek MA, and Donoghue MJ. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33:475-505.

Wiens JJ, and Graham CH. 2005. Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology. *Annual Review of Ecology, Evolution, and Systematics* 36:519-539.

Winkler H, and Leisler B. 1992. On the ecomorphology of migrants. Ibis 134 suppl. 1: 21-28

Xu J, Chen Y, Zhang L, Chai Y, Wang M, Guo Y, Li T, and Yue M. 2017. Using phylogeny and functional traits for assessing community assembly along environmental gradients: A deterministic process driven by elevation. *Ecology and Evolution* 7:5056-5069. 10.1002/ece3.3068

Zellweger F, Baltensweiler A, Ginzler C, Roth T, Braunisch V, Bugmann H, and Bollmann K. 2016. Environmental predictors of species richness in forest landscapes: abiotic factors versus vegetation structure. *Journal of Biogeography* 43:1080-1090. 10.1111/jbi.12696

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, and Smith GM. 2009. Mixed effects modelling for nested data. *Mixed effects models and extensions in ecology with R*: Springer, 101-142.