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

Gala Cortés-Ramírez Corresp., 1, 2 , **César A Ríos-Muñoz** 3 , **Adolfo G Navarro-Sigüenza** 1

1 Museo de Zoología "Alfonso L. Herrera", Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico City, Mexico
2 Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Mexico City, Mexico City, Mexico
3 Laboratorio de Arqueozoología, Instituto Nacional de Antropología e Historia, Mexico City, Mexico City, Mexico

Corresponding Author: Gala Cortés-Ramírez
Email address: g.cortes.ramirez@ciencias.unam.mx

Morphological variation has a strong relationship with the variation of ecological characteristics and the evolutionary history of each taxon, which in turn also vary in geography. To explore how the geographical variation of the morphology is related to different climatic gradients and the phylogenetic structure, we analyzed the variation of morphological traits (body size, bill, and wing) involved in the lifestyle of 64 species of tyrant flycatchers (Tyrannidae) distributed in Mexico. We measured morphological traits identifying variables in specimens from biological collections and we related them to climatic and topographic data of each locality. We calculate the phylogenetic structure of each locality in order to explore the influence of climatic variables and the phylogenetic structure over the morphological variation of tyrant flycatchers, by means of mixed-effects linear models. We mapped the spatial distribution of the scaling between the morphological and environmental variables 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 regional scale, the spatial distribution of body size shows a scaling pattern coincident with the ecogeographical Bergmann's rule, with an increase 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 highland forests and other types of vegetation, morphological traits increase northeast to southwest. Phylogenetic structure helps to explain the variation of morphology at lower assemblages but not at the regional scale. The scaling patterns, along lowlands and highlands, suggest that part of morphological variation at this scale is explained in both by the climatic gradients and lineage relatedness of communities.

Morphological variation is best explained by a varied set of variables, and scaling models representing this variation and integrating phylogenetic patterns at different geographic scales provide new understanding into the mechanisms underlying the link between biodiversity, its geographical setting, and the environmental change.

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Gala Cortés-Ramírez[1,2*], César A. Ríos-Muñoz[3] and Adolfo G. Navarro-Sigüenza[1]

[1]Museo de Zoología “Alfonso L. Herrera”, Facultad de Ciencias, Universidad Autónoma de México.

[2] Posgrado en Ciencias Biológicas, Universidad Autónoma de México, Mexico City, Mexico.

[3]Laboratorio de Arqueozoología, Instituto Nacional de Antropología e Historia, Mexico City, Mexico.

* Corresponding author e-mail address: g.cortes.ramirez@ciencias.unam.mx

Corresponding Author:

Gala Cortés-Ramírez[1,2]

Museo de Zoología “Alfonso L. Herrera”, Facultad de Ciencias, Universidad Autónoma de México.

Apartado postal 70-399, 04510 México City.

Email address: g.cortes.ramirez@ciencias.unam.mx

Abstract

Morphological variation has a strong relationship with the variation of ecological characteristics and the evolutionary history of each taxon, which in turn also vary in geography. To explore how the geographical variation of the morphology is related to different climatic gradients and the phylogenetic structure, we analyzed the variation of morphological traits (body size, bill, and wing) involved in the lifestyle of 64 species of tyrant flycatchers (Tyrannidae) distributed in Mexico. We measured morphological traits identifying variables in specimens from biological collections and we related them to climatic and topographic data of each locality. We calculate the phylogenetic structure of each locality in order to explore the influence of climatic variables and the phylogenetic structure over the morphological variation of tyrant flycatchers, by means of mixed-effects linear models. We mapped the spatial distribution of the scaling between the morphological and environmental variables 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 regional scale, the spatial distribution of body size shows a scaling pattern coincident with the ecogeographical Bergmann's rule, with an increase 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 highland forests and other types of vegetation, morphological traits increase northeast to southwest. Phylogenetic structure helps to explain the variation of morphology at lower assemblages but not at the regional scale. The scaling patterns, along lowlands and highlands, suggest that part of morphological variation at this scale is explained in both by the climatic gradients and lineage relatedness of communities. Morphological variation is best explained by a varied set of variables, and scaling models representing this variation and integrating phylogenetic patterns at different geographic scales provide new understanding into the mechanisms underlying the link between biodiversity, its geographical setting, and the environmental change.

Introduction

A long-standing goal in ecology and evolutionary biology is to understand the relationship among factors responsible for the observed patterns of morphological diversity, evolutionary history and its geographic distribution. Morphological diversity across species is driven by several ecological and evolutionary processes, and is usually studied as the evolution of form and function, or lifestyle (Losos & Miles, 1994). Also, the establishing of morphological diversity 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 lifestyle and may also reflect the response to environmental biotic and abiotic factors, and may determine the responses of species 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). Other factors such as evolutionary history also have been found to determine geographical gradients in species variation (Jetz & Rahbek, 2002, Kissling et al., 2007). Morphological variation occurs within and across species, so the complex interaction of evolutionary history and environment makes 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), thus limiting 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 response to climatic gradients among different groups of organisms and traits, has been found to be contrasting showing more or less influence 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 is established, it is necessary to explore and quantify how species' morphological traits related to lifestyle, vary geographically along environmental gradients, at broader and narrower spatial scales of the same region, taking into account 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, focused in specific functional groups with different patterns of distribution defined by varying biotic components, 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). Also, quantifying the geographical distribution of morphological variation may help disentangle trade-offs found at the scaling of morphology with environmental and phylogenetic variables, from local to regional scales, making this type of analysis necessary for improving regional and global predictions of morphological functional variation (Diniz-Filho, 2004; Rodríguez & Ojeda, 2014).

To evaluate broad scale patterns of morphological variation and the promoter processes, it is necessary to quantify the distribution of morphological traits associated to the lifestyle of related functional groups of species. In that sense, some authors have found that the global patterns of functional groups 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 scaling between a set of morphological variables and the climatic gradients of a mainly insectivorous assemblage of birds, the tyrant flycatchers (Tyrannidae) which constitute a functional group composed by 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, which are adapted to different elevations and occupy all vertical strata present in forests (Fitzpatrick et al., 2004, Ridgely and Tudor, 2009). We chose as model system the species of Tyrannidae of Mexico 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 the lifestyle (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 help, in order to explain how broad scale patterns in species variation are established and how historical contingencies influences the response of morphological variation to environment. Our specific objectives were to test (1) Climate conditions (including temperature, precipitation, and seasonality of both), are associated with the observed variation in morphology across tyrant flycatchers assemblages; (2) the influence of the phylogenetic structure of assemblages over the distribution of morphological variation and its response to climate; and (3) to map the spatial distribution of the scaling between morphological variables and climatic gradients. Despite the obvious expectation that environmental-morphological relationship vary across spatial gradients, the approach we used take into account varied ranges in climate and seasonality within a lineage, abiotic variables influencing the geographic distribution of species, and the phylogenetic relationships of tyrant flycatchers. Taking into account phylogenetic relationships of a community could facilitate the chance of observing any associated deviations in the relation with environment through the evaluation of the conjoint effects of the phylogenetic structuring of communities and the clinal environmental variation (Bonetti & Wiens, 2014; Maestri et al., 2016). We hypothesized that by taking into account historical and geographical factors, climatic variables should explain most of the remaining tyrant flycatchers morphological variation across the environmental setting.

METHODS

Morphological traits data and data treatment

*Morphological data***.** In order to construct regression models of environmental-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 belonging to 60 species of Tyrannidae distributed in Mexico (Table S1). We measured five traits: 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 with important avian use of environmental space (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, and 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 the surface area of the appendage functions to dissipate excess of heat in warm climates or retain heat in cold climates (Symonds & Tattersall, 2010; Greenberg, 2012). Bill is also the functional trait by which birds obtain its food so it can be related to habitat and lifestyle variation (Mazer & Wheelwright, 1993; Jones; 2012). The joint variation of bill measures represents its variation in size and form. 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 lifestyle.

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 to complete the sample and under the assumption that the variation between sexes is smaller than interespecific variation (Claramunt, 2010). We took all the measurements with a digital and an analog Mitutoyo calipers, with precision of 0.01 mm. For statistical analysis we use *log natural*-transformed measures in order to normalize the dataset, and because body size is strongly associated with other morphological traits, we extracted the effect of size in bill and wing measures by dividing each measure by the mass. Joint variation of the three bill measurements were 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.

Environmental and geographical 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 temperature annual variation, temperature range or seasonality, variation of precipitation in humid season, and variation of precipitation in the dry season. We decided to use the first principal components of each climatic index as they take into account most of the climatic variation in the study area (Table S3). For each specimen we obtained locality-specific climate data that were extracted from the climatic indexes. We used each climatic index as a fixed explanatory variable for the regression models; this information was later related to the morphological variables.

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

Historical distribution and relatedness data

Assemblages of the tyrant flycatchers. In order to discriminate the effects of contingencies related to the evolutionary distributional history of the tyrant flycatchers, we divided the data in three separate sets taking into account characteristics of three constructed assemblages of tyrant flycatchers distributed across Mexico, defined as temporal arrangements in which the species interact (Halffter & Moreno, 2005). 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 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 that represent the species distributed in all Mexico). Many of the characteristics of the assemblages that exist in a region depend on the species that the evolutionary history allows to exist in a given space as well as environmental factors. 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 richness, endemism, and habitat specialization of its biota, and patterns of biogeographic distribution define them as areas with a particular evolutionary history (Ríos-Muñoz & Navarro-Sigüenza, 2012; Olguín-Monroy et al., 2013). Type II and regional assemblage dataset were used to contrast the response of different scale assemblages to environmental gradients, because the influence of different variables over morphological variation can change at different scales (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. (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), values = 1 indicates that evolution of traits are consistent with Brownian motion, while $K<1$ indicates less similarity in the trait than expected under Brownian evolution, and $K>1$ indicates greater similarity in the trait than expected under Brownian evolution (Blomberg et al., 2003). Phylogenetic signal tests were conducted using *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 are 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 could potentially co-occur. We estimated the set of coexisting species at each location by extracting presence data from distributional hypothesis for Mexican Tyrannidae, generated elsewhere using ecological niche model algorithms (Navarro-Sigüenza et al., unpubl. data).

Statistical analyses

Assumptions

Given that climatic gradients and phylogenetic structure of an area potentially play a role as promoters or constrainers for morphological variation, and because this role may vary in strength and direction, we analyzed the morphological data by constructing regression models in order to explore the relationship between morphology, environment and phylogenetic structure influence. Our main hypothesis was that by taking into account evolutionary and geographical factors, climatic variables should explain most of the morphological variation of Tyrannidae species. Particular hypotheses considered here are: 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). For hypothesis 1, we assumed that morphology would show a clinal variation related to one or more climatic variables of temperature and precipitation, then a latitudinal pattern is expected to arise when the model is translated to a map. A significant association of climatic variables and change in morphology is evidence for hypothesis 1. Conversely, for hypothesis 2, we assumed that morphological change cannot solely be explained by climatic variables, but also phylogenetic structure would also be significantly associated to variation in morphology (evidence for hypothesis 2). Clinal 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 phylogenetically overdispersed. Phylogenetic structure unlikely explain alone 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)

The regression models

We explored the relationship between environmental gradients and phylogenetic structure with the morphological variation of traits of tyrant flycatchers, across the species distributed along Mexico, by the use of regression models. We constructed trait maps and obtained our inferences based on the fitting of a mixed multiple regression model predicting morphological variation of body size, bill and wing length. We used 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. From each specimen we obtained one measure of body size, bill variation and wing length giving three *log-natural* transformed responses for each individual (*see previous section)*. Hence, the measurements for each individual within a species are likely to be correlated because they belong to the same species within a subfamily. A diagram of the nested structure of the data is given in Fig. 2.

We used mixed-effects models fit in which the slope and intercept coefficients (i.e., the relationship between the morphological variation of the traits and environmental, topographic and phylogenetic structure variables) can be allowed to vary according to random effects. Random effects are the result of the nested structure of the data and variables that behave randomly; that is, variables which were not observed or measured but are known to affect the data. It implies that each individual within the same group is correlated because they belong to the same group, and each group can respond differentially to the variable (Militino et al., 2010). We considered that morphological variation (response variable) depends of predictor variables (fixed terms) which are: two topographic variables, four climatic indexes, and the phylogenetic structure at each location of each type of assemblage (regional, type I and type II). We included as random effect the phylogenetic membership of each individual (i.e., the belonging to the species to a given subfamily *sensu* Tello et al., 2009). We generated 144 different structures of regression models, fitting each response variable (body size, bill and wing length) to each predictor variable (temperature variation, temperature range, variation of precipitation in humid season, variation of precipitation in the dry season, phylogenetic structure, altitude, and topographic settings) for each assemblage dataset. In total, we fitted 16 models for each morphological variables at each assemblage, from which we selected the models that provided the best fit for each response (Table S3). 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). The fitting of the models involved a multi-step process which we will explain in the next section.

Obtaining the best fitting models

To find the best fitting models for each morphological variable (and assemblage dataset), we followed the protocol recommended by Zuur et al. (2009). First we start with a model that has as many explanatory variables as possible (in the fixed part of the model), then we find the optimal random structure, next the optimal fixed structure (including the optimal variance structure), and finally we choose the optimal model using restricted maximum likelihood (REML) estimation. 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. In this case, there are seven fixed predictor variables 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 adding a random intercept 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. Next, we used a random intercept and slope model, in which the response varies within 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). In other words, letting the slope to change implies that the variation of the response can change within each community in function of how much are related the Tyrannidae distributed on it. We found the optimal random structure model for each morphological variable by using the *anova* function to compare AIC, BIC and logLIK of the three models. We included the optimal variance structure to the optimal model for the random terms, (Table 2, Table S4 model 4), for which we added multiple variances for the residuals. We considered that different variances exists for the observations that have distinct phylogenetic membership (e.g. the model assumes a different variance for the set of observations that belong to “Species 1” in relation to the variance for the set of observations that belongs to “Species 2”). Using the AIC, BIC and logLIK, we selected the optimal model for the random terms with the optimal variance structure.

We selected the best fitting model structure for the fixed terms by adding each of the predictor variables and their interactions (Table 2), one by one sequentially, to the model with only the optimal random and variance structure (Table S4 models 5-16). First, we tested only for climate gradients explaining morphological variation (Evidence for hypothesis 1, Table S4 models 7-11), and then we selected the model structure that best explained the data. Next, we tested if phylogenetic structure influenced morphological variation (Evidence for hypothesis 2, Table S4 model 12) by adding the new predictor variable to the best fitting model with only explanatory climatic variables. Finally, we added to the selected model for each variable and dataset, altitude, the interaction with the climatic variable, and topographic setting as predictors (Table 2, Table S4 models 13-16), to test if any of those variables also influenced the variation of morphology (as assemblages were also recognized by means of altitude). The final products of the procedure described were nine best fitting models predicting each morphological variable, at each assemblage, scaling between climatic variables, phylogenetic structure and phylogenetic membership (Table S4, Table 3).

Mapping the spatial distribution of scaling patterns

To map the spatial distribution of scaling of 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 side) of Mexico and each assemblage. Then we translate the best-fitting model formulae 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 to place measures of the functional traits (Moles et al., 2011). We performed all analyses using Maptools (Lewin et al., 2011) package in R version 3.4.1 (R Core Team, 2017). Trait maps were visualized using the ArcGIS 10 (ESRI, 2011).

RESULTS

Relationship of climatic gradients and the morphological variation

Climatic gradients are associated positively with morphological variation of the three measured traits at all assemblages (Table 3). All best fitting models include as fixed term a climatic variable, specifically, temperature variables of seasonality (temperature range) or mean variation. Temperature seems to explain variation of morphology at all scales analyzed, from regional to lower scales of lowland and the other forests assemblages. At the regional scale, for body size, bill and wing length, temperature is related positively and significantly to the morphological change, and reflects increase in the morphology as seasonality increases. The magnitude of the response is higher for body and bill sizes (slopes 0.42 and 0.65, respectively), whereas the slope for wing is close to zero (slope=0.091), that means that although it is positive and reflects an increase in the morphological variable; this change is small. In other words, while the climatic seasonality increases importantly, wing length will not tend to increase as much as body and bill size, it reflects a poor association between wing and temperature range index.

For lower scale assemblages, type I and type II, the scaling between morphological variables and temperature range is also positive but not significant for all variables (*p-value*>0.05). For instance, the scaling between bill size and wing in the 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, for lowland forests assemblage, scaling between wing and temperature range is not significant ~~n~~either. Only body size scaling is significantly positive in both assemblages. Bill size scaling is significant in lowland forests assemblage but the magnitude of the response is less steep~~er~~ (slope=0.43).

Influence of phylogenetic structure over the morphological variation

Patterns of phylogenetic relatedness also helped to explain morphological variation at lower scale assemblages, for body size, bill and wing variables (Table 3). At highland forests and other types of vegetation, models for bill and wing were not significant (*p-value*>0.05), whereas body size is related positively to phylogenetic structure (slope= 0.60). A positive correlation with phylogenetic structure means that body size tend to increase at areas with more phylogenetically related co-occurring species (phylogenetic clustering), while decreases in areas with low phylogenetic relatedness (phylogenetic overdispersion). For lowland forests, bill variation is related slightly positively with phylogenetic structure, wing scaling is not significant, and body size is negatively related to phylogenetic structure. The latter means that, for these areas, there is a tendency of decrease in body size while communities became more phylogenetically clustered.

Besides of the scaling patterns showed by the best fitting models, phylogenetic structure exhibited a geographical pattern (Fig. 3). Both, highland and lowland forests assemblages presented 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 returned a value of K= 0.85 for body size, K= 0.88 for bill variation, and K= 0. 87 wing chord. All values were all statistically significant at α= 0.05. These values indicate that phylogenetic signal for each morphological variable at the species level although is lower than 1, values are close to Brownian evolution (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.

Spatial distribution of the scaling between morphological variables and environmental gradients

Overall trait variation was explained by temperature gradients, and also by phylogenetic structure at lower geographic scales (assemblages lower than regional). Mapping the predictions of the best fitting models (Table 3) yielded different patterns of spatial distribution for morphological variation (Figures 4-6), across the geography at different scales. We only mapped the statistical significant models. At the regional scale (Fig. 4), for the three morphological variables, morphology changes in a clinal way, where every trait increases in size in a south to north direction. Phylogenetic structure does no help to better explain variation of morphology at this scale. Lowland forests spatial distribution of traits showed a clinal variation from northeast to southwest (Fig. 5) in which body size and bill size increases towards the southwest. In lowland forests assemblage, bill size increases positively at areas with high phylogenetic structure. Conversely, body size shows an increase in areas with low phylogenetic structure (overdispersion) and decreases in areas phylogenetically clustered (Fig. 3A). Geographically that means that phylogenetic structure influences the decrease in size in areas where temperature gradients predict increase in size, and increase in size where temperature gradients predict decrease. For the type II assemblage (Fig. 6), we mapped body size and bill variation, which are explained by temperature seasonality. The geographic pattern of variation showed a morphological change where body size and bill increase northeast to southwest. Phylogenetic structure indicates the same pattern of increase where areas of higher phylogenetic clustering predict increase in both traits and are located in the southern region (Fig. 3B).

DISCUSSION

Environmental drivers of morphological diversity across geography have been extensively studied in many regions with different taxonomic groups, at a different geographic, taxonomic and functional scales (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; Mazel et al., 2018). As a result of previous studies that analyze the role of environment and geography as promoters of morphological diversity, many patterns of clinal variation have been detected for many groups; and among the main environmental promoters of morphological variation, climatic variables seem to strongly influence the distribution and variation of morphological traits, across different 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 in what extent and by which mechanisms such associations are maintained and may influence distribution patterns (Violle et al., 2014). It has been suggested that the conjoint action of variables may be acting at the same time promoting morphological variation at many taxonomic and geographic scales. For this reason, we intended to evaluate the influence of several variables already recognized as important predictors of morphological variation across geography.

When we focused on how climatic gradients explain the variation in morphology, our results suggest that temperature seasonality is the climatic variable that influences the most the geographical distribution of morphology, but the magnitude of the influence varies across different scales. This variable assumedly represents tolerance limits of species to variation in temperature, likely influencing morphological variation through maintaining habitat use through time, because species of a given lineage occupy a particular region for historical or ecological reasons, and they are adapted to the conditions of such region, so these species and their descendants are likely to remain in that region (Wiens & Graham, 2005). We also assumed that our results indicate a pattern that is latitudinally coincident with the expectations of 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 scale, latitudinal pattern is likely to show an increase in body size from south to north (Fig. 4), but some studies found exceptions at different geographic scales (e.g. James, 1970).

Scaling 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 the highlands and lowlands of western Mexico (Fig. 5 and Fig. 6), 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 scaling patterns of morphological variation in eastern lowlands, like the phylogenetically overdispersed Yucatan Peninsula or the Tehuantepec Isthmus, relatively constant (i.e., less seasonal) temperatures in the east, may have influenced the distribution of lineages and the variation of its 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 the environmental gradients influence the phylogenetic structure of the communities and therefore, patterns of phylogenetic clustering increases with decreasing temperature, meaning that closely related species tend to have a strong phylogenetic signal, and more similar trait 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). For instance, phylogenetic diversity of hummingbird communities of the Andean region tend to be phylogenetically clustered at higher elevations and colder areas, and 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 (Graham et al., 2009). We found similar results in which phylogenetically clustered communities are found in the western areas (Fig. 3) 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 in 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 of important dispersal barriers (Graham et al., 2009), or regions with a set of related species with a common and isolated history, like areas of endemism (Harold & Mooi, 1994). Phylogenetic overdispersion patterns are 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 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). As can be pointed out by our results, areas with higher phylogenetic overdispersion have been recognized 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).

Contradictory to the expectations of patterns of phylogenetic structuring is that 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 lower scales (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 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, and contain less related species of tyrant flycatchers, are distributed in areas of higher phylogenetic overdispersion, for example the southeastern tropical region.

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. 5). 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 both variables over variation in body size. An evolutionary trade off at this taxonomic and geographic scale suggests that the functional trait of size is limited by the action of another trait of evolutionary and ecological importance, like the structure of community. Trade offs can occur at different hierarchical levels, even situations can 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 one single level. For instance, area of distribution is considered a particular trait at the species level, the greater the distribution area, the lower the probability of extinction and vice versa (Ruggiero & Werenkraut, 2007). On the other hand, body size is an emerging feature of an individual and increases with increasing latitude according to the Bergman's rule (Salewski & Watt, 2017). But not all organisms are larger at higher latitudes, because the larger the size, the larger the area of distribution that is required to minimize the probability of extinction. At higher latitudes, there are more limitations of available habitat, therefore the areas of distribution are smaller. Species with smaller distribution ranges are favored, therefore, to minimize extinction rates, smaller body sizes are also favored (although the opposite is expected for these latitudes). 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, like distribution range (Diniz-Filho, 2004) or in our case, the structuring of communities.

CONCLUSIONS

Our analyses demonstrate that the environment has a biogeographic 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). To assess the distribution of morphological traits related to the lifestyle of organisms is the best way to predict change through an environmental gradient (Olson et al. 2009; Santos et al. 2016) and consequently, scaling models representing variation of functional traits provide new insights into the general mechanisms that relate biodiversity to the environmental and geographical changes (Violle et al. 2014). A spatial visualization of morphological scaling patterns can integrate individual and interspecific level responses to evaluate the importance of morphological adaptation in the explanation of broader scale processes. Finally, the integration of morphological and phylogenetic patterns at different geographic scales also helps to increase our understanding of the underlying mechanisms that establish communities and promote their evolution.

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Table 1(on next page)

Bioclimatic variables used to construct the climatic indexes.

Temperature mean variation index	**Temperature range index (seasonality)**	**Variation of precipitation in humid season**	**Variation of precipitation in the dry season**
BIO1 = Annual Mean Temperature **BIO5** = Max Temperature of Warmest Month **BIO6** = Min Temperature of Coldest Month **BIO8** = Mean Temperature of Wettest Quarter **BIO9** = Mean Temperature of Driest Quarter **BIO10** = Mean Temperature of Warmest Quarter **BIO11** = Mean Temperature of Coldest Quarter	**BIO4** = Temperature Seasonality (standard deviation *100) **BIO7** = Temperature Annual Range (BIO5-BIO6) **BIO2** = Mean Diurnal Range (Mean of monthly (max temp - min temp)) **BIO3** = Isothermality (BIO2/BIO7) (* 100)	**BIO13** = Precipitation of Wettest Month **BIO16** = Precipitation of Wettest Quarter **BIO12** = Annual Precipitation **BIO18** = Precipitation of Warmest Quarter	**BIO14** = Precipitation of Driest Month **BIO15** = Precipitation Seasonality (Coefficient of Variation) **BIO17** = Precipitation of Driest Quarter **BIO19** = Precipitation of Coldest Quarter

All bioclimatic variables taken from Worldclim 1.4 project (http://www.worldclim.org, Hijmans et al. 2005)

Figure 1

Geographical limits of the three delimited tyrant flycatchers datasets on the basis of the species distributed within Mexico.

Areas in green represent the distribution of the lowland tropical dry and humid forests (type I assemblage) and in brown the forests above 1500m (highland forests) or other types of vegetation (type II assemblage), the combination of both represent the regional assemblage. Modified from Ríos-Muñoz & Navarro-Sigüenza (2012) and Olguín-Monroy et al. (2013).

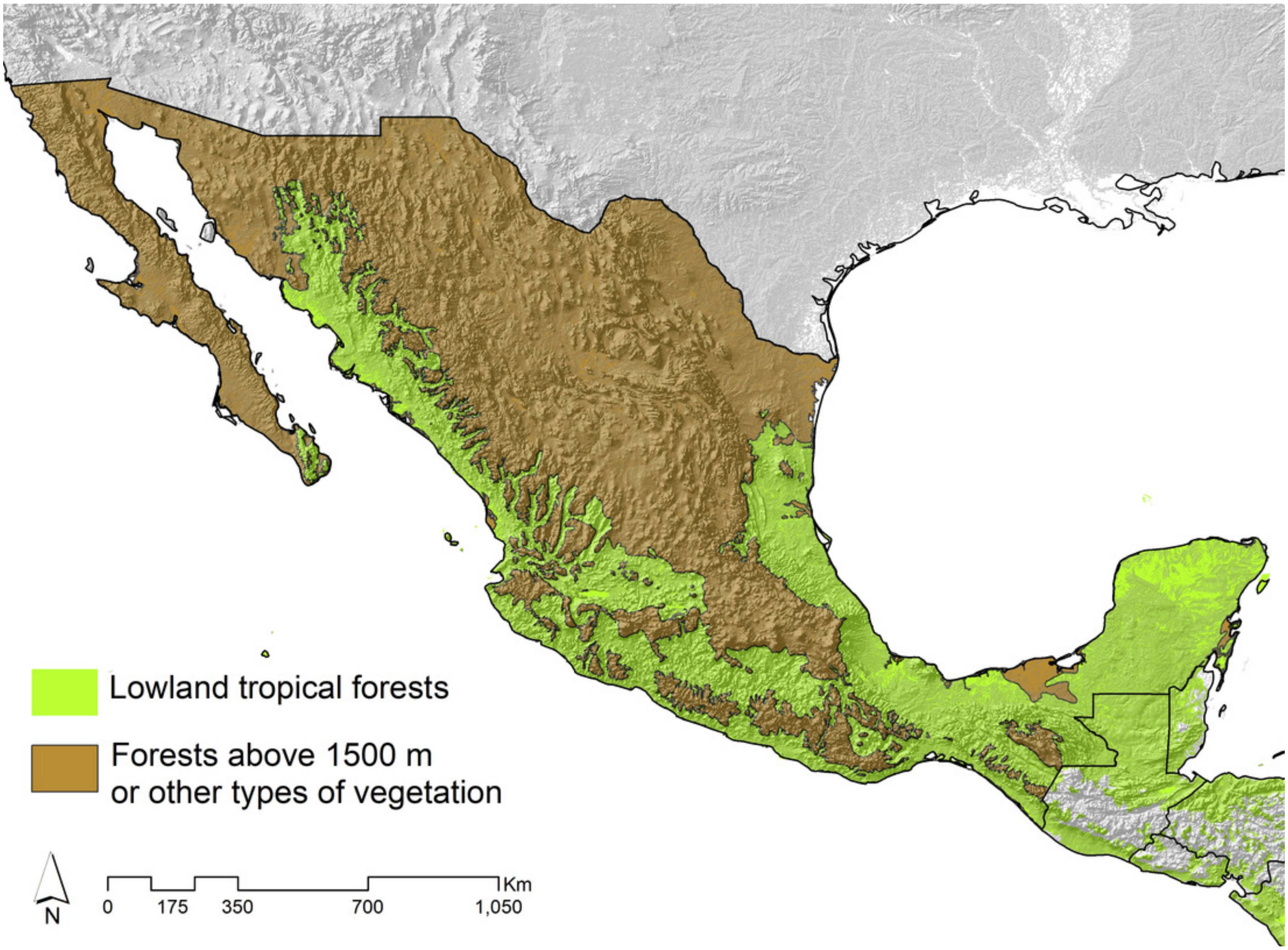

Figure 2

Nested structure of the database.

We measured the Tyrannidae data samples from multiple species, and from each species, we have various specimens, from each specimen we obtained one measure of body size, bill variation and wing length giving three responses for each individual.

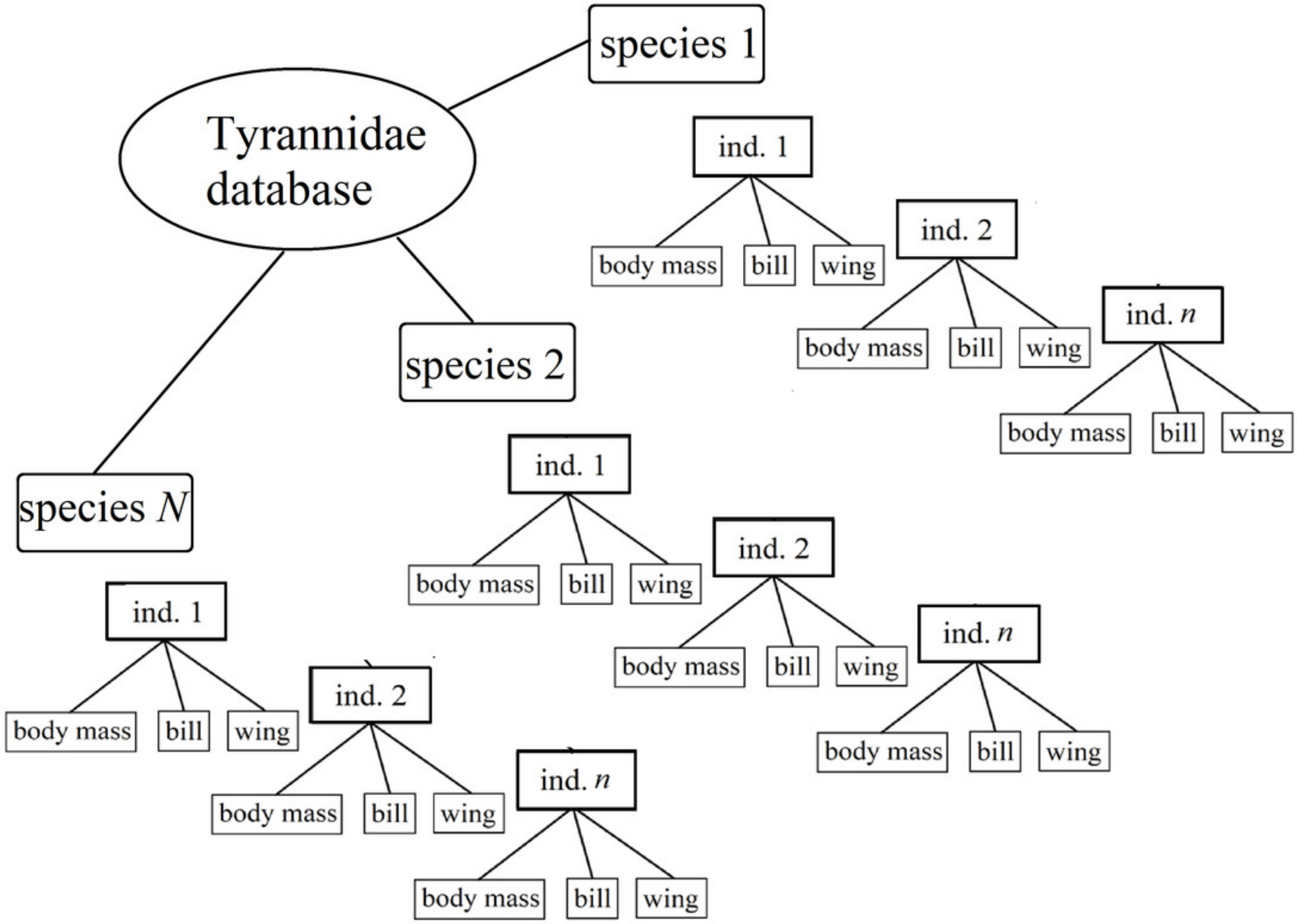

Table 2(on next page)

Variables used as fixed terms, interactions and random effects in the regression models for the Mexican tyrant flycatcher.

	Significance	**References**
Morphological variables	**Response variables**	
Body mass *(as size proxy)*	Body size is a major influential variable that explains most of the morphological and trait variation within an individual and a species. It is strongly related to lifestyle, and also imposes physical constraints to other morphological traits of birds. Body size can predict from the proportion of body parts to the distribution patterns of a species. Its variation has been related to variation in climate and other environmental and phylogenetic factors.	Schmidt-Nielsen (1984); Peters & Peters (1986); Olson et al. (2009); Bonner (2011); Salewski & Watt (2016)
Wing length	Wing is considered a major eco-evolutionary module of the birds, that is, a body part identified as an anatomical subregion of the musculoskeletal system that is highly integrated and act as functional unit during locomotion. Wing is related to the bird lifestyle, habitat exploitation and locomotion (bird flight), because of that, wing variation is very physically constrained. For tyrant flycatchers, wing is usually related to the type of habitat that the individual lives in and exploits, as they use a special flight called sallies to catch their prey.	Hamilton (1961); Fitzpatrick (1980); Fitzpatrick (1981); Fitzpatrick (1985); Miles & Ricklefs (1984); Gatesy & Dial (1996)
Bill variation	Bill is another major module of the birds, that is, a body part identified as an anatomical subregion of the head that is highly integrated and act as functional unit during specific processes of the individual, like feeding or communication. For this reason, bill is related to many features of the bird lifestyle, and varies and responds to environmental and evolutionary factors semi-autonomously from other body parts. For tyrants flycatchers, it is most related to their diet breadth and insectivorous feeding habits.	Fitzpatrick (1980);); Fitzpatrick (1985); Symonds & Tattersall (2010); Greenberg et al. (2012)
	Predictor variables **Fixed terms**	
Climatic variables Temperature means Temperature range Variation of precipitation in humid season Variation of precipitation in the dry season	Climatic gradients are part of the environment in which a species occurs. Variables of temperature and precipitation have been related to many functions of organisms and species, as they affect the variation of many morphological and lifestyle traits. For instance body size, distribution range, habitat and diet breadth (niche breadth), reproductive traits, trophic level, and others. In particular, for tyrants flycatcher's temperature means and range variation could define the suitable areas for occupation and habitat distribution. They also are supposedly major drivers of morphological trait variation. Precipitation seasonality may be related to the distribution of food, as insects abundance within forests and other habitats, is correlated to the humid season. Body size and appendages size may be related to climate gradients following the Bergmann's and Allen's rules, respectively, as temperature decrease, body size increases but appendages sizes decrease.	Diniz-Filho (2004); Zellweger et al. (2006); O'Donnel & Ignizio (2012), Symonds & Tattersall (2010); Salewski & Watt (2016)

Altitude **Topographic setting**	There is evidence that climatic patterns of precipitation and temperature are affected by altitude. For instance, temperature drops with altitude and precipitation patterns differs with the topographic orientation within a mountainous area (hillshade effect).	Seoane et al. (2004) Kobelkowsky-Vidrio et al. (2014)
Phylogenetic structure	Communities are assembled at the local level from regional pools of species, by means of competition and other biotic interactions, and also by the local dispersion or clustering of functional traits. But at regional scale, the sorting of species, in relation to its functional traits can be related to large-scale environmental and climatic gradients. The sorting of individuals at both scales is the result of the combination of the patterns and processes occurring at different scales, and includes an historical component by which the community (or assemblage) is constructed, that is the phylogenetic relatedness of the members of the community. Closely related species can coexist based in the distribution of their functional traits, so the trait composition of the community is predictable because of the sorting of individuals and the history of the community. Then, the phylogenetic structure of a community can potentially explain the distribution of trait at the community or assemblage scale.	MacArthur & Levins (1967); Webb et al. (2002); Cavender-Bares et al. (2009); Lawing et al. (2017)
Interaction terms		
Altitude x Climatic variables (one interaction with altitude per each climatic index)	As there is clear evidence of the relationship between climate and altitude, we considered that the interaction between the two types of variables (their conjoint effect) must be considered in the model as a term that might explain morphological variation.	Seoane et al. (2004)
	Predictor variables **Random effect**	
Species of a subfamily at an assemblage influenced by the phylogenetic structure of the communities	Individual's morphological traits are likely to resemble more to the morphology of another individual of the same species, simply because they belong to the same phylogenetic group (their share common ancestry). Measures from individuals of the same species are expected to be correlated; this nested structure potentially violates the statistical assumptions of independence among data, so it has to be considered in the analysis.	Blomberg & Garl& (2002); Blomberg et al. (2003); Zuur et al. (2009)
Variance structure		
Phylogenetic membership of species	Different species groups, have different response to the fixed terms, thus morphological variables show different dispersion of the data simply because they belong to different groups.	Blomberg & Garl& (2002); Blomberg et al. (2003); Zuur et al. (2009)

Table 3(on next page)

Best-fitting models for each morphological trait using mixed-effects model regression.

logLIK= Maximum Likelihood; AIC = Akaike's information criterion; BIC= Bayesian Information Criterion.

Assemblage	Morphological variable	AIC	BIC	logLIK	Model structure	Intercept	Slope	*p*-value
Regional								
	Body size	-167.095	-144.515	90.547	logMass~Temperature range	1.11	0.42	<0.001
	Bill	490.442	503.409	-241.221	logMass~Temperature range	-0.94	0.65	<0.05
	Wing	-431.851	-402.917	224.925	logMass~Temperature range	1.81	0.091	<0.001
Type I								
	Body size	-157.429	-128.495	87.714	logMass~Temperature range+phylostructure	1.12	0.56, -0.35	<0.001
	Bill	491.238	504.205	-241.619	logMass~Temperature range+phylostructure	-0.94	0.043, 0.03	<0.05
	Wing	-460.550	-444.368	235.275	logMass~Temperature range+phylostructure	1.81	-0.002,-0.014	0.45
Type II								
	Body size	-178.785	-162.602	94.392	logMass~ Temperature range+ phylostructure	1.11	0.65, 0.60	<0.001
	Bill	513.291	542.226	-247.645	logMass~Temperature range+phylostructure	-0.94	0.034, 0.029	0.06
	Wing	-475.085	-462.118	241.542	logMass~ Temperature mean variation+phylostructure	1.36	-0.004, -0.013	0.141

*** Assemblages explanation. Type I: Lowland tropical forests. Type II: Highlands above 1500 masl and other types of vegetation. Regional the combination of assemblages type I and II.**

Figure 3

Geographical patterns of phylogenetic structure.

(A) Phylogenetic structure at localities of the lowland forests. (B) Phylogenetic structure at localities of the highland forests or other types of vegetation.

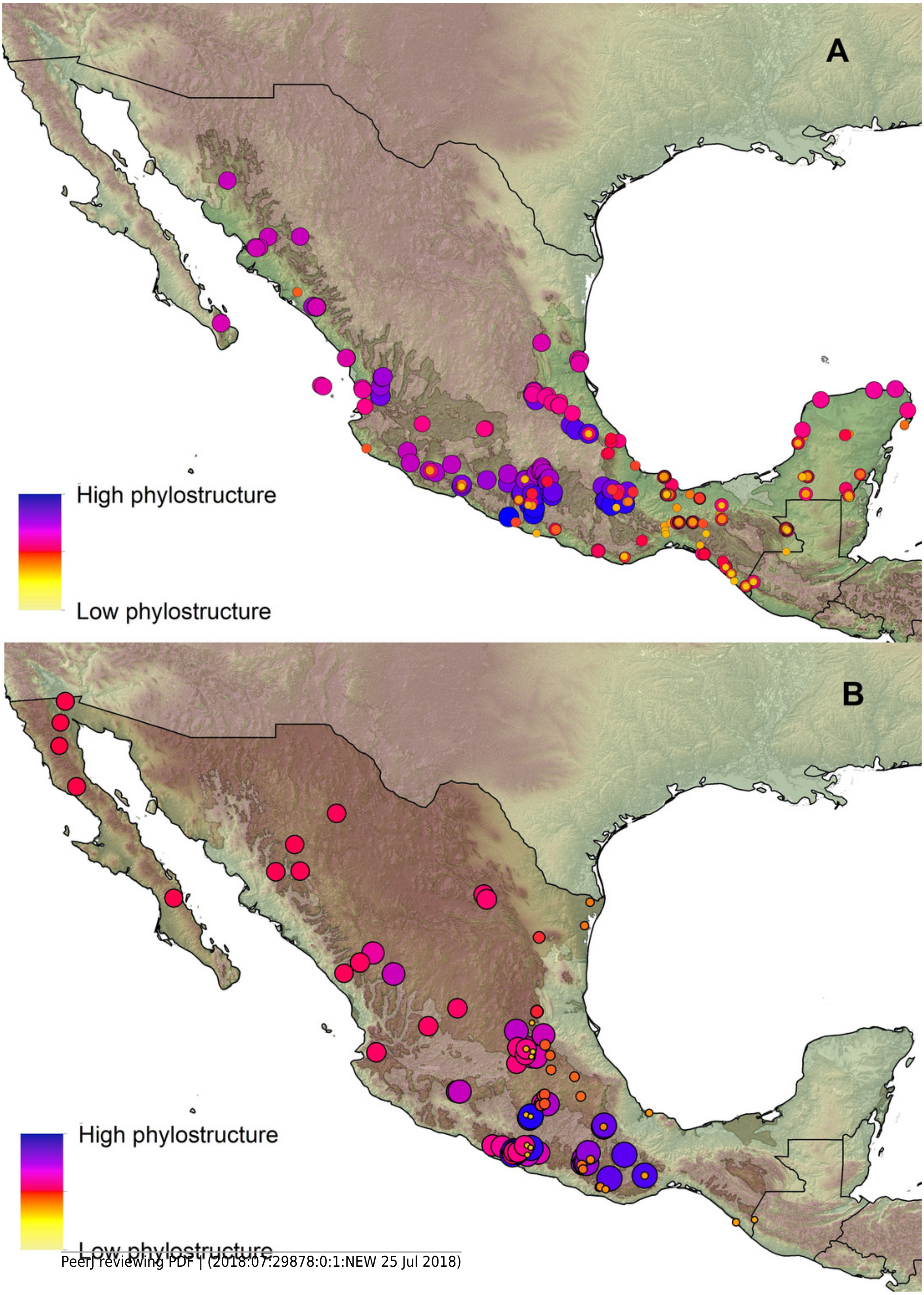
A
High phylostructure
Low phylostructure
B
High phylostructure
Low phylostructure

Figure 4

Spatial distribution of scaling patterns of body size, bill size and wing length fitted for the regional assemblage by temperature range index.

The scatterplot diagram and the regression lines show the predicted response of body size, bill and wing to the increase in seasonality (Temp. range).

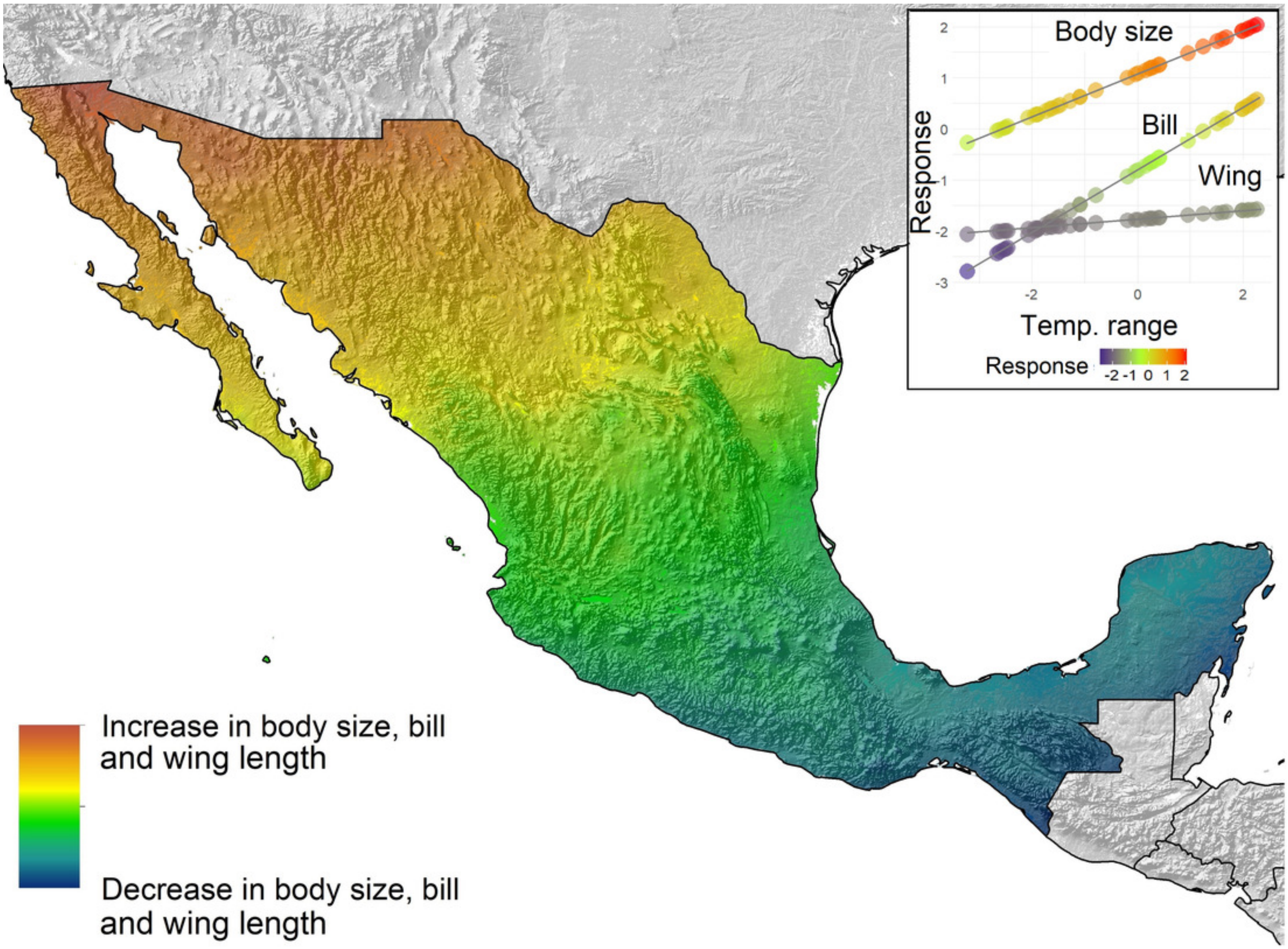

Figure 5

Spatial distribution of scaling patterns of body size and bill fitted for the type I assemblage by temperature range index.

The scatterplot diagrams and the regression lines show the predicted response of body size and bill to the increase in seasonality (Temp. range), and the increase in phylogenetic clustering (phylostructure).

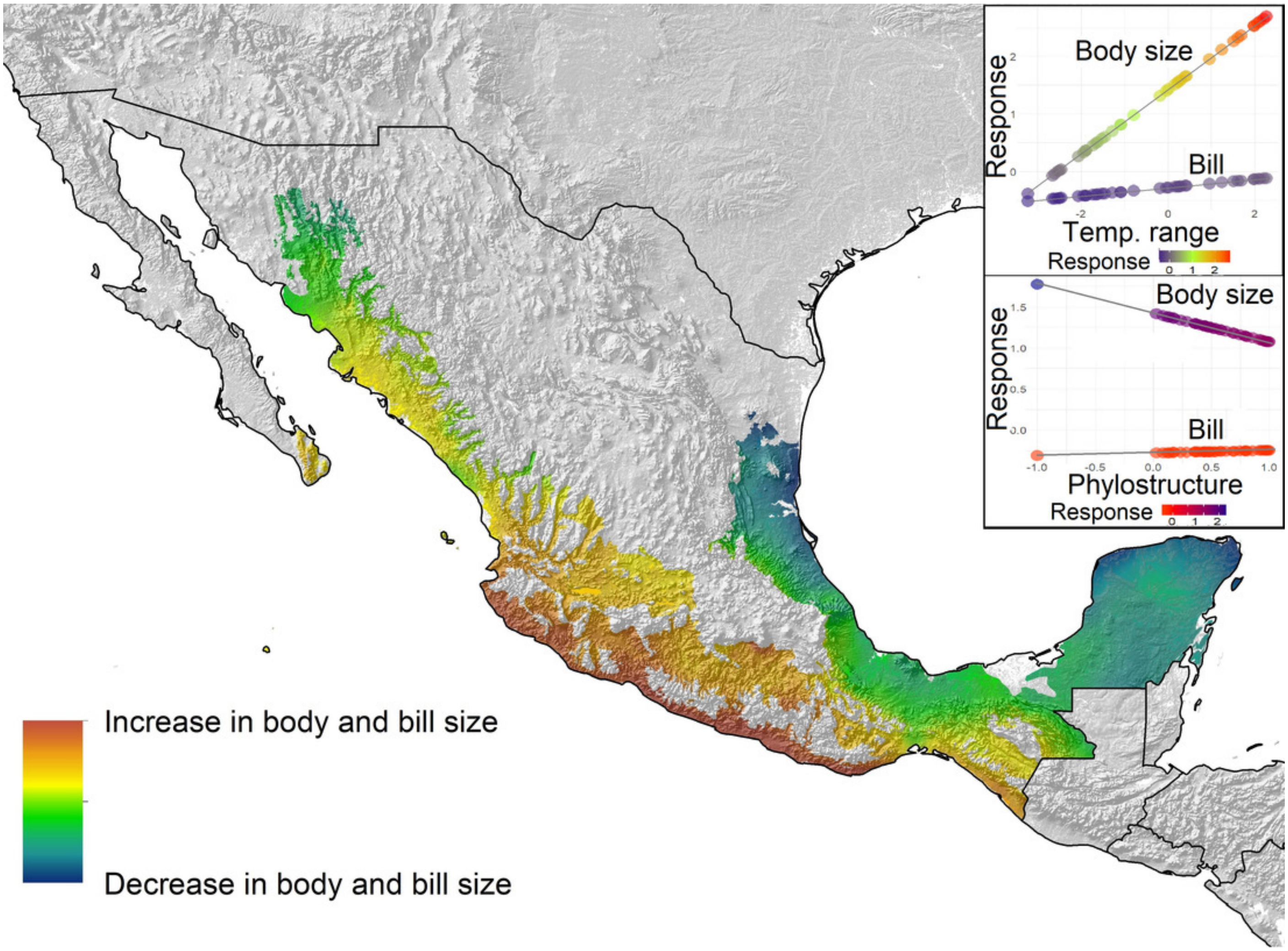

Figure 6

Spatial distribution of scaling patterns of body size fitted for the type II assemblage by temperature range index.

The scatterplot diagrams and the regression lines show the predicted response of body size to the increase in seasonality (Temp. range), and the increase in phylogenetic clustering (phylostructure).