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

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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 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 the regional assemblage, the spatial distribution of body size shows a 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 trait values increased. Phylogenetic structure helps to explain the variation of morphology at lower assemblages but not at the regional assemblage. The patterns of trait variation along lowlands and highlands assemblages, suggest that part of morphological variation 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 regression models representing this variation and integrating phylogenetic patterns at different community levels provide new understanding into the mechanisms underlying the link between biodiversity, its geographical setting, and the environmental change.

1 **Influence of phylogenetic structure and climate gradients on**

2 **geographical variation in the morphology of Mexican**

3 **flycatcher forests assemblages (Aves: Tyrannidae)**

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26 **Abstract**

27 Morphological variation is strongly related to variation in the ecological characteristics and

28 evolutionary history of each taxon. To explore how geographical variation in morphology is

29 related to different climatic gradients and phylogenetic structure, we analyzed the variation of

30 morphological traits (body size, bill, and wing) of 64 species of tyrant flycatchers (Tyrannidae)

31 distributed in Mexico. We measured these morphological traits in specimens from biological

32 collections and related them to the climatic and topographic data of each collection locality. We

33 also calculated the phylogenetic structure of flycatcher assemblages of each locality in order to

34 explore the influence of climatic variables and the phylogenetic structure over the morphological

35 variation of tyrant flycatchers, by means of linear mixed-effects models. We mapped the spatial

36 distribution of the variation of morphological traits in relation to environmental gradients taking

37 into account the phylogenetic structure. The climatic variables that better explained the

38 morphological variation were those of temperature ranges (seasonality) and the results suggest

39 that the phylogenetic clustering increases towards the highlands of Sierra Madre Oriental and

40 Sierra Madre del Sur, and the lowlands of Balsas Depression. At the regional assemblage, the

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42 rule, with an increase in size from south to north. In the tropical lowland forests assemblage,

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51   the mechanisms underlying the link between biodiversity, its geographical setting, and the

52   environmental change.

54

55   **Introduction**

56   A long-standing goal in ecology and evolutionary biology is to understand the relationships

57   among morphological diversity, evolutionary history, environment and geographic distribution.

58   Environmental drivers of morphological diversity across geography have been extensively

59   studied in many regions with different taxonomic groups, at different geographic, taxonomic and

60   functional scales (Losos & Miles, 1994; Cavender-Bares et al., 2009; Kluge & Kessler, 2011;

61   Violle et al., 2014; Jarzyna et al., 2015; Jarzyna & Jetz, 2016; Lawing et al., 2017; Schneider et

62   al., 2017; Seeholzer et al., 2017; Phillips et al. 2018; Mazel et al., 2018). As a result of previous

63   studies that analyze the role of environment and geography as promoters of morphological

64   diversity, patterns of gradual variation of traits have been detected for many groups. Climate

65   seems to be one of the main environmental promoters of morphological variation, strongly

66   influencing the distribution and variation of morphological traits across species and regions (e.g.

67   James, 1970; Graves, 1991; Kivelä et al., 2011; Maestri et al., 2016; Xu et al., 2017). However,

68   the role of climate and other environmental variables is poorly understood. Even though many

69   studies have demonstrated its associations with morphological traits, the question remains to

70   what extent and by which mechanisms such associations are maintained and may influence

71   distribution patterns (Violle et al., 2014). It has been suggested that several variables may act

72   simultaneously, promoting morphological variation at many taxonomic and geographic scales.

73

74   Morphological diversity across species is driven by several ecological and evolutionary

75   processes and is usually studied as the evolution of form and function, or ecomorphology (Losos

76   & Miles, 1994; Ricklefs, 2012; Dehling et al. 2014; Seeholzer et al. 2017; Phillips et al. 2018).

77   Also, variation in morphological diversity within communities can have effects in structuring

78   broad-scale biogeographical patterns of species richness along climatic and geographical

79   gradients (Deutsch et al., 2008; Cicero & Koo, 2012). Morphological variation is related to

80   ecology and reflects a response to biotic and abiotic environmental factors, and it may determine

81   species' responses to climate change (Wainwright and Reilly, 1994; Pontarotti, 2010; Cicero &

82   Koo, 2012). Climatic variables, such as temperature and precipitation, are recognized as major

83   factors determining geographical patterns of morphological variation (Hawkins et al., 2007). For

84   instance, bill size increases with higher temperatures, supporting the hypothesis that larger bills

85   are an adaptation to release heat while minimizing evaporative water loss in hot, dry

86   environments (Greenberg et al., 2012). In this way, overall bill size may be related to

87   physiological responses to regional climates, and the season of critical thermal stress may vary

88   geographically, even on relatively small spatial scales (Campbell-Tennant, Gardner & Kearney,

89   2015; Danner and Greenberg, 2015). Other factors such as evolutionary history also have been

90   found to determine geographical gradients in species variation (Jetz & Rahbek, 2002, Kissling et

91   al., 2007). For instance, habitat filtering is an ecological process by which species are eliminated

92   from a community because of morphological/ecological similarity with other established

93   members of the community (Wainwright and Reilly, 1994). Under this interpretation, the

94 variation of morphological variables across communities and geography is proportional to the

95 amount of phylogenetic dissimilarity among communities (Pillar and Duarte 2010), taking into

96 account that morphology is structured by phylogeny at the species level if there is phylogenetic

97 signal. Morphological variation occurs within and across species, so the complex interaction of

98 evolutionary history and environment makes difficult to identify the underlying causes of broad

99 scale patterns of variation (Endler, 1977; Ricklefs & Miles, 1994; Violle et al., 2014; Forister et

100 al., 2015).

101   The recognition of the promoters of broad scale patterns of morphological variation is

102 challenging due to the differential response of organisms' traits to environmental variation and

103 geographical settings (Violle et al. 2014). This limits our ability to elucidate the causes and

104 consequences of the patterns of species' morphological diversity. For instance, the geographical

105 patterns of community structure and morphological variation in response to climatic gradients

106 has shown contrasting effects of the same environmental variables (e.g. Forister et al., 2015; van

107 de Pol et al., 2016; Lawing et al., 2017). To understand how morphological diversity arises, it is

108 necessary to explore and quantify how species' morphological traits are related to their ecology,

109 how they vary geographically along environmental gradients, consider both large and small

110 spatial scales in the same region, and account for the historical contingencies limiting the

111 distribution of species assemblages and their traits (Cavender-Bares et al., 2009). In this sense,

112 phylogenetic structure and distributional data provide the historical framework to quantify

113 ecological, geographical and evolutionary patterns, in order to infer the processes that established

114 them (Saito et al. 2016; Sobral & Cianciaruso 2016, Phillips 2018). Also, quantifying the

115 geographical distribution of morphological variation may help disentangle trade-offs found in the

116 relationship between morphology and environmental and phylogenetic variables. Then, analyses

117   of the distribution of morphological variation are necessary for improving regional and global

118   predictions of morphological and functional change (Diniz-Filho, 2004; Rodríguez & Ojeda,

119   2014).

120   To evaluate broad scale patterns of morphological variation and the underlying processes

121   which promote them, it is necessary to quantify the distribution of morphological traits in

122   relation to the ecology of related functional groups of species. In that sense, some authors have

123   found that the global patterns of functional richness are associated with environmental variables

124   (Kissling et al., 2009; Brum et al., 2012). To describe how morphology varies geographically

125   with environment, we explored the spatial distribution of a set of morphological variables in

126   relation to climatic gradients of a mainly insectivorous assemblage of birds, the tyrant flycatchers

127   (Tyrannidae). The tyrant flycatchers constitute a functional group of species that use insects and

128   arthropods as their main food resource (Hespenheide 1971; Sherry 1984). This taxon includes

129   more than 400 species distributed across the Americas (IOU, 2018) occurring in almost every

130   habitat. They are adapted to different elevations and occupy all vertical forest strata (Fitzpatrick

131   et al., 2004, Ridgely and Tudor, 2009). We chose the Tyrannidae of Mexico as a model system

132   because: (1) they are widely distributed in the country (Ridgely et al., 2005; Berlanga et al.,

133   2008); (2) the natural history, phylogenetic structure, and functional significance of their

134   morphological traits is relatively well known (Ohlson, Fjeldså & Ericson, 2008; Tello et al.,

135   2009); (3) their morphology can be related to their ecology (e. g., Fitzpatrick 1980, 1981, 1985);

136   and (4) their morphology varies across environmental and geographical gradients (Brum et al.,

137   2012).

138   Our main goal was to investigate the variation of morphology across geography and to

139   determine the relationship of environmental climatic gradients as explanatory factors of

140   morphological function-related traits. We have considered the phylogenetic structure of Mexican

141   flycatchers as a factor that may help explain how broad scale patterns in species variation are

142   established and how historical contingencies influence the response of morphological variation

143   to the environment. Our specific objectives were to test (1) whether climate conditions

144   (temperature, precipitation, and their seasonality), are associated with the observed variation in

145   morphology across tyrant flycatchers assemblages; (2) the influence of the phylogenetic structure

146   of assemblages on the geographic distribution of morphological variation and its response to

147   climate; and (3) to map the spatial distribution of morphological variation along climatic

148   gradients. Because traits are related to the ecology of the organism, for instance foraging

149   behavior or habitat use (Fitzpatrick, 1985), morphological variation is expected to reflect

150   species' responses to environmental gradients. Then, the approach we used takes into account

151   varied ranges in climate and seasonality within a lineage, abiotic variables influencing the

152   geographic distribution of species, and the phylogenetic relationships among the tyrant

153   flycatchers. Taking into account phylogenetic relationships within a community by accounting

154   for phylogenetic structuring, may help to understand the influence of the composition of a

155   community on the response of traits to environmental variation (Bonetti & Wiens, 2014; Maestri

156   et al., 2016).

157

158   ***Hypothesis and assumptions***

159   Given that climatic gradients and phylogenetic structure of an area potentially play a role as

160   promoters or constrainers of morphological variation, and because this role may vary in strength

161   and direction, we analyzed the morphological data by constructing regression models in order to

162   explain the relationship between morphology, environment and phylogenetic structure. We

163   hypothesized that once historical and geographic factors are accounted for: Hypothesis 1) climate

164   gradients explain morphological change across geography; and hypothesis 2) phylogenetic

165   structure of a community should influence morphological variation of the co-occurring species.

166   For hypothesis 1, we assumed that morphology would show clinal variation related to one or

167   more climatic variables, then a latitudinal pattern when the model is translated to a map.

168   Conversely, for hypothesis 2, we assumed that morphological change cannot solely be explained

169   by climatic variables, but also phylogenetic structure would also be significantly associated to

170   variation in morphology (evidence for hypothesis 2). Latitudinal variation in morphology is

171   likely to be affected by the phylogenetic composition of the area, that is, the variation of

172   morphological traits across geography is expected to be proportional to the amount of

173   phylogenetic dissimilarity among communities (Duarte, 2011). Phylogenetically clustered areas

174   are expected to show different patterns of morphological variation than areas that are

175   phylogenetically overdispersed. Because of the tendency of species to remain in an

176   environmental space similar to that of their ancestors (Wiens & Graham, 2005) we expect that

177   morphological variation within assemblages will be constrained. Phyllogenetically clustered

178   assemblages are more likely to be restricted in their climatic ranges, whereas phyllogenetically

179   overdispersed assemblages are more likely to be found in the transition zones where there is a

180   high species turnover (Graham et al., 2009) sepecies competition influences the local trait

181   composition of a community (Wainwrigth & Reilly, 1994). Phylogenetic structure alone is

182   unlikely to explain the variation of morphology; instead it is expected to influence morphology

183   along with climatic variables, meaning that the response of the trait could be driven by either

184   environmental filtering (species are filtered from a community due to morphological or

185   ecological similarity with other co-occurring species), other biotic interactions (e.g. competition),

186   or random factors (Cavender-Bares et al., 2009; Lawing et al., 2017).

187

188   **METHODS**

189   ***Morphological traits data and data treatment***

190   *Morphological data.* In order to construct regression models of environmentally-related

191   morphological variation, the morphological traits were associated to locality-specific climate,

192   topographic and phylogenetic structure data. We obtained morphological data from a sample of

193   296 skin specimens from 60 species of Tyrannidae distributed in Mexico (Table S1). We

194   measured five traits (Claramunt, 2010, following recommendations by Eck et al., 2011): body

195   size (using mass data as a proxy), bill length, bill width, and bill depth (the last two taken at the

196   anterior border of the nostrils), and wing chord (wing length from the carpal joint to the tip of the

197   longest primary feather without flattening the wing). We selected these traits because they have

198   been associated use of environmental space in birds (Miles & Ricklefs, 1984). Size is a

199   significant attribute at all levels of organization, as it predicts and explains the variation of many

200   organismal and species traits, from the proportion of parts to metabolic rates to the distribution

201   patterns (Schmidt-Nielsen, 1975; Brown, 1995; Diniz-Filho, 2004; Bonner, 2011). Bill size can

202   be positively correlated with temperature in avian taxa (Allen's rule), and the common

203   explanation for this pattern is that larger surface area of the appendage functions to dissipate

204   excess heat in warm climates and small area to retain heat in cold climates (Symonds &

205   Tattersall, 2010; Greenberg, 2012). The bill is also the functional trait by which birds obtain

206   food, so it can be related to habitat and ecomorphological variation (Mazer & Wheelwright,

207   1993; Jones; 2012). The relative variation of bill measures represents its variation in size and

208   shape. Finally, wing chord plays a role in determining the aerodynamics and mechanical aspects

209   of the avian wing, thus it interacts with the effective exploitation of habitat; so it is strongly

210   related with ecology and behavior (Hamilton, 1961; Lockwood, 1998, Swaddle & Lockwood,

211   1998, Gatesy & Dial; 1996). Together, body size, bill size and wing chord represent

212   morphological traits that are related to the flycatcher ecology.

213   In general, we only measured adult male specimens to homogenize the data set and to

214   avoid morphological variations associated with sexual dimorphism. In some cases, we had to

215   measure female specimens (~8% specimens) to complete the sample, and used these data based

216   on a previous test (Cortés-Ramírez, Ríos-Muñoz & Navarro-Sigüenza, 2012) that showed that

217   the variation between sexes is smaller than interspecific variation (*sensu* Claramunt, 2010). We

218   took all the measurements with digital or analog Mitutoyo calipers, with a precision of 0.01 mm.

219   For statistical analysis we used *natural log*-transformed measures in order to normalize the

220   dataset, and because all morphological measurements may scale with overall body size, we made

221   bill and wing size measurements relative to body size by dividing each measurement by body

222   mass. Relative variation of the three bill measurements was obtained by performing a principal

223   component analysis (PCA) to reduce the dimensionality of bill variation (Table S2), retaining the

224   first principal component as representative of bill variation and size. The first principal

225   component represented 86% of bill variation and overall size of the bill. Each morphological

226   variable was evaluated independently from the other variables.

227

228   ***Environmental and geographic data.***

229   *Climatic variables.* We considered the geographic location of each specimen to obtain locality-

230   specific climate data based on a set of 19 bioclimatic variables (Hijmans et al., 2005). To reduce

231   the dimensionality without eliminating bioclimatic variables, we constructed four climatic

232   indexes by applying a PCA on climatic variables following Alvarado-Cárdenas et al. (2013,

233   Table 1). These four indexes represent annual temperature variation, temperature range or

234   seasonality, variation of precipitation in the most humid season, and variation of precipitation in

235   the driest season. We decided to use the first principal component of each climatic index, as they

236   account for most of the climatic variation in the study area (Table S3). For each specimen we

237   extracted locality-specific climate index data using a geographic information system. We used

238   the climatic index data for each individual as a fixed explanatory variable in the regression

239   models.

240

241   *Topographic variables.* In order to separate the effects of the geographical setting, we used the

242   USGS Digital Elevation Model (altitude, USGS, 2015, https://lta.cr.usgs.gov/GTOPO30) and

243   aspect as predictor variables in all regression models. To facilitate the use of aspect as a variable

244   that describes topographic orientation, we transformed it using the cosine to express northness

245   and the sine for eastness following Kobelkowsky-Vidrio, Ríos-Muñoz, & Navarro-Sigüenza

246   (2014).

247

248   ***Historical distribution and relatedness data***

249   *Assemblages of the tyrant flycatchers.* In order to discriminate the effects of the

250   evolutionary/historical distributional of the tyrant flycatchers, we divided the data into three

251   separate sets taking into account characteristics of three constructed assemblages of tyrant

252   flycatchers distributed across Mexico. We defined an assemblage as a temporal and spatial

253   arrangement in which species potentially occur and interact; i.e., the pool of species in a

254   geographic area (Halffter & Moreno, 2005, Lessard et al., 2016). We defined three assemblages

255   on the basis of environmental factors delimited by elevation and vegetation type (Fig. 1, Table

256   S1): Type I- Assemblage of the lowland forests (species distributed only below 1500 m), Type

257   II- Assemblage of the highland forests (species present mainly above 1500 masl) and other types

258   of vegetation, and the Regional assemblage (species distributed in both assemblages, which

259   represent the species distributed in all Mexico). We assigned the species to each assemblage and

260   carried out statistical analysis independently for each data set. We focused on the type I

261   assemblage data because Mexican lowland forests are characterized by high levels of species

262   richness, endemism, and habitat specialization, and patterns of biogeographic distribution define

263   them as areas with a particular evolutionary history (Ríos-Muñoz & Navarro-Sigüenza, 2012;

264   Olguín-Monroy et al., 2013). The Type II and Regional assemblage datasets were used to

265   contrast the response of morphological variation to environmental gradients at different spatial

266   scales and community levels. It is known that the influence of different variables on the

267   morphological variation change at different scales of analysis (Lawing et al., 2017).

268

269   *Phylogenetic signal and phylogenetic structure.* We reconstructed a phylogenetic tree for the

270   species of Tyrannidae distributed in Mexico using Jetz et al.'s (2012) bird tree with the Hackett

271   et al. (2008) backbone (Fig. S1), in order to calculate the phylogenetic signal of traits and the

272   phylogenetic structure of the localities. The phylogenetic signal was calculated for each

273   morphological variable using the generalized K statistics (Adams, 2014). Phylogenetic signal

274   indicates the tendency of related species to resemble each other more than species drawn at

275   random from the same tree (Blomberg & Garland, 2002). Generalized K statistics tests a null

276   model of evolution of a trait by Brownian motion (drawn at random from the tree), $K = 1$

277   indicates that trait evolution is consistent with Brownian motion model, while K<1 indicates less

278   similarity in the trait than expected under Brownian motion model, and K>1 indicates greater

279   similarity in the trait than expected under Brownian motion model (Blomberg et al., 2003).

280   Phylogenetic signal tests were conducted using *geomorph* package (Adams & Otarola-Castillo,

281   2013) in R version 3.4.1 (R Core Team, 2017).

282   To determine if the species in a particular area were more closely related than expected

283   by chance, we measured the phylogenetic structure of the Tyrannidae distributed at each locality.

284   To calculate the metric, we used the Net Relatedness Index (NRI, Webb et al., 2002) in the R-

285   package *PhyloMeasures* (Tsirogiannis & Sandel, 2016). Values of NRI greater than zero indicate

286   phylogenetic clustering and values lower than zero indicate phylogenetic evenness or

287   overdispersion. Phylogenetic clustering is found when the co-occurring species of an area are

288   more closely related than expected by chance. Phylogenetic evenness or overdispersion is found

289   when the coexisting species of an area are less related than expected by chance (Webb et al.,

290   2002). To calculate the NRI for each locality, we used the reconstructed phylogenetic hypothesis

291   and we established which species likely co-occur by extracting presence data from distributional

292   hypotheses for Mexican Tyrannidae, generated elsewhere using ecological niche models

293   (Navarro-Sigüenza et al., unpubl. data).

294

295   ***Statistical analyses***

296   ***The regression models***

297   We evaluated the effects of environmental gradients and phylogenetic structure on

298   morphological variation in the tyrant flycatchers of Mexico using regression models. We

299   constructed trait maps (see below) and obtained our inferences based on the fitting of linear

300   mixed-effects models predicting morphological variation in body size, bill and wing length. We

301   used linear mixed-effects modeling because our data are nested in the sense that samples derive

302   from multiple species, and from each species we have various specimens.

303   To find the best fitting models for each morphological variable (and assemblage dataset),

304   we followed the protocol recommended by Zuur et al. (2009). In the first step, we started with a

305   model for each morphological variable that contained all the predictor variables and their

306   interaction in the fixed part of the model. There are seven fixed predictor variables (temperature

307   variation index, temperature range or seasonality index, variation of precipitation in humid

308   season, variation of precipitation in the dry season, topographic setting, altitude, and

309   phylogenetic structure) and four interactions (relationships between altitude and the temperature

310   and precipitation indexes, Table 2, Table S4 model 1). After obtaining the more complex linear

311   model, we made a new model allowing random intercepts for the nested structure of individuals

312   of a species within a subfamily (Table 2, Table S4 model 2). The random intercept implies that

313   the basal value of the response is influenced by the nested structure of the data, so measures

314   within a species are more likely to be correlated just because they belong to the same

315   phylogenetic group (Militino et al., 2010). Next, we allowed random slopes and intercepts for

316   individuals of a species within a subfamily (random intercept), influenced by the phylogenetic

317   structure of the communities (random slope, Table 2, Table S4 model 3). Letting the slope to

318   change implies that morphological traits can change between communities in function of how

319   closely related are the species distributed on it. Then, we included the optimal variance structure

320   to the optimal model for the random terms (Table 2, Table S4 model 4). We considered that

321   different variance exist for the observations that have distinct phylogenetic membership. Next,

322   we selected the best fitting model structure for the fixed terms by sequentially adding each

323   predictor variable and their interactions (Table 2) to the optimal random and variance structure

324   model (Table S4 models 5-16). We tested if phylogenetic structure influenced morphological

325   variation (Evidence for hypothesis 2, Table S4 model 12) by including it to the best fitting model

326   for the fixed terms. Finally, we included the interaction term between phylogenetic structure and

327   the climatic variables that best explained the morphological variation (temperature seasonality,

328   model 17). The interaction between phylogenetic structure and temperature seasonality implies

329   that phylogenetic structure modifies the effect of temperature seasonality on the morphological

330   variation within assemblages. The final products of the procedure described were nine best

331   fitting models predicting each morphological variable, at each assemblage, in relation to climatic

332   variables, phylogenetic structure and phylogenetic membership (Table S4, Table 3). We

333   considered the best-fitting model for each variable the one with the highest maximum likelihood

334   (ML), the Akaike information criterion (AIC), and Bayesian informative criterion (BIC,

335   Burnham & Anderson, 2002). We performed all statistical analyses using the *nlme* (Pinheiro et

336   al., 2013) package in R version 3.4.1 (R Core Team, 2017).

337

338   ***Mapping the spatial variation of morphological traits***

339   To map the spatial variation of the morphological traits, we extrapolated the best-fitting models

340   into GIS layers. First, we extracted the value of the predictor climatic variable in each pixel (30

341   seconds per side) of Mexico within each assemblage. Then, we translated the best-fitting model

342   formula for the climatic index value at each pixel. For instance, if the model was: "*Size expected*

343   *at pixel X = slope*value of climatic index at pixel X + intercept*", we obtained a different value

344   for the morphological variable at each pixel according to the model and the variation of the

345   predictor variable, generating a map of the measurements of the functional traits (Moles et al.,

346   2011). We performed all analyses using the Maptools (Lewin et al., 2011) package in R version

347   3.4.1 (R Core Team, 2017). Trait maps were visualized using ArcGIS 10 (ESRI, 2011).

348

349   **RESULTS**

350   ***Relationship between climatic gradients and morphological variation***

351   Climatic gradients were associated positively with morphological variation of the three measured

352   traits in all three assemblages (Table 3). All best fitting models included at least one climate

353   variable among the fixed terms, specifically, temperature seasonality (temperature range) or

354   mean variation. Temperature appears to explain variation in morphology at all levels analyzed.

355   At the regional assemblage, for body size, bill and wing length, temperature is related positively

356   and significantly to morphological change, and reflects increase in the morphological variables

357   values as temperature seasonality increases. The magnitude of the response is higher for body

358   and bill sizes (slopes 0.42 and 0.65, respectively), whereas for wing is close to zero

359   (slope=0.091); that means that although it is positive and reflects an increase in the

360   morphological variable values, this change is small. In other words, while the climatic

361   seasonality increases, wing length will not tend to increase as much as body and bill size, it

362   reflects a poor association between wing and temperature range index.

363   For type I and type II assemblages, the relationship between morphological variables and

364   temperature range is also positive but not significant for some variables (*p-value*>0.05). For

365   instance, the regression model for bill size and temperature range, and wing length and

366   temperature range, in the highland forests and other types of vegetation assemblage indicates that

367   the relationship is not significantly different from 0 (there is no relationship between the

368   morphological variable and temperature range). Also, for the lowland forests assemblage,

369   regression model for wing and temperature range is not significant either. Only the relationship

370   between body size and temperature range is significantly positive in all assemblages. The

371   relationship between bill variation and temperature range is significant in lowland forests

372   assemblage but the magnitude of the response is less steep (slope=0.43).

373

374   ***Influence of phylogenetic structure on morphological variation***

375   Linear mixed-effects models results indicated that phylogenetic relatedness also helped to

376   explain morphological variation in type I and type II assemblages, for body size, bill and wing

377   variables (Table 3). At highland forests and other types of vegetation assemblage, models for bill

378   and wing were not significant (*p-value*>0.05), whereas the model for body size is significant and

379   positively related to phylogenetic structure (slope= 0.60). A positive correlation between body

380   size and phylogenetic structure means that body size values increase at areas with more

381   phylogenetically related species occurring at the community (phylogenetic clustering), and

382   decreases in areas with less phylogenetically related species (phylogenetic overdispersion). For

383   lowland forests, phylogenetic structure was positively correlated to bill variation, and negatively

384   correlated to bosy size. The relationship between wing and phylogenetic structure was not

385   significant. The results indicate that there is a tendency of decrease in body size while

386   communities became more phylogenetically clustered.

387   Our results indicate that phylogenetic structure exhibits a geographical pattern (Fig. 2).

388   Both highland and lowland forests assemblages presented areas with phylogenetic overdispersion

389   and phylogenetic clustering (Table S5). Areas of higher phylogenetic clustering appeared to be

390   distributed along the lowland areas of the Balsas Depression, and the highlands of Sierra Madre

391   del Sur (mountain range in the southern Mexico) and Sierra Madre Oriental (mountain range in

392   eastern Mexico). Areas with high phylogenetic overdispersion are mainly distributed in

393   southeastern Mexico (i.e. southeastern Yucatan Peninsula, Tehuantepec Isthmus).

394   We also measured the phylogenetic signal of the morphological traits, in order to explore

395   the tendency of the traits to resemble each other taking into account phylogenetic relatedness.

396   Phylogenetic signal analysis returned a value of K= 0.85 for body size, K= 0.88 for bill variation,

397   and K= 0. 87 wing chord. All values were statistically significant at α= 0.05. These values

398   indicate that although the phylogenetic signal for each morphological variable at the species

399   level is lower than 1, values are close to Brownian motion model (no tendency of traits to

400   resemble each other due to phylogenetic relatedness), which means that they are slightly less

401   similar than expected due to phylogenetic relatedness.

402

403   ***Spatial variation of morphological traits in relation to environmental gradients***

404   Overall, trait variation was explained by temperature gradients and phylogenetic structure at

405   assemblages other than regional. Mapping the predictions of the best fitting models (Table 3)

406   yielded different patterns of spatial distribution for morphological variation (Figures 3-5), across

407   the geography at different scales. Maps represent the gradient of change of the morphological

408   traits with respect to the environmental variable that better explain their variation. We only

409   mapped the statistically significant models. At the regional assemblage (Fig. 3), for the three

410   morphological variables, morphological trait values increase with increasing latitude.

411   Phylogenetic structure does not help to explain morphological variation in the regional

412   assemblage. Lowland forests assemblage showed a morphological trait variation from northeast

413   to southwest (Fig. 4), in which body size and bill size increases towards the southwest. In the

414   lowland forests assemblage, bill size increases with increasing phylogenetic structure.

415   Conversely, body size increases in areas with low phylogenetic structure (overdispersion) and

416   decreases in areas phylogenetically clustered (Fig. 2A). Geographically, that means that

417   phylogenetic structure decreases size in areas where temperature gradients predict increase in

418   size, and increase in size where temperature gradients predict decrease. For the type II

419   assemblage (Fig. 5), we mapped body size and bill variation, which are explained by temperature

420   seasonality. Increases in body size and bill variation were predicted in areas of higher

421   phylogenetic clustering and in southwestern Mexico (Fig. 2B).

422

423   **DISCUSSION**

424   Our results suggest that both climatic variables and phylogenetic structure influence the

425   morphological variation of Mexican tyrants, but the influence of the phylogenetic structure

426   varies between different assemblages and morphological traits. When we focused on how

427   climatic gradients explain the variation in morphology, our results suggest that temperature

428   seasonality is the most influential climatic variable, but the magnitude of the influence varies

429   across different assemblages. This variable assumedly represents tolerance limits of species to

430   variation in temperature, likely influencing morphological variation through maintaining habitat

431   use through time (Wiens & Graham, 2005). Our results showed a latitudinal pattern that is

432   consistent with the Bergmann's rule for birds: as temperature increases, body mass is likely to

433   decrease (McNab, 1971). This is a common finding in many studies, because the total surface

434   area of an animal is a proxy for heat dissipation, and predicts that a larger size can be reached in

435   colder climates than in warmer ones, which is linked to the temperature economy of the animal

436   (Salewski and Watt, 2017). Due to the distribution of temperature at the regional assemblage,

437   latitudinal pattern is likely to show an increase in body size from south to north (Fig. 3), but

438   some studies found exceptions at another regions (e.g. James, 1970).

439   Patterns of morphological variation in western Mexico type I and II assemblages showed

440   a pattern in which the tendency to increase in size was predicted in direction to both highlands

441   and lowlands of western Mexico (Fig. 4 and Fig. 5), which also contain areas with the highest

442   values of phylogenetic structure. A larger body size in less vegetated or highly seasonal areas

443   may be an adaptation to live in these types of isolated environments, and higher phylogenetic

444   structuring agrees with the fact that western areas have been identified as a complex

445   biogeographical and ecological setting in which a highly endemic and phylogeographically

446   structured bird fauna occurs (e.g. García-Trejo & Navarro-Sigüenza, 2004; Navarro-Sigüenza et

447   al., 2004; Ríos-Muñoz & Navarro-Sigüenza, 2012; Arbeláez-Cortés et al., 2014). For patterns of

448   morphological variation in eastern lowlands, like the phylogenetically overdispersed Yucatan

449   Peninsula or the Tehuantepec Isthmus, relatively constant (i.e., less seasonal) temperatures in the

450   east, may have influenced the distribution of lineages and the variation of its morphological

451   traits, and consequently the particular phylogenetic community structure in those regions (Martin

452   et al., 2018).

453   The results of several studies support the idea that environmental gradients influence the

454   phylogenetic structure of the communities and therefore, phylogenetic clustering increases with

455   decreasing temperature, meaning that closely related species tend to have a strong phylogenetic

456   signal, and more similar traits and geographic distributions than expected by chance (Helmus et

457   al., 2007; Donoghue, 2008; Graham et al., 2009; Flynn et al., 2011; Tedersoo et al., 2012; Miller

458   et al., 2013). For instance, Miller et al. (2013) found that the tendency of species to remain in an

459   environmental space similar to that of their ancestors (niche conservatism, Wiens & Graham,

460   2005) constrains honeyeater assemblages in arid regions, along a gradient of decreasing

461   precipitation. Instead, we found that tyrant's assemblages became more phylogenetically

462   clustered along a gradient of increasing temperature seasonality, but with low phylogenetic

463   signal. Our findings might reflect that variation in morphological traits of phyllogenetically

464   clustered assemblages is more restricted in their climatic ranges. Moreover, on another study,

465   Graham et al. (2009) found that phylogenetic diversity of hummingbird communities of the

466   Andean region tend to be phylogenetically clustered at higher elevations and colder areas, and be

467   overdispersed at lower elevations, whereas in the transition zone between lowlands and

468   highlands there is a species turnover of relatively distant related species that can be associated to

469   the environmental gradient. We found similar results in which phylogenetically clustered

470   communities are found in the western areas (Fig. 2) which includes mountainous ranges above

471   1500 masl (southern Sierra Madre Oriental, and the Sierra Madre del Sur), although lowland

472   areas like the Balsas Depression also show high values of phylogenetic clustering.

473   Phylogenetic clustering at higher elevations supports the idea of environmental filtering,

474   a pattern where similar traits are selected above other variations because they have an advantage

475   within the community and the environment, also allowing the coexistence of close relatives

476   (Webb et al., 2002). Phylogenetic clustering in lowlands like the Balsas Depression supports the

477   idea of the effect of dispersal barriers over community structuring, where communities are

478   phylogenetically similar despite their large differences in species composition, a pattern

479   reflecting the influence biogeographic barriers (Graham et al., 2009) that promote regions with a

480   set of related species with a common and isolated history, like areas of endemism (Harold &

481   Mooi, 1994).

482   The phylogenetic overdispersion patterns we found could be more related to the

483   expectation that competition influences the local trait composition of a community by promoting

484   the filling of the morphological and ecological space exploited (Wainwright & Reilly, 1994); but

485   it can also be associated with the distribution of a lineage along a transition zone, that is, an area

486   where a mixed set of distinct biotic elements overlap (Morrone 2004). Areas found with higher

487   phylogenetic overdispersion have been recognized by other authors as areas where different

488   biotic elements overlap, e.g parts of the Mexican Transition Zone (Sierra Madre Oriental),

489   Yucatan Peninsula and the limits of the Tehuantepec Isthmus (Morrone, 2006, 2014).

490   Contradictory to the expectations of patterns of phylogenetic structuring, our data show

491   low phylogenetic signal, so traits are less similar than expected due to phylogenetic relatedness.

492   We would have expected a strong phylogenetic signal, as closely related species of a community

493   tend to occupy similar morphological space due to common ancestry, especially in

494   phylogenetically clustered areas. Overdispersion of traits driven by competitive interactions and

495   divergent trait evolution, as well as the taxonomic and spatial scale, may have influenced the

496   results by masking phylogenetic signal patterns at different assemblages (Webb et al., 2002;

497   Cavender-Bares et al., 2006; Lawing et al., 2017). The latter seems to be the case for tyrant

498   flycatchers, as many closely related clades that supposedly have similar distribution of traits, are

499   concentrated in the same areas of high phylogenetic structure. For example, closely related and

500   morphologically similar *Empidonax* and *Contopus* are concentrated southeastward, while another

501   set of closely related *Empidonax* are found concentrated westward (i.e. *E. difficilis, E.*

502   *occidentalis, E. fulvifrons* and *C. cooperi, C. pertinax and C. sordidulus*). On the other hand, the

503   areas that have more phylogenetically diverse communities (phylogenetic overdispersion) are

504   found in southeastern tropical region, for example the Yucatan Peninsula.

505   Another contradicting pattern revealed by our analyses was defined by the discordant

506   response of variation in body size in relation to temperature seasonality and phylogenetic

507   structure (Fig. 4). Our results indicate that body size increases as temperature seasonality

508   increases, but as communities became more phylogenetically clustered, body size decreases,

509   resulting in a trade-off between the influences of temperature seasonality and phylogenetic

510   structure over variation in body size. An evolutionary trade off suggests that the functional trait

511   of size is limited by the action of another trait of evolutionary and ecological importance, like the

512   relatedness of the species occurring within the community. Trade offs can occur at different

513   hierarchical levels, and situations can even occur in which the selection on traits of individual

514   organisms is opposed to the selection on an emergent characteristic at the species level

515   (Jablonski, 2007), establishing variation patterns that cannot be fully explained by analyzing a

516   single level. Then, the variation of a characteristic of the individual like body size could be

517   opposed to the selection of a property at the species level (Diniz-Filho, 2004), like the structuring

518   of communities.

519

520   **CONCLUSIONS**

521   Our analyses demonstrate that the environment has an effect on morphological variation that is

522   mediated by the phylogenetic structure of communities across geography. The use of different

523   environmental variables to elucidate patterns of morphological change in lineages, with distinct

524   levels of phylogenetic signal, and varied patterns of lineage composition across space provides

525   greater explanatory power than only taking into account species richness or abundance, or simply

526   presence/absence distributional data (Olson et al., 2009; Maestri et al., 2016; Lawing et al.,

527   2017). Several authors have noticed that morphological variation is best explained by a varied set

528   of variables, given that the effect of a single climatic variable, most of the time explains variation

529   only at one scale (taxonomic or geographic, James 1970; Dial 2008; Olson et al. 2009; Martínez-

530   Monzón et al. 2017). Assessing the distribution of ecomorphological traits of organisms is the

531   best way to predict change over an environmental gradient (Olson et al. 2009; Santos et al. 2016)

532   and consequently, regression models representing variation of functional traits provide new

533   insights into elucidating the general mechanisms that relate biodiversity across environmental

534   and geographical changes (Violle et al. 2014). A spatial visualization of the predicted response of

535   trait variation in relation to environmental factors can integrate individual and interspecific level

536   responses to evaluate the importance of morphological adaptation in the explanation of broader

537   scale processes. Finally, our results highlight that to allow a better understanding of the spatial

538   distribution patterns of morphological traits, and the processes that promote them in different

539   assemblages, it is necessary to consider the relationship of different ecomorphological traits of

540   the species in conjunction with the phylogenetic composition of the communities.

541

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852

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

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

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 their ecology, 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 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 flights called sallies to catch their prey. Wing shape directly influences evasive movements against predators. Also, the shape and length of the wing are important factors as they directly influence the dispersal ability of birds. Several species of tyrant flycatchers are migratory, so wing length is an important aspect that is directly related to migratory movements.	Hamilton (1961); Fitzpatrick (1980); Fitzpatrick (1981); Fitzpatrick (1985); Miles & Ricklefs (1984); Winkler & Leisler (1992), Gatesy & Dial (1996), Swaddle & Lockwood (1998); Bowlin & Wikelski (2008); Dawideit et al. 2009; Förschler & Barlein 2011
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 acts as functional unit during specific processes of the individual, like feeding or communication. For this reason, bill is related to many features of the ecology of the bird, and varies and responds to environmental and evolutionary factors semi-autonomously from other body parts. For tyrant flycatchers, it is most related to their diet breadth and insectivorous feeding habits.	Fitzpatrick (1980); Fitzpatrick (1985); Symonds & Tattersall (2010); Greenberg et al. (2012); Felice & Goswami (2017)
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 traits. For instance body size, distribution range, habitat and diet breadth (niche breadth), reproductive traits, trophic level, and others. In particular, for tyrant flycatchers, 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 insect abundance within forests and other habitats is correlated with the humid season. Body size and appendage size may be related to climate gradients following the Bergmann's and Allen's rules, respectively, as temperature decrease, body size increases but appendage sizes decrease.	Diniz-Filho (2004); Zellweger et al. (2006); O'Donnel & Ignizio (2012), Symonds & Tattersall (2010); Salewski & Watt (2016)

Altitude Topographic setting (northness and eastness)	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 the regional scale, the sorting of species, in relation to 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 a 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 on 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 the 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) 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 the morphology of another individual of the same species more closely, simply because they belong to the same phylogenetic group (their shared 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 may have different responses 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)

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

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

2 **combination of assemblages type I and II.**

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).
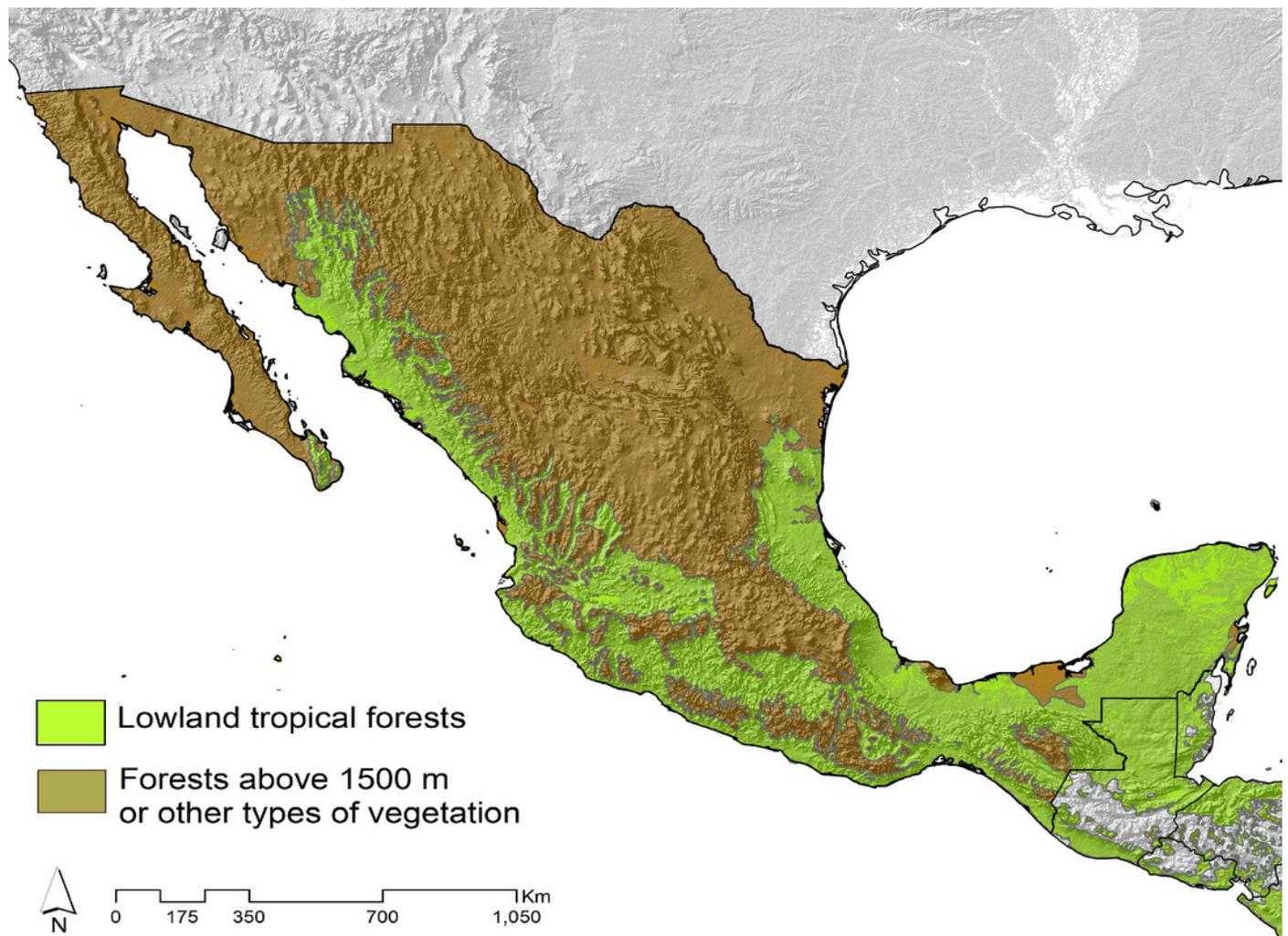
Figure 2

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
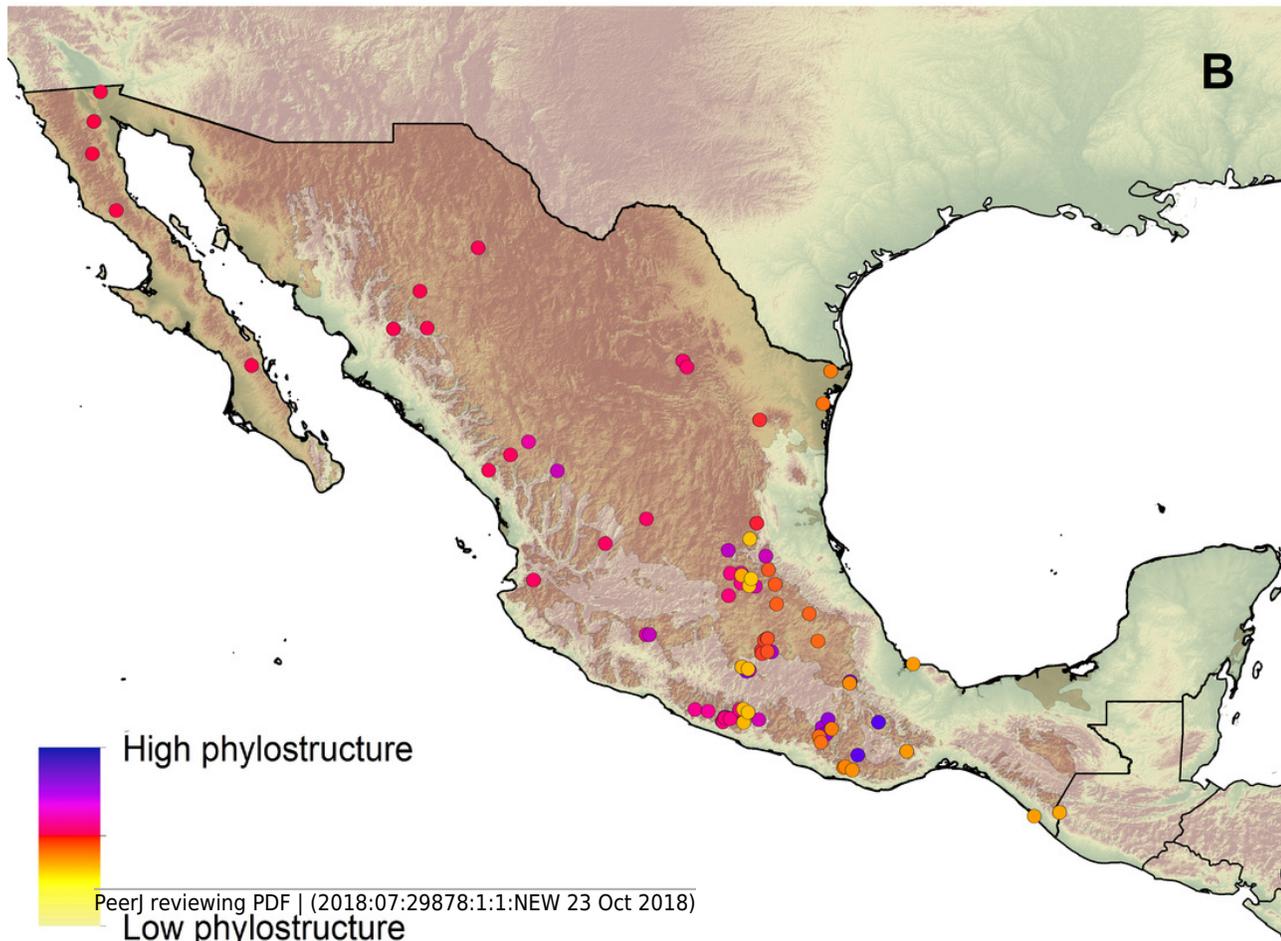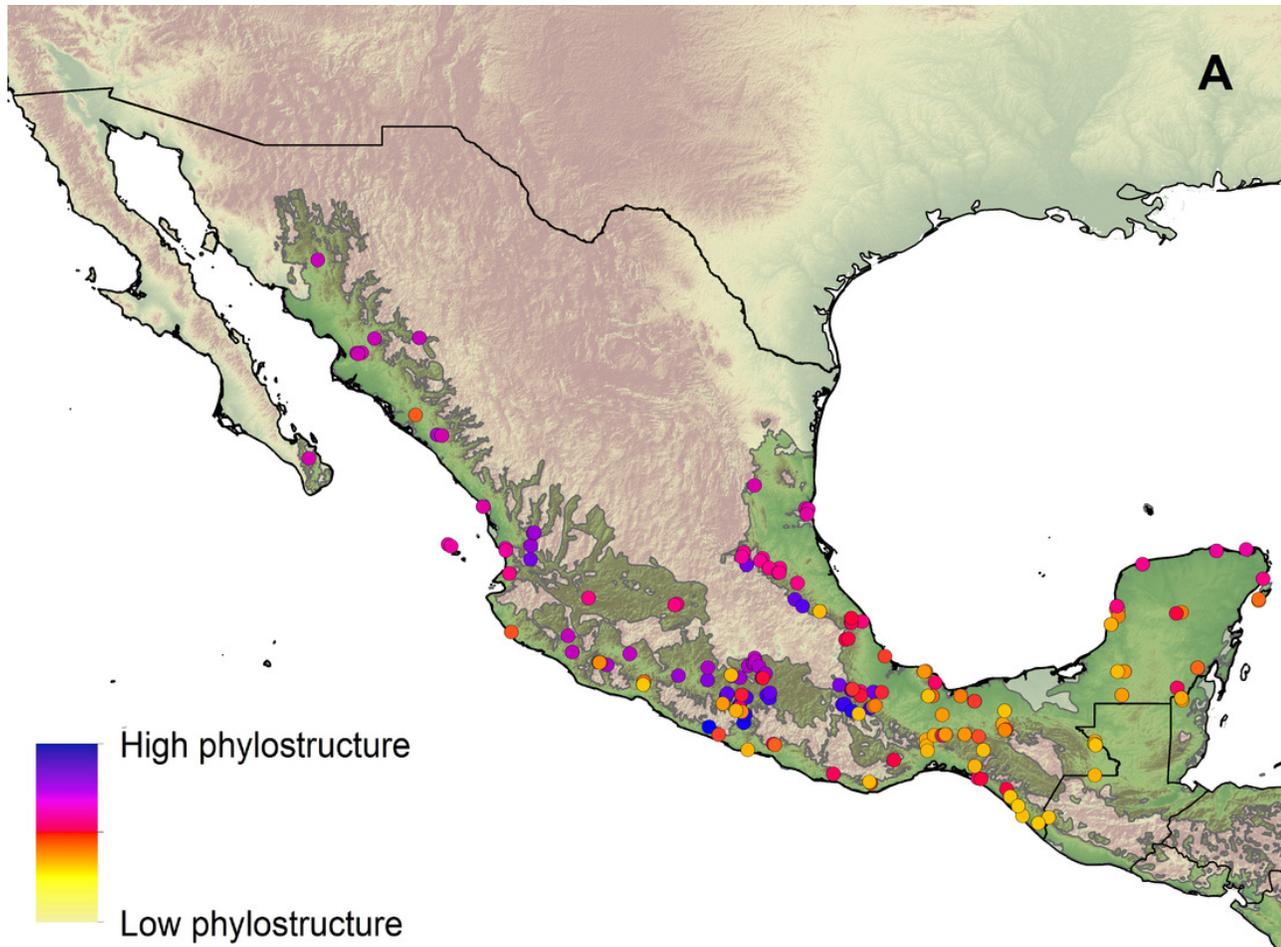
Figure 3

Spatial distribution of morphological variation 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).
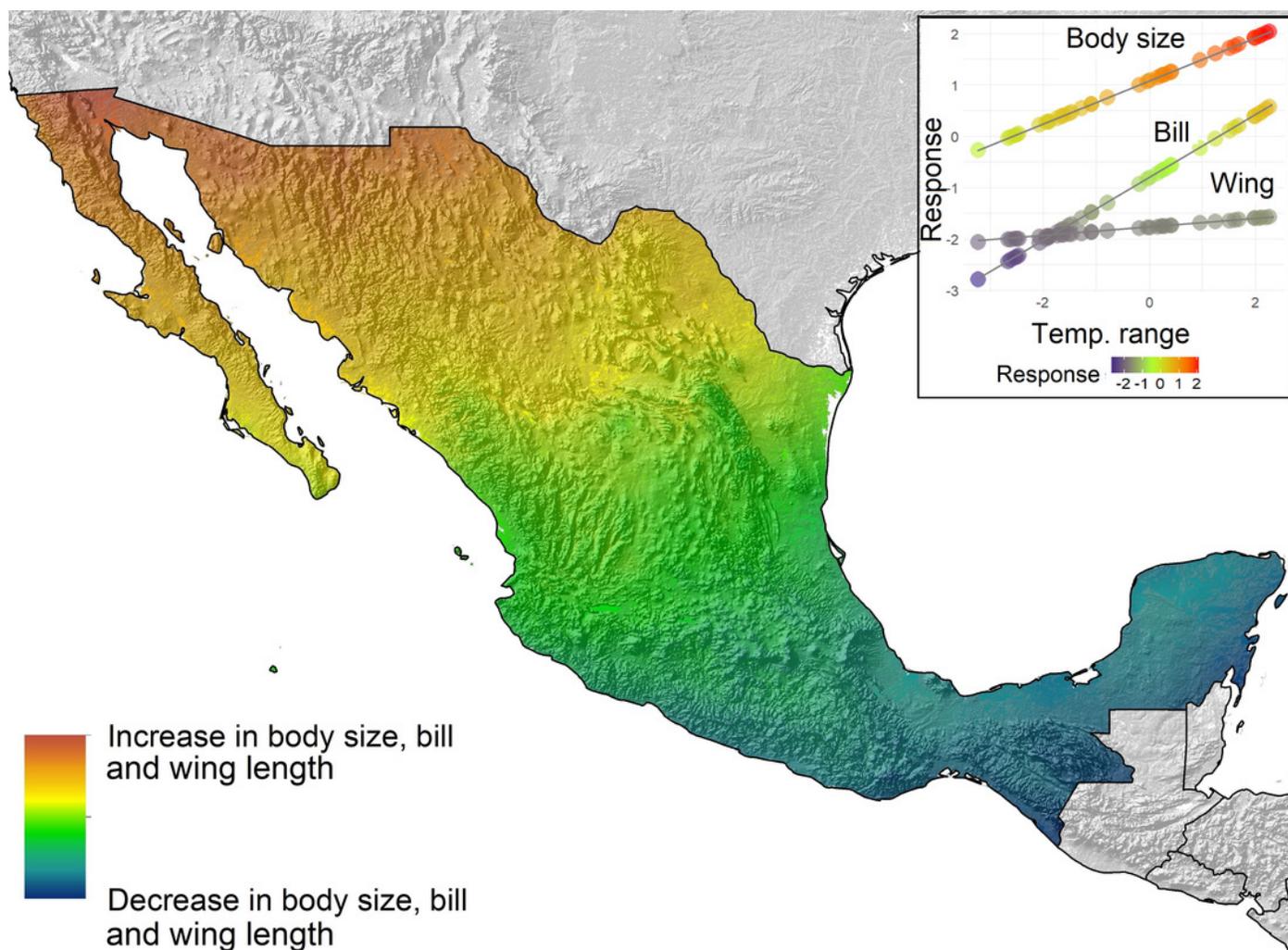
Figure 4

Spatial distribution of morphological variation 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).
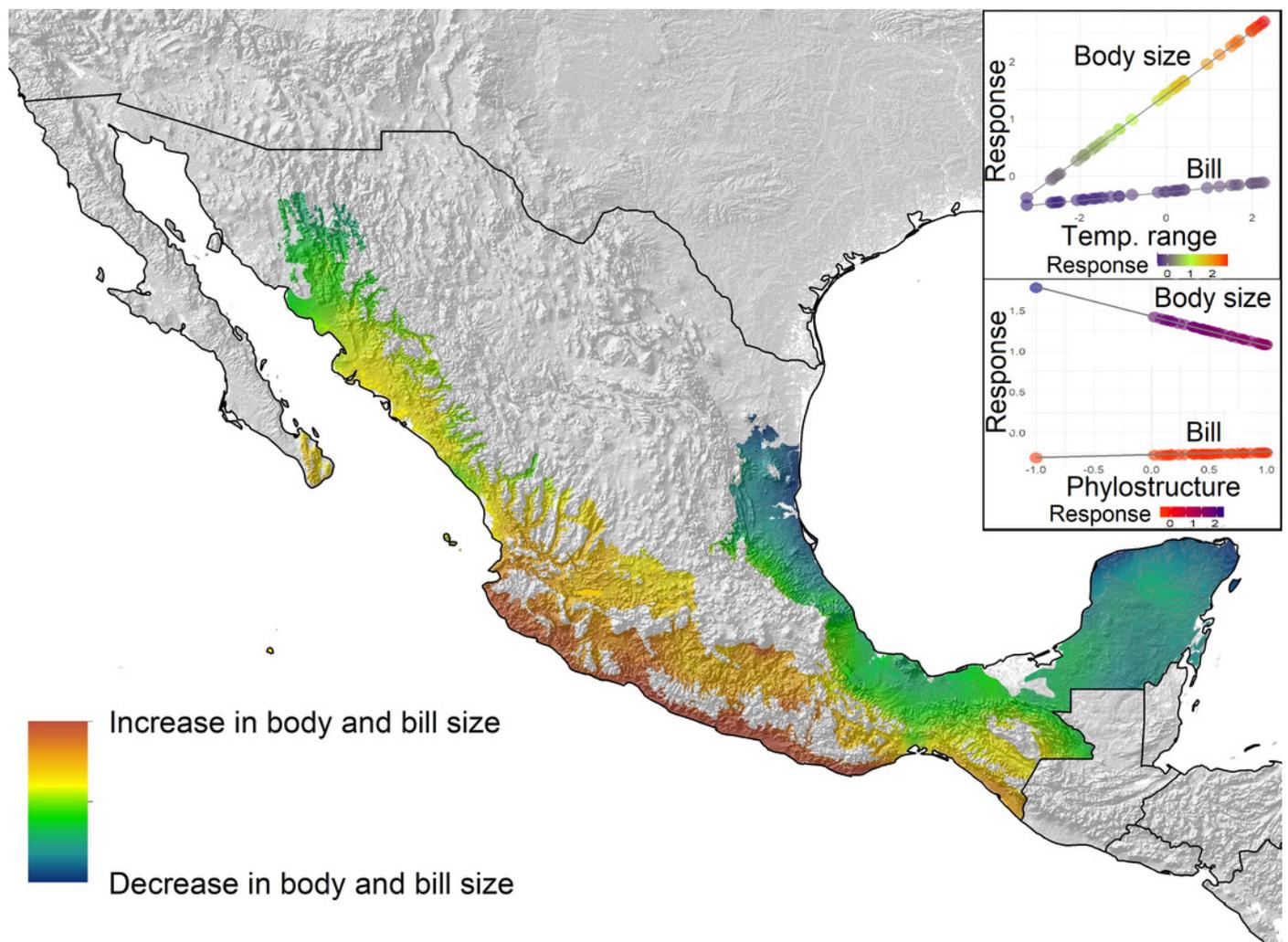
Figure 5

Spatial distribution of morphological variation of 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).