1   **Mapping diversification metrics in macroecological studies: Prospects and**

2   **challenges**

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Abstract

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18 The intersection of macroecology and macroevolution is one of the most active

19 research areas today. Macroecological studies are increasingly using phylogenetic

20 diversification metrics to explore the role of evolutionary processes in shaping

21 present-day patterns of biodiversity. Evolutionary explanations of species richness

22 gradients are key for our understanding of how diversity accumulated in a region.

23 For instance, the present-day diversity in a region can be a result of *in situ*

24 diversification, extinction, or colonization from other regions, or a combination of

25 all of these processes. However, it is unknown whether these metrics capture well

26 these diversification and dispersal processes across geography. Some metrics

27 (e.g., mean root distance -MRD-; lineage diversification-rate -DR-; evolutionary

28 distinctiveness -ED-) seem to provide very similar geographical patterns

29 regardless of how they were calculated (e.g., using branch lengths or not). The

30 lack of appropriate estimates of extinction and dispersal rates in phylogenetic

31 trees can limit our conclusions about how species richness gradients emerged.

32 With a review of the literature and complemented by an empirical comparison, we

33 show that phylogenetic metrics by itself are not capturing well the speciation,

34 extinction and dispersal processes across the geographical gradients.

35 Furthermore, we show how new biogeographic methods can improve our

36 inference of past events and therefore our conclusions about the evolutionary

37 mechanisms driving regional species richness. Finally, we recommend that future

38 studies include several approaches (e.g., spatial diversification modelling,

39 parametric biogeographic methods) to disentangle the relative the role of

40   speciation, extinction and dispersal in the generation and maintenance of species

41   richness gradients.

42

43   Keywords: Phylogeny, Geography, Spatial diversification, Macroevolution, Species

44   richness, Regional assemblages

Introduction

The causes of spatial variation of biodiversity are one of the most fundamental questions in ecology, biogeography and macroecology (Brown 1995, 2014, Brown and Lomolino 1998, Hawkins et al. 2012, Fine 2015, Jablonski et al. 2017). Current studies are integrating in a single framework the ecological and evolutionary mechanisms driving regional species diversity (McGaughran 2015, Pärtel et al. 2016, Cabral et al. 2017, Leidinger and Cabral 2017). However, only three macroevolutionary processes ultimately can modify the number of species in a region: speciation, extinction and dispersal (Wiens 2011, Fine 2015, Jablonski et al. 2017) (Figure 1). These processes can be modulated by species' traits varying within clades (Paper et al. 2016, 2017, Jezkova and Wiens 2017, Moen and Wiens 2017), age of region (e.g., time-for-speciation effect; Stephens & Wiens, 2003), geographical area (Losos and Schluter 2000), or climatic conditions (Condamine et al. 2013, Lewitus and Morlon 2017).

The integration of different disciplines such as molecular phylogenetics, palaeontology, and historical biogeography have allow to infer a series of macroevolutionary processes across geography (Diniz-Filho et al. 2013, Fritz et al. 2013). It is well-known that fossil information is key to estimate with high confidence rates of speciation and extinction (Sepkoski 1998, Foote 2000, Quental and Marshall 2010, Rabosky 2010b). New methods correcting for sampling bias are able to generate improvements in the estimates of the speciation, extinction and net diversification rates (Silvestro et al. 2014, 2016).

67   However, the causal mechanisms that underlying the geographical diversity

68   gradients only can be established with greater confidence for a few taxonomic

69   groups with adequate fossil record, such as marine bivalves (Jablonski et al. 2006,

70   2017), mammals (Silvestro et al. 2014) or plants (Antonelli et al. 2015).

71   As fossil data is not available or incomplete for most extant groups, model-

72   based approaches used to estimate speciation and extinction rates in

73   palaeontology were adapted to study the macroevolutionary dynamics using

74   phylogenetic information (Nee et al. 1994, Morlon et al. 2010, Stadler 2013).

75   Molecular phylogenies are becoming essential to the study of diversification

76   dynamics across temporal and spatial scales for extant taxa (Wiens and

77   Donoghue 2004, Rabosky and Lovette 2008, Stadler 2013, Morlon 2014, Schluter

78   and Pennell 2017). Therefore, it is possible to reconstruct past diversification

79   process based on the branching events of a phylogeny using a set of birth-death

80   models (Nee et al. 1994, Nee 2006, Morlon et al. 2010, Stadler 2013, Morlon

81   2014). These birth-death models allow infer either a homogeneous process for an

82   entire clade (Nee et al. 1994, Magallón and Sanderson 2001) or a heterogeneous

83   process varying in time or in specific subclades of a tree (Paper et al. 2006,

84   Rabosky and Lovette 2008, Alfaro et al. 2009). However, these birth-death models

85   only account for temporal variation of the macroevolutionary processes and how

86   translate these processes to the geography is still a matter of debate.

87   Macroecological studies use two main approaches to link the estimates of

88   diversification with the geographical ranges of species (Hawkins et al. 2007, Algar

89   et al. 2009, Qian et al. 2014, Pinto-Ledezma et al. 2017, Velasco et al. 2018). The

90   first one uses a set of phylogenetic metrics as a proxy to capture the geographical

91   signature of lineage diversification dynamics (Diniz-Filho *et al.*, 2013; Fritz *et al.*,

92   2013; Table 1; Figure 2). These metrics provide either an estimate of a per-species

93   rate of diversification (e.g., mean root distance –MRD-, residual phylogenetic

94   diversity –rPD-, mean diversification rate –MDR-), the phylogenetic structure of

95   regional assemblages (e.g., phylogenetic species variability –PSV-) or the average

96   age of co-occurring lineages in a given area (e.g., mean age; see Table 1). Each

97   metric is calculated for each species in the phylogeny; therefore, we can associate

98   the species' values to its corresponding geographical range and generate a map

99   with average values for cells or regions. Although these phylogenetic metrics only

100   account for speciation events, macroecologists have used these maps as a proxy

101   to test some evolutionary-based hypothesis in macroecological research (Diniz-

102   Filho *et al.*, 2013; Fritz *et al.*, 2013; see Table 2 for a compendium of these

103   hypotheses).

104   The second approach used by macroecologists consists in the explicit

105   estimation of diversification parameters across geography (Goldberg et al. 2005,

106   2011, Ramiadantsoa et al. 2017). For instance, the geographic state speciation

107   and extinction model –GeoSSE (Goldberg et al. 2011; Table 1) allows estimating

108   speciation, extinction and dispersal parameters across two regions. It is possible

109   to disentangle the relative role of each one of these processes on the generation

110   and maintenance of the geographical diversity gradients (Rolland et al. 2014,

111   Pulido-Santacruz and Weir 2016, Pinto-Ledezma et al. 2017). In addition, a

112   recently developed Bayesian approach (BAMM; Rabosky 2014, Rabosky et al.

113   2014) allows to infer the balance of speciation and extinction in the generation of

114   these biodiversity gradients (Rabosky et al. 2015, Sánchez-Ramírez et al. 2015,

115   Morinière et al. 2016, Pinto-Ledezma et al. 2017). The BAMM approach allows

116   both the inference of macroevolutionary dynamics for an entire clade (i.e., a

117   macroevolutionary regime; Rabosky 2014) and also get estimates of per-species

118   diversification rates (i.e., as a phylogenetic metric; Rabosky 2016) that can be

119   mapped in a geographical domain. Although all these methods aim to obtain a

120   geographical picture of the diversification processes, it remains unexplored if they

121   can effectively capture these dynamics across regions.

122   In this paper, we conducted a review on macroecological literature to

123   evaluate how evolutionary and biogeographic processes contribute to shape

124   geographical species richness gradients. We review only those papers that make

125   explicit use of phylogenetic metrics and/or explicit diversification approaches

126   (Table 1). We divided our review in three main sections. In the first one, we

127   discuss how studies use phylogenetic metric to test some evolutionary-based

128   hypotheses underlying geographical diversity gradients and we explore some

129   limitations of these metrics (see also Table 2). Also, we discuss to what extent

130   these metrics are able to capture macroevolutionary dynamics in a spatial explicit

131   context. We illustrate these using three case studies (Furnariides birds, Hylid

132   frogs, and *Anolis* lizards; Figure 1) and explore how another approaches (e.g.,

133   diversification modelling and biogeographical approaches) can complement our

134   inferences about diversification process across geography. In the second section,

135   we discuss how dispersal and extinction processes are limiting these

136   diversification inferences and we propose some research avenues to attempt to

137   solve these problems. Using an explicit biogeographical approach, we test the

138   role of dispersal on the geographical species richness patterns of the three case

139   studies. Finally, in the third section, we call for the adoption of complementary

140   approaches (e.g., extensive simulations, parametric biogeographical methods) in

141   macroecological research with the aim to evaluate the relative role of speciation,

142   extinction and dispersal process driving geographical biodiversity gradients.

143

144   ***LITERATURE REVIEW***

145   We conducted a literature search in Web of Science for studies that

146   explicitly have addressed questions on how speciation, extinction and dispersal

147   have shaped geographical species richness gradients. We selected those papers

148   that used either phylogenetic metrics (e.g., mean root distance -MRD-,

149   phylogenetic diversity -PD-, phylogenetic species variability -PSV-; diversification

150   rate –DR-; mean Ages; Table 1) or explicit macroevolutionary approaches (e.g.,

151   GeoSSE, BAMM; Goldberg *et al*., 2011; Rabosky 2014). We compiled a list of 44

152   papers (Table A1), but we are aware that this likely is not an exhaustive search.

153   The majority of papers reviewed are testing historical process shaping latitudinal

154   diversity gradients (LDG) in various taxa.

155

156   ***TESTING EVOLUTIONARY HYPOTHESIS USING PHYLOGENETIC METRICS***

157   ***AND EXPLICIT DIVERSIFICATION APPROACHES***

158   Here, we discuss how phylogenetic metrics are used to test evolutionary

159   hypotheses related to the generation and maintenance of geographical diversity.

160   Several studies used the mean root distance -MRD- metric to evaluate whether

161   regional assemblages are composed of "basal" or "derivate" linages. First, this

162   terminology should be avoided because it provides an incorrect interpretation of

163   the phylogenetic trees (Baum et al. 2005, Crisp and Cook 2005, Omland et al.

164   2008). Although this metric does not incorporate information from branch lengths

165   (Algar et al. 2009, Qian et al. 2015), it does provide the average number of nodes

166   separating each species in a given region from the root of the phylogeny (Kerr and

167   Currie 1999). MRD therefore provides information about the number of

168   cladogenetic events (splits) that have occurred through the history of co-occurring

169   lineages in each region (Pinto-Ledezma et al. 2017, Velasco et al. 2018). Under

170   this view, MRD should be interpreted as a metric of total diversification (Rabosky

171   2009), where high MRD values indicating regional assemblages dominated by

172   extensive cladogenesis and low MRD values indicating assemblages with few

173   cladogenetic events. A main concern with this metric concern with the fact that it

174   does not provide any information about what macroevolutionary dynamics have

175   taken place in a region. For example, it is very hard to establish whether MRD

176   allows to distinguish between diversity-dependent (Rabosky 2009, Rabosky and

177   Hurlbert 2015) or time-dependent (Wiens 2011, Harmon and Harrison 2015)

178   processes dominating regional diversity. Although the distinction between these

179   two dynamics, and its relationship with the origin and maintenance of regional

180   diversity, is an intense topic in the macroevolutionary literature (Rabosky 2009,

181 2013, Wiens 2011, Cornell 2013, Harmon and Harrison 2015, Rabosky and

182 Hurlbert 2015). However, more empirical and theoretical work is necessary to

183 establish what scenario plays a significant role in regional species richness

184 assembly (Rabosky 2012, Etienne et al. 2012, Valente et al. 2015, Graham et al.

185 2018). It might worth to establish whether local ecological process scaling up to

186 regional scales or emergent effects (i.e., the existence of a strong equilibrium

187 process) governed the build-up of regional diversity (Cornell 2013, Harmon and

188 Harrison 2015, Rabosky and Hurlbert 2015, Marshall and Quental 2016).

189   The time-for-species effect hypothesis state that the regional build-up of

190 species richness is directly proportional to the colonization time of its constituent

191 clades (Stephens and Wiens 2003b; Table 2). However, many phylogenetic

192 metrics used to test this hypothesis, did not incorporate any age information (Fritz

193 and Rahbek 2012, Qian et al. 2015). Qian et al. (2015) did some additional

194 predictions for the time effect hypothesis regarding the phylogenetic structure of

195 regional assemblages. We suggest that these predictions are not easily deduced

196 from the original statement of the time-for-speciation effect hypothesis (Stephens

197 & Wiens 2003). For instance, Qian et al. (2015, p. 7) predicted that regions with

198 low species richness (e.g., extra-tropical regions) should be composed of more

199 closely related species than regions with high species richness (e.g., tropical

200 regions). This assumes that regions with low species richness were colonized

201 recently and therefore these lineages had little time for speciation. However, it is

202 also plausible consider that high extinction occurred in these poor species

203 richness regions by marginal climatic niche conditions preventing adaptive

204   diversification (Wellborn and Langerhans 2015). By contrast, regions with high

205   species richness might also be assembled by multiple dispersals from nearby

206   regions becoming to be a macroevolutionary sink (Goldberg et al. 2005). In this

207   latter case, the species richness was not build-up by *in situ* speciation mainly but

208   by continued dispersal through time. To evaluate which of these scenarios is more

209   plausible it is necessary to adopt an approach that explicitly infer the number of

210   the dispersal and cladogenetic events across areas (Roy and Goldberg 2007,

211   Dupin et al. 2017).

212   Differences in species diversification are also considered as a main driver of

213   the geographical diversity gradient for many groups (Kennedy et al. 2014, Pinto-

214   Ledezma et al. 2017). This hypothesis states (Table 2) that differences in net

215   diversification rates between areas are the main driver of differences in regional

216   species richness between areas. Davies and Buckley (2011) used the phylogenetic

217   diversity controlled by species richness (i.e., residual PD –rPD-) to distinguish

218   areas with different evolutionary processes. These authors predicted that areas

219   where rapid speciation and low immigration events from other areas occurred, are

220   dominated by large adaptive radiations (e.g., large islands; Losos and Schluter

221   2000). By contrast, areas with slow speciation and colonized by multiple lineages

222   through time should have high values of residual PD.

223   The "out of the tropics" -OTT- hypothesis (Jablonski et al. 2006; Table 2)

224   states that latitudinal diversity gradient is due to that the majority of lineages

225   originated in the tropics and then migrated to extratropical regions. Under this

226 hypothesis, tropics harbour higher net diversification rates (higher speciation and

227 lower extinction) than extratropical regions and dispersal rates are higher from the

228 tropics to extratropical regions than the reverse (Jablonski et al. 2006; Table 1).

229 For instance, Rolland et al. (2014) used the GeoSSE model to test this hypothesis

230 in the generation of the latitudinal mammal diversity gradient. They found that net

231 diversification rates (i.e., the balance of speciation minus extinction) was higher in

232 tropical than in temperate regions and dispersal rates were higher from the tropics

233 to temperate regions than the reverse. Also, Pinto-Ledezma et al. (2017) used the

234 GeoSSE model to test an analogue hypothesis to OTT, as form of Out of the

235 Forest hypothesis (OTF), using Furnariides birds as a clade model. Their favoured

236 a model where open areas have higher speciation, extinction and dispersal rates

237 than forest habitats. All these results suggest that it is reasonable to use either

238 phylogenetic metrics or explicit diversification approaches (e.g., the GeoSSE

239 model) to evaluate a set of evolutionary-based hypotheses as a main driver of

240 geographical diversity gradients. However, we show here (see below) that these

241 approaches fail to capture the evolutionary and biogeographic processes at

242 spatial scales.

243

244 ***Are phylogenetic metrics capturing well the diversification process across***

245 ***geography?***

246 A deep understanding of evolutionary processes affecting regional species

247 assemblages is coming from the integration of molecular phylogenies and fossil

248   record (Quental and Marshall 2010, Marshall 2017). From this integration of

249   neontological and paleontological perspectives, it is clear that both approaches

250   are necessary to test evolutionary-based hypothesis in macroecological research.

251   Several hypotheses were proposed to explain geographical diversity patterns,

252   particularly the latitudinal diversity gradient –LDG- (see Table 2 for a summary and

253   compilation of the main hypotheses reported in the literature). Although the ideal

254   approach is to generate robust conclusions from multiple lines of evidence (e.g.,

255   fossil record, molecular phylogenies, biogeographical inference) it is clear that this

256   information is scarce for many taxonomic groups. Many macroecological studies

257   have adopted either phylogenetic metrics or explicit diversification approaches

258   (e.g., the GeoSSE model) to evaluate the relative contribution of speciation,

259   extinction and dispersal on the resulting geographical diversity gradients (Table

260   S1).

261   Phylogenetic metrics can be easily visualized in a geographical context and

262   several inferences about ecological (e.g., dispersal) and evolutionary (e.g.,

263   speciation) process can be done. As these metrics provide a *per-species level*

264   *diversification* metric for each species in a phylogeny, it is possible to associate

265   these values with the corresponding species' geographical range and obtain a

266   mean value for cells or regions in a given geographical domain (Table 1; Figure 2).

267   By contrast, explicit diversification approaches (e.g., GeoSSE; BAMM; fitting

268   models) provide a *per-lineage level diversification* metric for a given clade or a

269   regional assemblage (Rabosky 2016a). However, in some cases, it is possible to

270   generate a *per-species level diversification* metric with these approaches. For

271   instance, Pérez-Escobar et al. (2017) used the function GetTipsRates in

272   BAMMtools (Rabosky et al. 2014) to map speciation rates for Neotropical orchids.

273   These two approaches (phylogenetic metrics and lineage diversification)

274   potentially can provide complementary pictures about how macroevolutionary

275   dynamics have taken place in the geography. One the one hand, it is possible to

276   estimate diversification rates for a given clade using the number of species, its

277   age and a birth-death models (Magallón and Sanderson 2001, Nee 2006,

278   Sánchez-Reyes et al. 2017). These model-fitting approaches allow to whether

279   diversity- or time-dependent diversification process has taken place in a regional

280   assemblage (Etienne et al. 2012, Rabosky 2014, Valente et al. 2015). On the other

281   hand, per-species diversification rate metrics allow establishing the potential of

282   each individual species to generate more species (Jetz et al. 2012, Rabosky 2014,

283   2016a). However, these approaches imply at least a different process, which left a

284   different signature on the geography. Phylogenetic metrics captures a total

285   diversification process (Rabosky 2009), whereas lineage diversification

286   approaches (e.g., BAMM) can potentially provide information about an individual

287   diversification process (Rabosky 2013). In addition, still is not clear whether

288   phylogenetic metrics can provide an accurate description of the diversification

289   dynamics across geography.

290   The first step to clarify how well these phylogenetic metrics behave is to

291   establish a comparison within and between different taxonomic groups. To

292   evaluate how different phylogenetic metrics vary across geography and their

293   relationship with species richness, we used two empirical data sets from our own

294   empirical work (furnariid birds and anole lizards; (Pinto-Ledezma et al. 2017,

295   Velasco et al. 2018) and a data set compiled from several sources (hylid frogs;

296   (Wiens et al. 2006, Algar et al. 2009, Pyron 2014a). We mapped across geography

297   five phylogenetic metrics (Table 1, Figure 2). We selected these three data sets

298   because previous work analysed how evolutionary-based hypotheses affected the

299   present-day species richness gradient (Wiens et al. 2006, Algar et al. 2009, Pinto-

300   Ledezma et al. 2017, Velasco et al. 2018).

301   Figure 2 shows the geographical pattern of species richness and the five

302   phylogenetic metrics for *Anolis* lizards, hylid frogs and Furnariides birds. For all

303   clades, there is a higher species concentration near to the Ecuador. Higher

304   species concentration for hylids and Furnariides can be found in the Amazon and

305   the Atlantic forest and for *Anolis* lizards in Central America and the Caribe (Figure

306   2A-C; see also Algar et al. 2009, Pinto-Ledezma et al. 2017, and Velasco et al.

307   2018, for a detailed description of the geographical species richness pattern for

308   these clades, respectively). In terms of the geographical pattern of each

309   phylogenetic metric (Figure 2D-R), in most of the cases cells with higher metric

310   values are related to cells that contain high species richness and vice versa

311   (Figure 2D-R; Figure A1). However, the degree and the direction of this

312   relationship changes according to the phylogenetic metric used. For example,

313   MRD, a metric of species derivedness, shows a negative correlation with species

314   richness (Figure 2J-L; Figure A1). Importantly, the spatial relationships between

315   species richness and phylogenetic metrics found in our analysis could simply be

316   the result of aggregated species-level attributes within cells or assemblages

317   (Hawkins et al. 2017). Hence, any conclusion derived from these relationships

318   needs to be considered carefully. In addition, there are different levels of

319   correlation between phylogenetic metrics (Figure A1). For example, MDR - MA

320   present a high but negative correlation, and rPD - PSV and MRD - MDR present a

321   mid-high positive correlation (Figure A1). Although there are few studies

322   comparing correlations between metrics (Vellend et al. 2010, Miller et al. 2017), to

323   our knowledge, none previous study compares the similarity of these

324   diversification metrics (Table 1). However, some of these metrics sharing

325   mathematical assumptions, which increase the likelihood of correlation between

326   them. For example, for ultrametric trees, metrics as MDR could be approximated

327   by considering the mean root distance (i.e. MRD metric) from the tips to the root

328   (Freckleton et al. 2008), so further studies exploring the mathematical relation

329   between metrics are needed.

330   In order to assess if the cells/assemblages on average do not represent a

331   random sampling from the species pool, we applied a simple permutation test to

332   explore the non-randomness in each of the phylogenetic metrics. We applied a

333   null model where the presence-absence matrix (i.e., PAM) was randomly shuffled

334   1000 times, but maintaining the frequency of species occurrence and observed

335   richness in the cells/assemblages (Gotelli 2000). This kind of null model is

336   standard in studies at the community/assemblage level that use phylogenetic

337   information (Cavender-Bares et al. 2004, 2006). Interestingly, none of the

338   phylogenetic metrics deviates from the null expectation for the three clades

339   (Figure 3). Also, very few cells/assemblages present p-values below the 0.05

340   threshold, thus indicating that the cells/assemblages present random association

341   among species (Figure 3). These results should be supported by repeating

342   analyses with more clades at different spatial extents, but again, we stress that

343   any result obtained with the use of phylogenetic metrics need to be interpreted

344   carefully.

345

346   ***A brief comparison between phylogenetic metrics and explicit diversification***

347   ***and biogeographic approaches***

348   We compared the phylogenetic metrics enunciated in Table 1, which have

349   been the most used in macroecological research. We explored whether the

350   geographical patterns of these phylogenetic metrics in three empirical examples

351   coincide with the macroevolutionary dynamics inferred using explicit modelling

352   diversification approaches. In particular, we implemented the GeoSSE model to

353   estimate the three parameters (speciation, extinction, and dispersal) between two

354   areas in each taxonomic group (Table 3 and 4). In addition, we used the BAMM

355   approach to generate the per-species level diversification metric implemented in

356   the software BAMM 2.5.0 (Rabosky 2014). In the following section, we discuss

357   each metric and we compare them with the explicit diversification approaches.

358

359   *Residual Phylogenetic Diversity (rPD)*

360   In the case of furnariid birds, we show that forest areas tend to exhibit

361   slightly higher values of rPD in contrast with open areas (Figure 4; see also Figure

362   2). According to Davies and Buckley's logic, these areas exhibit slow

363   diversification and frequent dispersal from open areas. Pinto-Ledezma et al.

364   (2017) using GeoSSE and BAMM approaches indicated that open areas exhibit

365   higher net diversification rates than open areas (Table 3). For hylid frogs, we found

366   that tropical areas tend to exhibit higher rPD values than extratropical regions

367   (Figure 5). However, by adopting an explicit diversification approach (GeoSSE and

368   BAMM), we found that net diversification rates were similar in both regions (Table

369   3). In the case of *Anolis* lizards, the rPD values were higher in the continent than in

370   the island areas (Figure 6). However, using GeoSSE and BAMM, we found that

371   both rates were similar (Table 3). In a recent paper, Poe et al. (in press) also found

372   that macroevolutionary rates are similar between insular and mainland clades. All

373   these results suggest that rPD likely does not provide an accurate signature of the

374   macroevolutionary dynamic at spatial scales. In fact, it seems that rPD tends to

375   overestimate differences between regions when a stationary diversification

376   process is occurring across geography. A potential solution might be rethinking

377   the way in which we visualize rPD across geography in contrast with the original

378   meaning by Davies & Buckley (2011; see also Forest et al. 2007).

379

380   *Mean root distance (MRD)*

381   As we discussed, *MRD* captures a total diversification value portraying the

382   number of cladogenetic events co-occurring in a given region. In the case of

383   furnariid birds, we found that MRD values tend to be higher in open than forest

384   areas (Figure 4). Accordingly, this metric suggests that more cladogenetic events

385   were accumulated in open areas (i.e., more total diversification; Rabosky 2009).

386   Therefore, this metric, for this bird clade, is consistent with results from explicit

387   diversification approaches (Table 3). For hylid frogs, it seems that there are no

388   differences in MRD values between extratropics and tropics areas (Figure 5).

389   However, tropical areas have some cells with very high values. Again, MRD

390   provide an accurate description of the total diversification pattern in this clade

391   across the latitudinal gradient. In *Anolis* lizards, we found that MDR values tend to

392   be lower in islands in comparison with mainland areas (Figure 6). In this case,

393   MRD did not provide an accurate description of the evolutionary processes

394   occurring between the mainland and insular anole assemblages. However, there is

395   also a high probability that the high MRD values in the mainland are a direct reflect

396   of an idiosyncratic evolutionary trajectory of each one of the two clades that

397   radiated there (i.e., *Draconura* and *Dactyloa* clade; see Poe et al. 2017, Velasco et

398   al. 2018). These two clades seems to exhibit differential diversification dynamics

399   across geography (Velasco et al. 2018) but further research might be necessary to

400   evaluate these differences.

401

402   *Phylogenetic species variability (PSV)*

403   The PSV metric provides information about how related are the species in a

404   given regional assemblage. In hylid frogs, we found that tropical assemblages

405   tend to be composed of more related species than extratropical assemblages

406   (Figure 5). Hylid assemblages in extratropical areas are composed of multiple

407   lineages that dispersed from tropical areas and then diversified there. We found

408   higher dispersal rates from tropical to temperate regions than vice versa (Table 3

409   and 4). The same tendency is present in the case of furnariid birds where open

410   areas exhibit higher PSV values than forest areas (Figure 4) and dispersal rates

411   were higher from open to forest areas than the reverse (Table 3). By contrast, we

412   did not find any evidence for differences in PSV values between island and

413   mainland *Anolis* assemblages (Figure 6). In addition, the dispersal rates were very

414   low between these two regions (Table 3; Poe et al. 2017). All these results confirm

415   that the PSV metric can provide some insights about how dispersal process have

416   shaped regional assemblages. We find evidence that low PSV values (i.e.,

417   phylogenetically over-dispersed faunas) are influenced by multiple dispersals

418   along its evolutionary history.

419

420   *Mean diversification rate (MDR)*

421   Jetz et al. (2012) proposed MDR metric as a species-level speciation rate

422   metric based in the branch length along the path from the root of a tree to each

423   individual species. In furnariid birds, we noted that MDR was slightly higher in

424   open versus forest areas and the same pattern is present using the BAMM

425   approach (Pinto-Ledezma et al. 2017; Figure 5; Table 3). For hylid frogs,

426   extratropical regions tend to exhibit higher values than tropical regions (Figure 5).

427   MDR seems to capture well the differences in macroevolutionary diversification for

428   these taxa along the latitudinal diversity gradient. A similar pattern is present when

429   the BAMM approach is used (Table 3). We consider that both metrics (MDR vs

430   per-species diversification rate from BAMM) leave the same signature in the

431   geography. In *Anolis*, we found that insular assemblages tend to exhibit higher

432   MDR values than continental assemblages (Figure 6), However, there is no

433   difference in the macroevolutionary dynamic between these two areas for the

434   *Anolis* lizards clade (Poe et al. in press, Velasco et al. 2018).

435

436   *Mean ages (MA).*

437   The average of ages of co-occurring lineages are used to test evolutionary

438   hypothesis about whether a region maintains older lineages than others (e.g., a

439   museum) or a combination of old and recent lineages (e.g., OTT hypothesis, Table

440   1). Although this metric does not provide any inference of the ancestral area of the

441   clade, it is possible to implement an explicit biogeographic approach to test this

442   (see below). For example, in hylid frogs, we found that extratropical areas are

443   composed of older lineages than tropical regions (Figure 5). The biogeographic

444   parametric approach infers this same area as ancestral for the entire lineage

445   (Figure A2). In furnariid birds, mean ages metric revealed that older lineages have

446   accumulated more in forest than open areas (Figure 4). In accordance, the

447   ancestral area inferred with a parametric biogeographic method was the forest

448   area (Figure A3). In the case of the anole lizards, insular settings tend to be

449   composed of older lineages than continents. However, the ancestral area for the

450   entire anole clade is the mainland, particularly South America (Poe et al. 2017).

451   The mainland *Anolis* radiation is composed of two clades, one clade that

452   originated in South America (the *Dactyloa* clade; Poe et al. 2017) and colonized

453   Caribbean islands, and the other clade (the *Norops* clade; Poe et al. 2017) that

454   originated in the Caribbean islands and then colonized back the mainland in

455   Middle America and then dispersed to South America. Therefore, the

456   biogeographical history of the *Anolis* radiation is complex and involves multiple

457   dispersals between islands and mainland areas (Poe et al. 2017; Figure A4). In

458   general, mean ages does not provide enough information about the biogeographic

459   origin and maintenance of a clade. This happens because multiple dispersals and

460   *in situ* cladogenesis might erase any simplistic pattern elucidated for this metric,

461   as found in the case of the *Anolis* lizards.

462

463   ***HOW DISPERSAL AND EXTINCTION AFFECT INFERENCES OF***

464   ***GEOGRAPHICAL DIVERSIFICATION GRADIENTS?***

465   Dispersal is another key macroevolutionary process that ultimately determines the

466   number of a species in a region (Roy and Goldberg 2007, Eiserhardt et al. 2013,

467   Rolland et al. 2014, Chazot et al. 2016). However, few studies evaluated explicitly

468   how the direction of dispersals between region contributes to the generation of

469   regional differences between areas (Chown and Gaston 2000, Goldberg et al.

470   2005, 2011, Jablonski et al. 2006). Roy and Goldberg (2007) showed with

471   simulations that dispersal asymmetry between areas had a strong impact in the

472   regional species richness and the average age of these lineages. Accordingly,

473   phylogenetic metrics can be sensitive to dispersal between areas because it is

474   impossible to distinguish which lineages originated by *in situ* speciation or simply

475   due to dispersal from nearby areas. Goldberg et al. (2011) developed the GeoSSE

476   model to evaluate how range evolution affected diversification rates in a

477   phylogenetic comparative approach. The GeoSSE model only considers three

478   states (A: endemic species to a region; B: endemic species to another region; and

479   AB for widespread species) and makes a series of assumptions that can be

480   problematic. The first assumption of the GeoSSE model is that a time-dependent

481   process dominates the diversification dynamic in each region (Stephens and

482   Wiens 2003, Wiens 2011). This assumption conflicts with a diversity-dependent

483   process assumption and this debate is far from being resolved (Cornell 2013,

484   Harmon and Harrison 2015, Rabosky and Hurlbert 2015). The second problematic

485   assumption has to do with the fact that the GeoSSE model consider dispersal

486   rates as stable through time and lineages. In other words, the dispersal ability and

487   therefore the frequency of transitions between areas are constant across the

488   evolutionary history of a clade. There are many empirical evidence showing that

489   dispersal rates vary across time and space among lineages (McPeek and Holt

490   1992, Sanmartín et al. 2008, Robledo-Arnuncio et al. 2014).

491   Regardless of these major assumptions, the GeoSSE model has been

492   adopted to evaluate relative contributions of speciation, extinction and dispersal

493   to the generation of species richness gradients (e.g., Rolland et al. 2014, Pyron

494   2014b, Staggemeier et al. 2015, Looney et al. 2016, Morinière et al. 2016, Pulido-

495   Santacruz and Weir 2016, Alves et al. 2017, Hutter et al. 2017, Pinto-Ledezma et

496   al. 2017). In a recent study, Rabosky and Goldberg (2015) found that state-

497   dependent diversification models tend to inflate excessively the false discovery

498   rates (i.e., type I error rates). In particular, Rabosky and Goldberg (2015) found

499   that these models tend to find false associations between trait shifts and shifts in

500   macroevolutionary dynamics. Although the Rabosky and Goldberg's study was

501   not based on the GeoSSE model, it is clear that transitions between areas (i.e.,

502   dispersal events) can be falsely associated with shifts in speciation and extinction

503   rates across the phylogeny. Alves et al. (2017) also found that geographical

504   uncertainties in the assignment of species to a given area affect the parameter

505   estimates (i.e., speciation, extinction and dispersal rates) in the GeoSSE model.

506   Same authors also evaluated how incorrect assignments of bat species to tropical

507   or extra-tropical regions can generate erroneous conclusions about the relative

508   role of speciation, extinction and dispersal on a latitudinal diversity gradient. From

509   these studies, it is clear that dispersal is a major issue that needs to be evaluated

510   explicitly in macroecological studies.

511   Pulido-Santacruz and Weir (2016) also used the GeoSSE model to disentangle

512   the relative effect of speciation, extinction and dispersal on the latitudinal bird

513   diversity gradient. They found that extinction was prevalent across all bird clades

514   and therefore they suggest this as a main driver of the geographical bird diversity

515   gradient. Pyron (2014c), also using the GeoSSE model, found that temperate

516   diversity in reptiles is due to higher extinction in these areas. We consider that

517   extinction inferences from the GeoSSE model should be treated with caution. For

518   the few clades where fossil record is abundant (e.g., marine bivalves; Jablonski et

519   al. 2006), studies point out to conclude that extinction differences between

520   regions should be treated with caution due to the potential sampling bias

521   (Jablonski et al. 2006, 2017). In addition, studies based on extensive simulations

522   found that extinction inferences based only in molecular phylogenies are not

523   reliable (Rabosky 2010a, 2016b, Quental and Marshall 2010), although extinction

524   rates can be estimated relatively well using medium to large phylogenies (Beaulieu

525   & O'Meara 2015).

526   In a recent review, Sanmartín and Meseguer (2016) proposed that it is possible

527   to detect the extinction signature in molecular phylogenies using extensive

528   simulations and lineage-through-time –LTT- plots (see also Antonelli and

529   Sanmartín 2011). These authors also found that many birth-death models leave a

530   similar phylogenetic imprint, which make indistinguishable some scenarios. In

531   addition, extinction events can affect substantially the ancestral range estimates,

532   and therefore dispersal and extinction parameters in several parametric

533   biogeographic methods (e.g., Dispersal-Vicariance –DIVA- and Dispersal-

534   Extinction-Cladogenesis –DEC- models; Ronquist 1997, Ree et al. 2005).

535   Sanmartín and Meseguer (2016) finally proposed that the adoption of a

536   hierarchical Bayesian approach using continuous-time Markov Chain models will

537   allow a better estimation of extinction both in geography and in the phylogeny

538   (Sanmartín et al. 2008, Sanmartin et al. 2010).

539   Recently, Rabosky and Goldberg (2017) developed a semi-parametric

540   method (FiSSE) to correct the statistical problems found in BiSSE models by

541   themselves in a previous paper (Rabosky and Goldberg 2015). However, the

542   FiSSE method does not allow the evaluation of the contribution of dispersal on

543   regional species richness. In any case, the best suitable framework to estimate

544   relative contributions of speciation, extinction and dispersal might be the GeoSSE

545   model (or parametric biogeographic models; e.g., Matzke 2014; see below),

546   although it requires the simulation of a series of null scenarios to evaluate the

547   statistical power in each case (see Alves et al. 2017, Pinto-Ledezma et al. 2017 for

548   a few examples). For instance, Pinto-Ledezma et al. (2017) developed a

549   parametric bootstrapping approach simulating traits to evaluate whether empirical

550   inferences are different from the simulated. They simulated 100 datasets of neutral

551   characters along a set of empirical phylogenies and using this new information

552   repeated the same procedure with empirical data (see Appendix S1 in Pinto-

553   Ledezma et al. 2017 for details of the bootstrapping approach). This

554   bootstrapping procedure assumes no direct effect of the geographic character

555   states on the parameter estimations (Feldman et al. 2016, Pinto-Ledezma et al.

556   2017).

557   Finally, it should be clear that more research would be necessary to

558   establish how extinction affect estimation parameters in state-dependent

559   diversification approaches (e.g., the GeoSSE model). For instance, the inclusion-

560   exclusion of extinct species in simulated phylogenies using birth-death models

561   could substantially affect the geographical inferences of speciation, extinction and

562   dispersal parameters in the GeoSEE model. This kind of approach might provide

563   some lights on how to biased can be the parameter estimates with only molecular

564   phylogenies using the GeoSSE model or any other modeling approach.

565

566   ***Parametric biogeographical approaches in macroecological studies.***

567   The use of parametric biogeographic approaches is an optimal solution to

568   estimate dispersals across time and space (Matzke 2014, Dupin et al. 2017).

569   These methods are promising in identifying the relative roles of cladogenetic and

570   anagenetic processes shaping regional species richness. Recently, Dupin et al.

571   (2017) developed a biogeographical stochastic mapping to infer the number of

572   dispersals, and other biogeographical events, in the evolutionary history of

573   Solanaceae plants across the world. This approach allows the inference from

574   multiple process including sympatric speciation, allopatric speciation, founder-

575   event speciation, range expansion (i.e., dispersal without speciation) and local

576   extinction (i.e., range contractions) based on a time-calibrated phylogenetic tree

577   and the occurrence of species in geographical regions (see also Matzke 2014 for

578   more detailed description of the method). These explicit biogeographical

579   approaches are promising in macroecological studies since they allow to test

580   simultaneously a set of evolutionary process during the diversification of a clade in

581   a region (Velasco 2018). In addition, with these new approaches it is possible to

582   differentiate effectively between macroevolutionary sources and sink areas

583   (Goldberg et al. 2005, Castroviejo-Fisher et al. 2014, Poe et al. 2017). For

584   instance, Poe et al. (2017) used a parametric biogeographical approach to

585   estimate the number of events among regions and distinguish those areas where

586   many cladogenetic events occurred (i.e., *in situ* speciation) and areas where

587   almost all its diversity was build-up from extensive colonization of other regions.

588   The biogeographical stochastic mapping (BSM) method developed by

589   Dupin et al. (2017) is promising to estimate more accurately the number of

590   dispersal events between regions based on a better estimation of the ancestral

591   area for a clade. We evaluated how dispersal rates between regions can affect

592   inferences drawn only from phylogenetic metrics in our three data sets. We

593   implemented GeoSSE and BSM approaches for each data set (Table 3 and 4). For

594   the case of hylid frogs, we counted the inferred number of dispersal events

595   between tropical and extra-tropical regions in the Americas (Table 3; see also

596   (Wiens et al. 2006, Algar et al. 2009). For furnariid birds, we counted the number

597   of dispersal events between open and forest areas (Table 3; see also Pinto-

598   Ledezma et al. 2017). Finally, for anole lizards, we counted the number of

599   dispersal events between insular and mainland areas (Table 3; see also Algar and

600   Losos 2011, Poe et al. 2017, Velasco et al. 2018).

601   Using biogeographical stochastic mapping –BSM-, we inferred the number

602   of dispersal events from one region to another for each one of the three

603   taxonomic groups examined (Table 3). The BSM approach allows us to

604   disentangle which dispersals were only range expansions and which dispersals

605   generated a speciation event (i.e., a founder-event speciation; (Barton and

606   Charlesworth 1984, Templeton 2008). For furnariid birds, we found that range

607   expansions were three times higher from forest areas to open areas than the

608   reverse and founder events were twice higher from forest to open areas than the

609   opposite (Table 3). This result suggests that differences in species richness

610   between forest and open areas are due by recurrent dispersal events along the

611   furnariid diversification history (Pinto-Ledezma et al. 2017). Pinto-Ledezma et al.

612   (2017) found a similar result using the GeoSSE approach, but they conducted a

613   parametric simulation approach to evaluate whether there was a direct effect of

614   the geographic location on the parameter estimates. Their results show that the

615   GeoSSE approach, in this case, had limited power to detect a signature of

616   geographic region on speciation, extinction and dispersal rates. With the

617   implementation of the BSM approach here, we corroborate Pinto-Ledezma et al.'s

618   findings with improved statistical power. In the case of hylid frogs and the

619   transitions between tropical and extra-tropical areas, we found that the BSM

620   approach inferred more dispersal events from tropical to extra-tropical regions

621   (Table 3 and 4). However, the number of founder events was relatively low in

622   comparison with range expansions (Table 3). These results suggest that few

623   dispersal events have occurred across the diversification of hylid frogs and

624   corroborate that the species richness in each region largely originated by *in situ*

625   speciation modulated by climatic factors (Wiens et al. 2006, Algar et al. 2009).

626   Finally, for *Anolis* lizards, we found that dispersal events between insular and

627   mainland regions were relatively low (Table 3 and 4). We did not find evidence of

628   any expansion range events from mainland to island or vice versa. This also

629   corroborates previous findings that evolutionary radiation of anole in insular and

630   mainland settings is due to extensive *in situ* diversification (Poe et al. in press,

631   2017, Algar and Losos 2011).

632   These results point out that the BSM approach (Dupin et al. 2017) is a

633   promising approach when we are interested in testing the role of anagenetic and

634   cladogenetic events on the resulting geographical species richness gradients.

635   Although parametric biogeographic approaches are still in their infancy (Sanmartín

636   2012, Matzke 2014, Dupin et al. 2017), these methods allow us to evaluate

637   macroevolutionary dynamics (i.e., speciation and extinction) in an explicit

638   geographical context. These methods are statistical powerful and make use of a

639   series of explicit geographic range evolution models (Velasco 2018).

640

641   ***TOWARD AN INTEGRATION OF BIOGEOGRAPHICAL AND SPECIES***

642   ***DIVERSIFICATION APPROACHES IN MACROECOLOGICAL STUDIES.***

643   Although different parametric biogeographic methods have been

644   developing at least for the last 20 years (Ronquist 1997, Ree et al. 2005, Landis et

645   al. 2013, Matzke 2014, Dupin et al. 2017), the adoption of these methods to test

646   evolutionary-based hypotheses underlying geographical diversity gradient has

647   been rare. For instance, few studies examined here tested the effect of dispersal

648   events in the generation of regional species richness assemblages. It should clear

649   that the current paradigm in biogeography makes a call for an evaluation of the

650   relative frequency of cladogenetic and anagenetic process during the

651   biogeographical history of lineages. The adoption of parametric approaches in

652   future macroecological studies will contribute to an improvement of the estimation

653   of speciation, extinction and dispersal processes as drivers of the geographical

654   diversity gradients. In addition, we also think that it is necessary to establish which

655   macroevolutionary dynamics govern regional assemblages. Phylogenetic

656   approaches based on fitting diversification models help to test whether regional

657   species richness is due to diversity dependence (i.e., ecological limits), time

658   dependence, or environmental factors (Rabosky and Lovette 2008, Etienne et al.

659   2012, Etienne and Haegeman 2012, Condamine et al. 2013). We also stress that

660   the adoption of many approaches providing multiple lines of evidence will help to

661   disentangle the evolutionary and ecological causes of biodiversity gradients.

662   Some recent studies have pointed toward this strategy and have begun to provide

663   evidence from many lines to understand how evolutionary processes underlying

664   species richness gradients works (Hutter et al. 2017, Pinto-Ledezma et al. 2017).

665

666   ***Conclusions and recommendations***

667   The resulting geographical pattern of several phylogenetic metrics did not

668   provide any robust evidence of a spatially explicit diversification dynamic. As we

669   have shown, these resulting geographical patterns did not differ from that

670   generated by a simple null model. It is hard to untangle causal mechanisms (i.e.,

671   speciation, extinction, and dispersal) from only the geographical signature that

672   these metrics attempt to capture. We recommend that phylogenetic metrics

673   should be used only to visualize geographical patterns of total diversification (e.g.,

674   MRD, residual PD; MDR), phylogenetic structure (e.g., PSV), or mean ages of co-

675   distributed species (e.g., MA) (Table 1). We suggest that conclusions about the

676   role of evolutionary processes in the generation and maintenance of species

677   richness gradients based only in these phylogenetic metrics should be avoided

678   and additional approaches always should be used.

679   Some explicit diversification approaches (e.g., model fitting approaches;

680   (Etienne et al. 2012, Rabosky 2014, Valente et al. 2015) are useful to establish the

681   macroevolutionary dynamics operating at regional scales. Although some

682 approaches (e.g, the GeoSSE model) allow us to evaluate the relative role of the

683 ultimate process that modify the regional species diversity, its statistical power

684 (e.g., high Type I errors) has been challenged by simulation and empirical studies.

685 Furthermore, the extinction and dispersal estimates inferred by the GeoSSE model

686 tend to be unbiased. Parametric biogeographic approaches are becoming a

687 standard tool to evaluate how evolutionary processes can explain the

688 geographical distribution of extant taxa. These approaches are promising and

689 should be extensively used because allow us to estimate the relative frequency of

690 cladogenetic and anagenetic process shaping the regional species richness.

691 It is necessary that macroecological studies use a combination of explicit

692 diversification approaches and parameter biogeographic methods with the aim to

693 clarify how evolutionary process have shaped regional species richness

694 assemblages. As Jablonski et al. (2017) have outlined, one of the main obstacles

695 to generate an appropriate understanding of the causal mechanisms underlying

696 geographical diversity gradients has been that many studies have tested a single

697 hypothesis, either evolutionary or ecological, as an explanatory factor. We suggest

698 that ecological and evolutionary hypotheses should be tested simultaneously to

699 explain the relative contribution of each process to the regional diversity. As

700 shown by our empirical comparison of phylogenetic metrics, explicit

701 diversification models, and historical biogeographic methods have showed, it is

702 necessary to obtain evidence of different approaches to guarantee sound

703 conclusions about the evolutionary causes of these biodiversity gradients.

704

Acknowledgments

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1011   Diversity Gradient in Hylid Frogs: Treefrog Trees Unearth the Roots of High

1012   Tropical Diversity. - Am. Nat. 168: 579–596.

1013

1014 Table 1: Phylogenetic metrics and explicit diversification approaches used in
1015 macroecological studies to address evolutionary questions related with the
1016 geographical diversity gradients.

Metric	Author	Description	Software / R package
MRD	Kerr and Currie 1999	MRD is calculated by counting the number of nodes separating each terminal species in a regional assemblage or cell from the tips to root of the phylogenetic tree. This metric does not need that trees be ultrametric or have branch lengths.	metricTester
PD (residual)	Faith 1992	PD is calcultated by summing all the branch lengths of species co-occurring in a regional assemblage or cell. Residual PD is obtained from an ordinary least square regression between PD and species richness.	picante, metricTester, pez
PSV	Helmus et al. 2007, Algar et al. 2009	PSV is calculated from a matrix where their diagonal elements provide the evolutionary divergence (based on the branch lengths) of each terminal species from the root to the tips of the tree, and the off-diagonal elements provide the degree of shared evolutionary history among species. Values close to zero indicates that all species in a regional assemblage or cell are very close related whereas values close to one indicate that species are not related.	picante, metricTester, pez
mean DR	Jetz et al. 2012	DR is calculated as the inverse of a measure of evolutionary isolation (Redding & Mooers 2006) which sum all the edge lengths from a species to the root of the tree. The inverse of this evolutionary isolation metric therefore capture the level of splitting rate of each species (i.e., its path to a top).	FiSSE
Mean age	Latham and Ricklefs 1993	The mean age of co-occurring species in a regional assemblage or cell simply is calculated tallying the age of each most recent common ancestor (MRCA) for each species and the averaged.	None
GeoSSE	Goldberg et al. 2011	The geographic state speciation and extinction -GeoSSE- model is a trait-dependent diversification method linking geographic occurrence with diversification rates. These method allow to infer both speciation and extinction rates as movement (dispersal) rates among two regions.	Diversitree R package
BAMM	Rabosky 2014	BAMM is a method that attempt to identify whether a phylogeny exhibit a single or various macroevolutionary regimes (i.e., different diversification dynamics). As speciation, extinction and net diversification rates are considered to be heterogeneous across the phylogeny it is possible to estimate a rate for each branch or species in the tree.	BAMM software and BAMMtools R package

1017

1018   Table 2. Description of some evolutionary hypothesis tested in macroecological studies as causal mechanisms of
1019   regional species richness.

Hypothesis	References	Description	Predictions	Metrics and/or methods used to test	Limitations
Phylogenetic niche conservatism (PNC)	Wiens and Graham 2005	Phylogenetic niche conservatism is the tendency of related species to inherit niche requirements from its the most recent common ancestors (Wiens & Graham 2005).	PNC predicts that regions where a clade originated will accumulate more species simply due to more occupation time and diversification rates tend to be similar between regions. The tropical niche conservatism hypothesis (TNC; Wiens and Donoghue 2004) is based on PNC to explain differences in species richness in tropical and temperate regions.	MRD, Mean age, GeoSSE, BAMM	1) MRD metric fails to capture spatially dynamics of the balance of speciation and extinction and it is very hard to establish whether species richness in a region is only generated by higher speciation rates. Furthermore, MRD does not capture dispersal dynamic across regions and species richness in a given region can be generated from only dispersals from nearby regions (e.g., macroevolutionary sinks; CITA). 2) Mean age provide partial is able to test the role of PNC on geographical species richness because only it is possible to establish which regions have, in average, old clades and this not reflects whether many speciation events occurred there. 3) GeoSSE is potentially the only one approach that allow to disentangle these three process but it is only limited to two regions (e.g., tropical vs. temperate). In addition, GeoSSE has been criticized due its low statistical power (see Rabosky and Goldberg 2015).
Regional diversification (RD)	Buckley et al. 2010	Differences in the balance of speciation and extinction across geography can explain differences in species richness between regions.	RD predicts that regions with striking differences in species richness are due to differences in macroevolutionary dynamics between regions.	residual PD, GeoSSE, BAMM	1) Residual PD can be used to discriminate regions with rapid and slow diversification based on the expected phylogenetic diversity given species richness (Buckley et al. 2010). However, this metric ignores the contribution to dispersal to PD in a given region or cell. 2) GeoSSE can estimate speciation, extinction and dispersal rates between regions but again is limited to two regions. 3) BAMM potentially could be used to estimate speciation rates for regional clades but this method is unable to estimate dispersal rates between regions.

Out of the tropics (OTT)	Jablonski et al. 2006	Species were generated in the tropical regions and dispersed to extratropical regions but maintain its presence in its ancestral areas	High rates of speciation are predicted in tropical regions in contrast with temperate regions. Asymmetric dispersal have occurred along the biogeographical history of a taxa from tropical to temperate areas.	MRD, Mean age, GeoSSE	These metrics are the same used to test the PNC/TNC hypothesis as we discuss above.
Time for speciation effect (TEE)	Stephens and Wiens 2003	Tropical regions accumulated more species because their clades had more time to speciate than temperate regions.	Regions recently colonized had lower species richness than regions where clades colonized very early in the history of a clade.	Mean age	1) Mean age does not provide an accurate description of which lineages colonized first a region. To test this hypothesis, it might be necessary to perform an ancestral range reconstruction of all co-occurring clades and estimate its diversification rates (i.e., total diversification for each independent colonized clade; Rabosky 2009; 2012).

1020

1021 Table 3. Parameter estimates from the GeoSSE model for three taxonomic groups
1022 (Furnariides birds, hylid frogs, and *Anolis* lizards) across two regions. Areas for each
1023 taxonomic group as follows: Furnariides birds: A: Forest; B: Open areas; Hylid frogs: A:
1024 Extra tropics; B: Tropics; *Anolis* lizards: A: Islands; B: Mainland.

Group	Rates	A	B	AB
Furnariides birds	Speciation	0.139 ± 0.020	0.223 ± 0.065	0.041 ± 0.020
	Extinction	0.040 ± 0.025	0.107 ± 0.075	-
	Dispersal	0.021 ± 0.004	0.311 ± 0.114	-
	Net diversification	0.099 ± 0.005	0.116 ± 0.01	-
Hylid frogs	Speciation	0.044 ± 0.003	0.044 ± 0.003	0.041 ± 0.025
	Extinction	0.002 ± 0.002	0.002 ± 0.002	-
	Dispersal	0.001 ± 0.001	0.035 ± 0.010	-
	Net diversification	0.042 ± 0.003	0.042 ± 0.003	-
Anolis lizards	Speciation	0.058 ± 0.003	0.058 ± 0.003	1.245 ± 1.303
	Extinction	0.001 ± 0.001	0.001 ± 0.001	-
	Dispersal	0.002 ± 0.001	0.0003 ± 0.000	-
	Net diversification	0.057 ± 0.002	0.057 ± 0.002	-

1025

1

1026 Table 4. Frequency of dispersal events inferred using biogeographical stochastic
1027 mapping (BSM) for three taxonomic groups (Furnariides birds, hylid frogs, and *Anolis*
1028 lizards) across two regions. Areas for each taxonomic group as follows: Furnariides
1029 birds: A: Forest; B: Open areas; Hylid frogs: A: Extra tropics; B: Tropics; *Anolis* lizards:
1030 A: Islands; B: Mainland.
1031

Event	Group	Regions	A	B
Range expansions	Furnariides birds	A	0	92.62 ± 4.39
		B	31.4 ± 4.29	0
	Hylid frogs	A	0	0.64 ± 0.78
		B	12.92 ± 0.88	0
	Anolis lizards	A	0	0
		B	0	0
Founder events	Furnariides birds	A	0	24.46 ± 2.54
		B	10.88 ± 2.22	0
	Hylid frogs	A	0	0.66 ± 0.66
		B	4.3 ± 1.42	0
	Anolis lizards	A	0	2.02 ± 0.14
		B	0.12 ± 0.33	0

1032
1033

1034   FIGURE LEGENDS

1035   Figure 1. Diagram illustrating how differences in speciation, extinction, and dispersal

1036   rates between regions can generate a geographical species richness gradient. The

1037   phylogenetic trees below illustrate how the differences in speciation and extinction

1038   rates between two regional assemblages can shape a gradient of species richness

1039   (degraded blue colour).

1040

1041   Figure 2. Geographical patterns of some phylogenetic metrics used in macroecological

1042   studies to explore evolutionary process underlying geographical diversity gradients

1043   (see also Table 1 for a detailed explanation). Left column *Anolis* lizards; Middle column:

1044   Hylid frogs; Right column: Furnariides birds. (A-C) observed richness patterns; (D-F)

1045   rPD: residual phylogenetic diversity (i.e., after controlling for species richness); (G-I)

1046   PSV: phylogenetic species variability; (J-L) MRD: mean root distance; (M-O) MDR:

1047   mean diversification rate; (P-R) Mean ages: average ages of species.

1048

1049   Figure 3. P-values distribution for each phylogenetic metric obtained through the null

1050   model (see main text for details). The vertical red lines represent the empirical 0.05 cut-

1051   off. Note that for all cases very few cells are below the 0.05 cut-off. (A-C) rPD: residual

1052   phylogenetic diversity (i.e., after controlling for species richness); (D-F) PSV:

1053   phylogenetic species variability; (G-I) MRD: mean root distance; (J-L) MDR: mean

1054   diversification rate; (M-O) Mean ages: average ages of species.

1055

1056   Figure 4. Variation of phylogenetic metric values for Furnariides birds in forest and

1057   open areas. rPD: residual phylogenetic diversity (i.e., after controlling for species

1058   richness); PSV: phylogenetic species variability; MRD: mean root distance; MDR: mean

1059   diversification rate; Mean ages: average ages of species.

1060

1061   Figure 5. Variation of phylogenetic metric values for Hylid frogs in tropics and extra-

1062   tropics regions. rPD: residual phylogenetic diversity (i.e., after controlling for species

1063   richness); PSV: phylogenetic species variability; MRD: mean root distance; MDR: mean

1064   diversification rate; Mean ages: average ages of species.

1065

1066   Figure 6. Variation of phylogenetic metric values for *Anolis* lizards in continental and

1067   insular areas. rPD: residual phylogenetic diversity (i.e., after controlling for species

1068   richness); PSV: phylogenetic species variability; MRD: mean root distance; MDR: mean

1069   diversification rate; Mean ages: average ages of species.

1070

DIVERSITY GRADIENTS

**Higher speciation
Lower extinction
Dispersal (out)**

**Lower speciation
Higher extinction
Dispersal (in)**
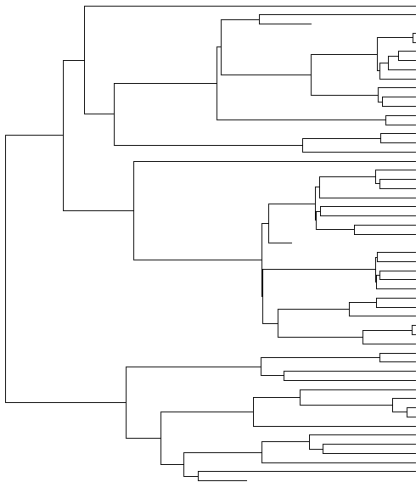
Speciation = 0.5; Extinction = 0.05
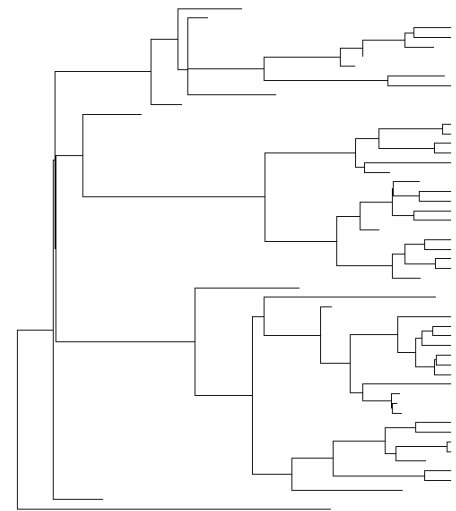
Speciation = 0.3; Extinction = 0.15

Anolis (A)
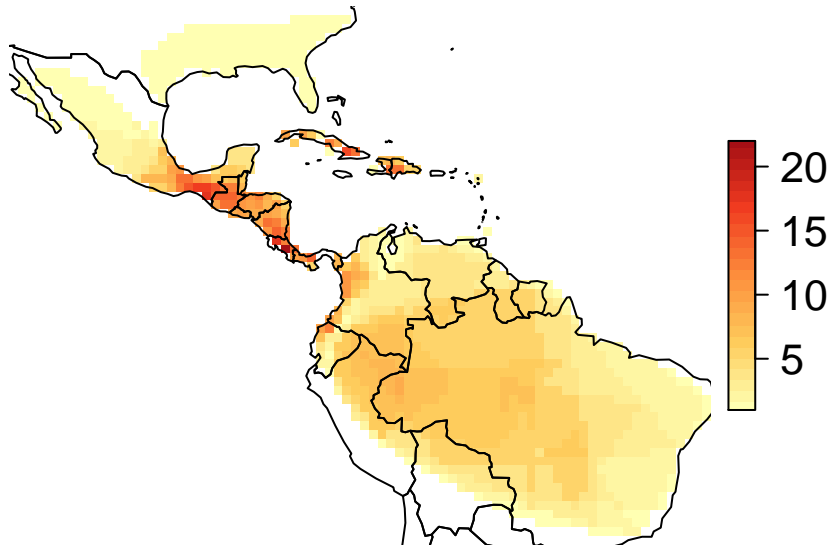
Hylids (B)
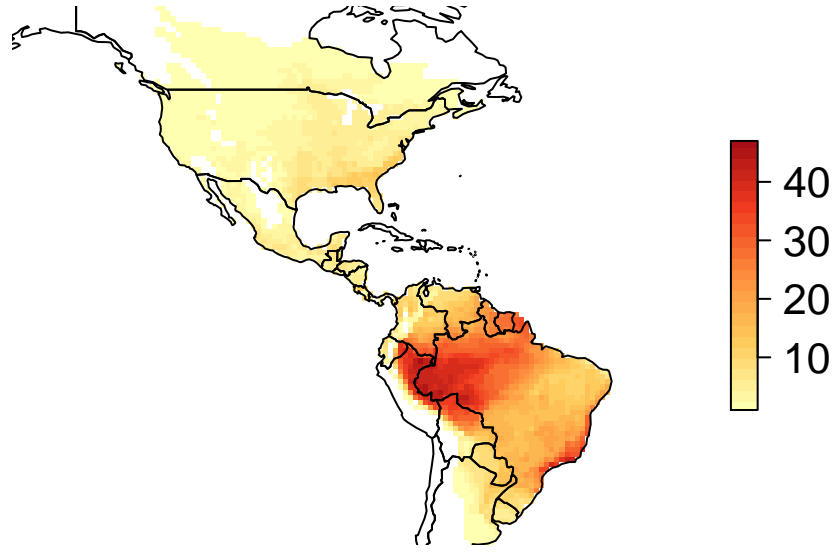
Furnariides (C)
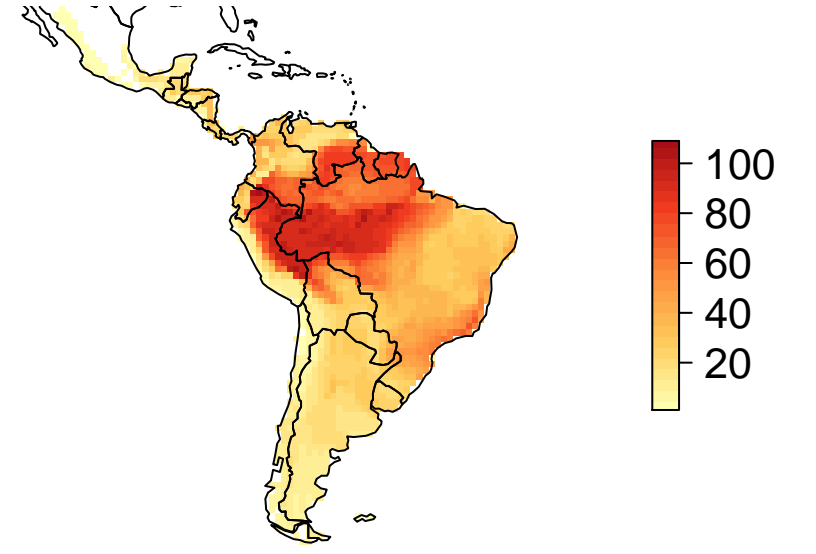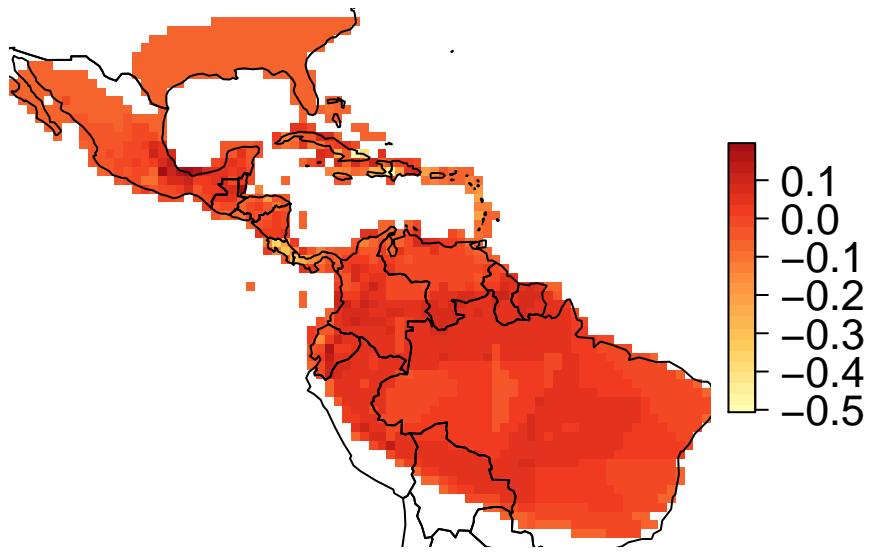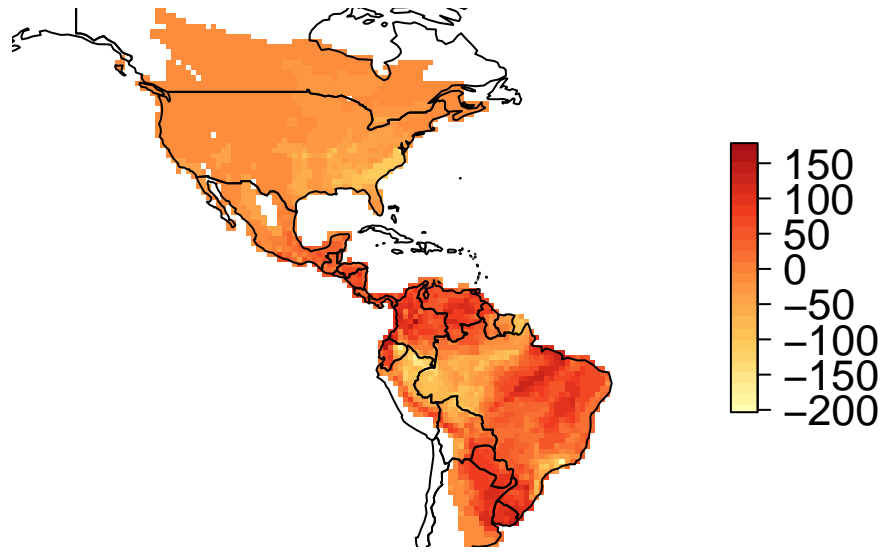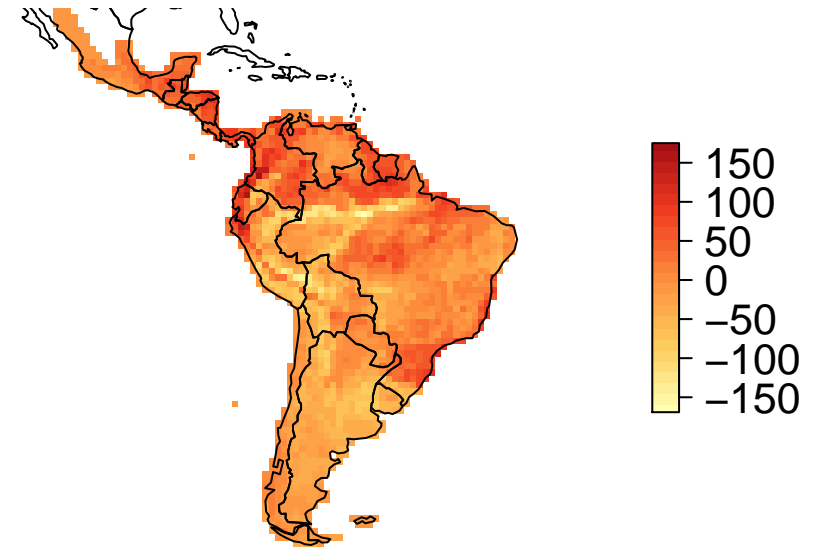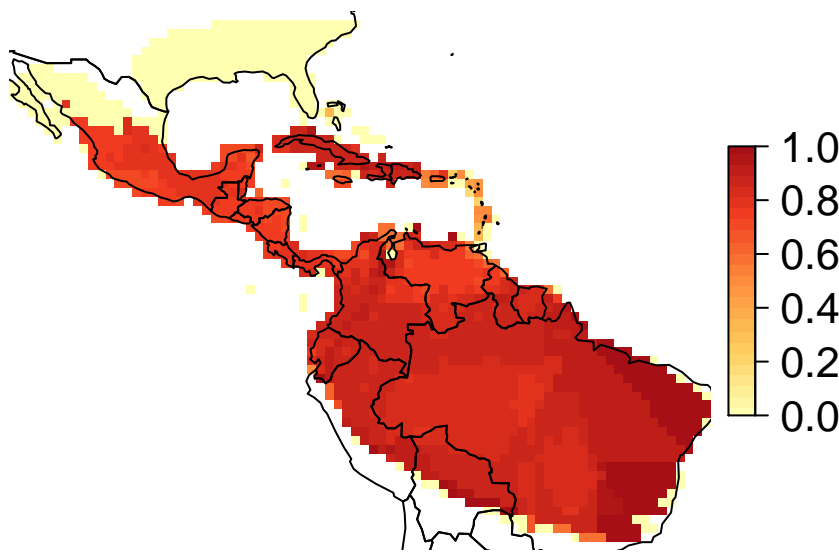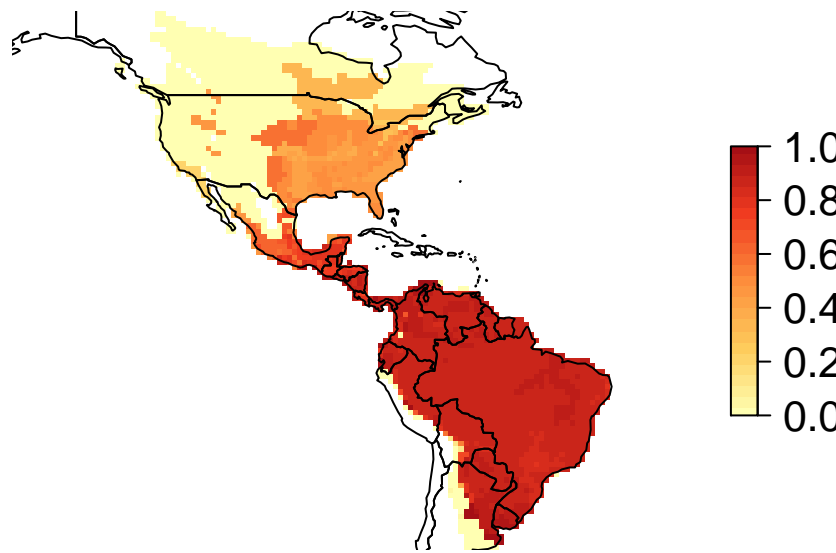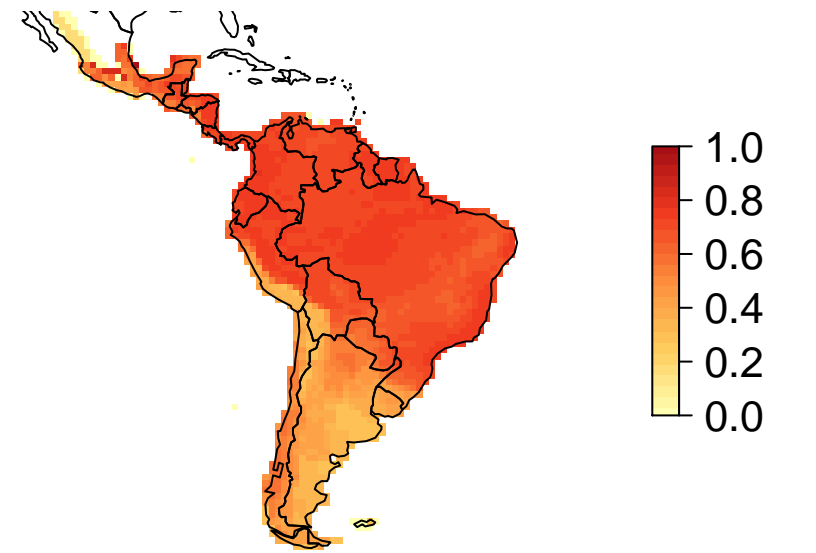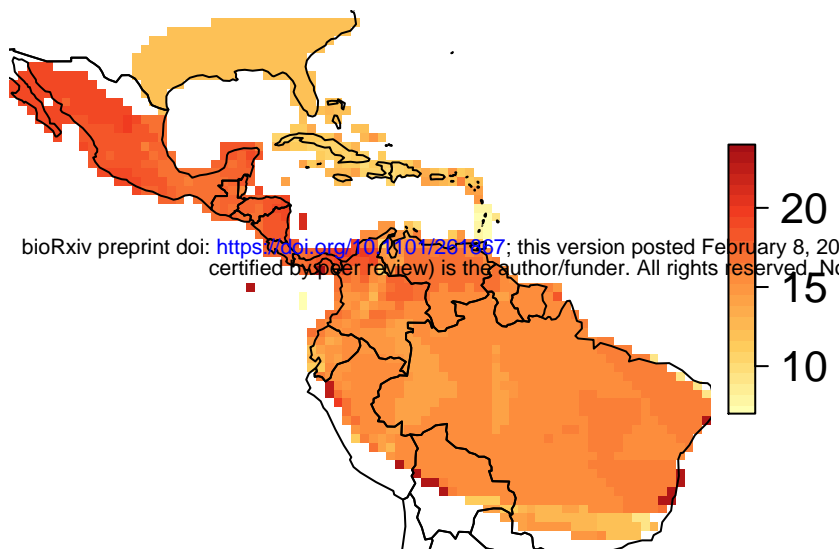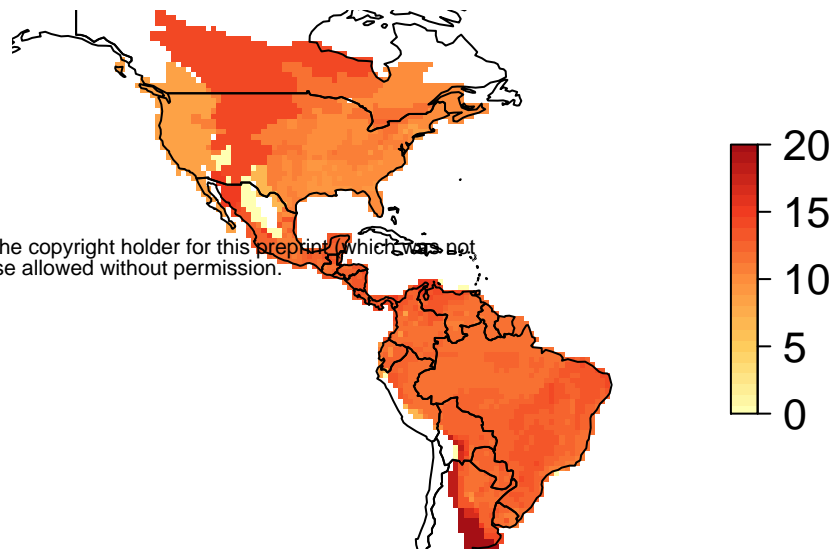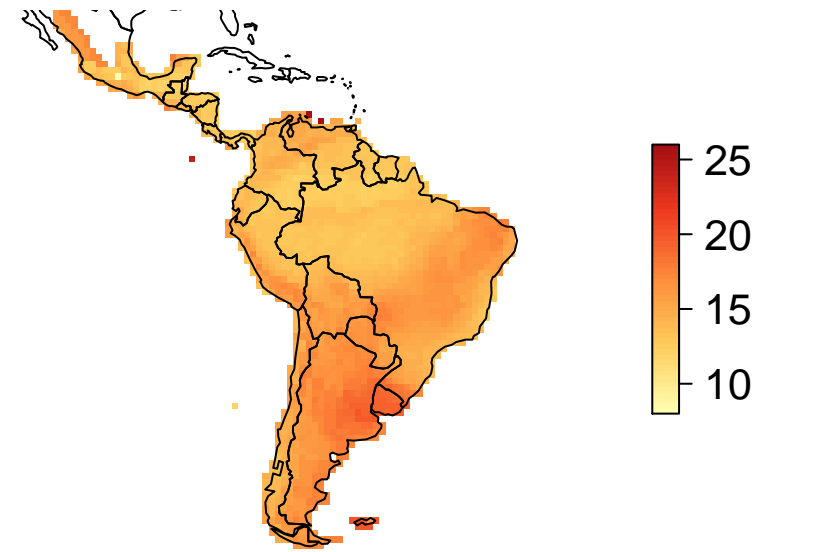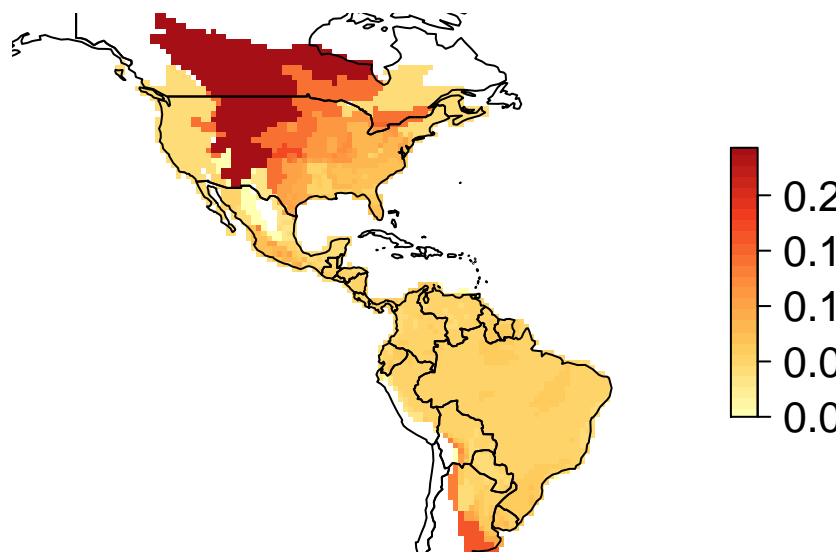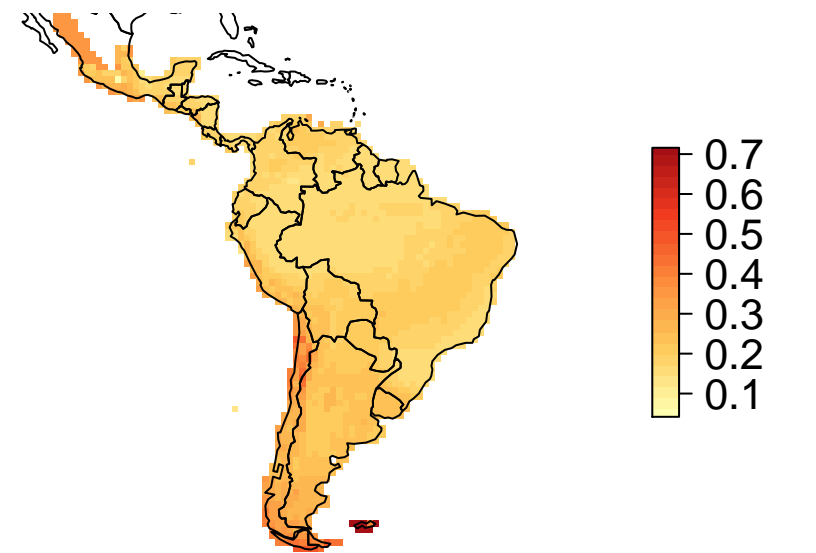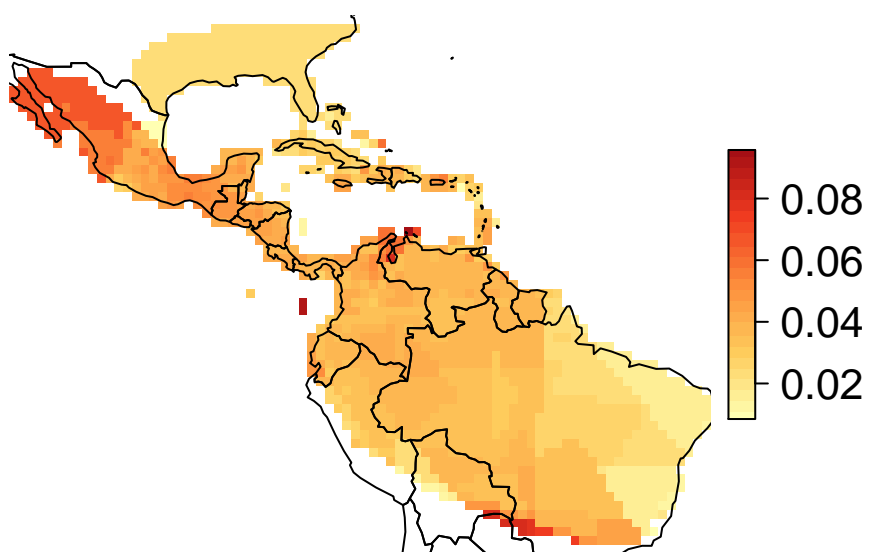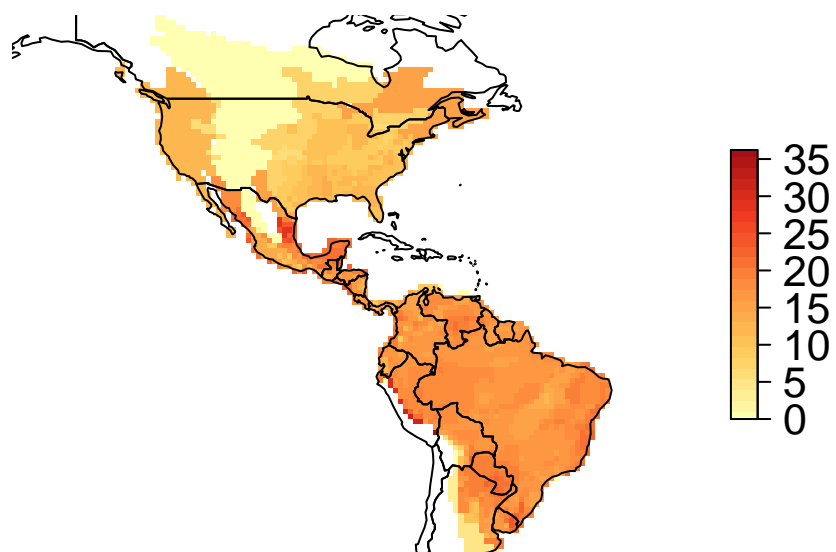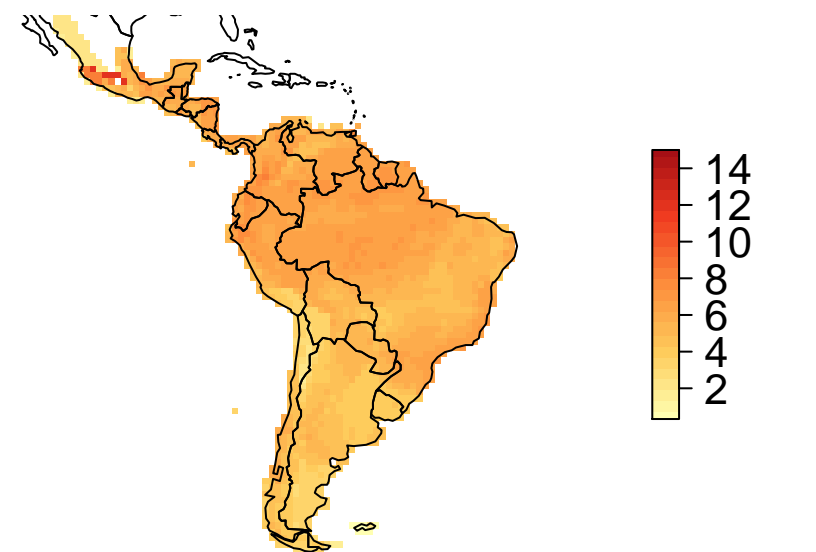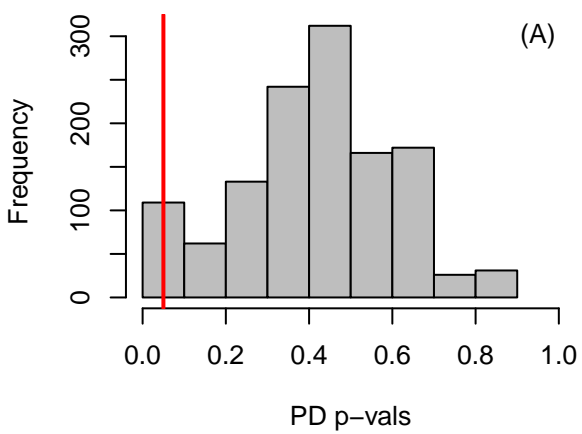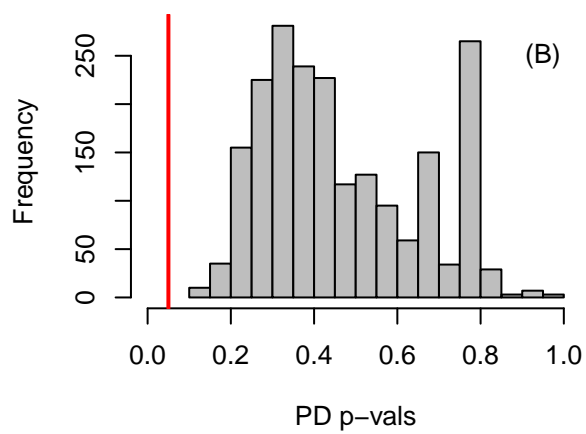
Anolis

Hylids

Furnariides

Stochastic map
ancstates: global optim, 2 areas max. d=5; e=0; j=2.9172; LnL=−102.92

Millions of years ago

Stochastic map
ancstates: global optim, 2 areas max. d=5; e=0; j=2.9704; LnL=−899.05

Millions of years ago

Stochastic map
ancstates: global optim, 2 areas max. d=0.7012; e=0; j=2.713; LnL=−20.91

Millions of years ago