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

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16   **Abstract**

17   The intersection of macroecology and macroevolution is one of the most active research areas

18   today. Macroecological studies are increasingly using phylogenetic diversification metrics to

19   explore the role of evolutionary processes in shaping present-day patterns of biodiversity.

20   Evolutionary explanations of species richness gradients are key for our understanding of how

21   diversity accumulated in a region. For instance, the present-day diversity in a region can be a

22   result of *in situ* diversification, extinction, or colonization from other regions, or a combination of

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

24   diversification and dispersal processes across geography. Some metrics (e.g., mean root distance

25   -MRD-; lineage diversification-rate -DR-; evolutionary distinctiveness -ED-) seem to provide very

26   similar geographical patterns regardless of how they were calculated (e.g., using branch lengths

27   or not). The lack of appropriate estimates of extinction and dispersal rates in phylogenetic trees

28   can limit our conclusions about how species richness gradients emerged. With a review of the

29   literature and complemented by an empirical comparison, we show that phylogenetic metrics by

30   itself are not capturing well the speciation, extinction and dispersal processes across the

31   geographical gradients. Furthermore, we show how new biogeographic methods can improve our

32   inference of past events and therefore our conclusions about the evolutionary mechanisms

33   driving regional species richness. Finally, we recommend that future studies include several

34   approaches (e.g., spatial diversification modelling, parametric biogeographic methods) to

35   disentangle the relative the role of speciation, extinction and dispersal in the generation and

36   maintenance of species richness gradients.

37

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

39   richness, Regional assemblages

40   **Introduction**

41   The causes of spatial variation of biodiversity are one of the most fundamental questions

42   in ecology, biogeography and macroecology (Brown 1995, 2014, Brown and Lomolino 1998,

43   Hawkins et al. 2012, Fine 2015, Jablonski et al. 2017). Current studies are integrating in a single

44   framework the ecological and evolutionary mechanisms driving regional species diversity

45   (McGaughran 2015, Pärtel et al. 2016, Cabral et al. 2017, Leidinger and Cabral 2017). However,

46   only three macroevolutionary processes ultimately can modify the number of species in a region:

47   speciation, extinction and dispersal (Wiens 2011, Fine 2015, Jablonski et al. 2017) (Figure 1). These

48   processes can be modulated by species' traits varying within clades (Paper et al. 2016, 2017,

49   Jezkova and Wiens 2017, Moen and Wiens 2017), age of region (e.g., time-for-speciation effect;

50   Stephens & Wiens, 2003), geographical area (Losos and Schluter 2000), or climatic conditions

51   (Condamine et al. 2013, Lewitus and Morlon 2017).

52   The integration of different disciplines such as molecular phylogenetics, palaeontology,

53   and historical biogeography have allow to infer a series of macroevolutionary processes across

54   geography (Diniz-Filho et al. 2013, Fritz et al. 2013). It is well-known that fossil information is key

55   to estimate with high confidence rates of speciation and extinction (Sepkoski 1998, Foote 2000,

56   Quental and Marshall 2010, Rabosky 2010b). New methods correcting for sampling bias are able

57   to generate improvements in the estimates of the speciation, extinction and net diversification

58   rates (Silvestro et al. 2014, 2016). However, the causal mechanisms that underlying the

59   geographical diversity gradients only can be established with greater confidence for a few

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

61   2017), mammals (Silvestro et al. 2014) or plants (Antonelli et al. 2015).

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

63 approaches used to estimate speciation and extinction rates in palaeontology were adapted to

64 study the macroevolutionary dynamics using phylogenetic information (Nee et al. 1994, Morlon

65 et al. 2010, Stadler 2013). Molecular phylogenies are becoming essential to the study of

66 diversification dynamics across temporal and spatial scales for extant taxa (Wiens and Donoghue

67 2004, Rabosky and Lovette 2008, Stadler 2013, Morlon 2014, Schluter and Pennell 2017).

68 Therefore, it is possible to reconstruct past diversification process based on the branching events

69 of a phylogeny using a set of birth-death models (Nee et al. 1994, Nee 2006, Morlon et al. 2010,

70 Stadler 2013, Morlon 2014). These birth-death models allow infer either a homogeneous process

71 for an entire clade (Nee et al. 1994, Magallón and Sanderson 2001) or a heterogeneous process

72 varying in time or in specific subclades of a tree (Paper et al. 2006, Rabosky and Lovette 2008,

73 Alfaro et al. 2009). However, these birth-death models only account for temporal variation of the

74 macroevolutionary processes and how translate these processes to the geography is still a matter

75 of debate.

76 Macroecological studies use two main approaches to link the estimates of diversification

77 with the geographical ranges of species (Hawkins et al. 2007, Algar et al. 2009, Qian et al. 2014,

78 Pinto-Ledezma et al. 2017, Velasco et al. 2018). The first one uses a set of phylogenetic metrics as

79 a proxy to capture the geographical signature of lineage diversification dynamics (Diniz-Filho *et*

80 *al.*, 2013; Fritz *et al.*, 2013; Table 1; Figure 2). These metrics provide either an estimate of a per-

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

82 rPD-, mean diversification rate –MDR-), the phylogenetic structure of regional assemblages (e.g.,

83 phylogenetic species variability –PSV-) or the average age of co-occurring lineages in a given area

84 (e.g., mean age; see Table 1). Each metric is calculated for each species in the phylogeny;

85 therefore, we can associate the species' values to its corresponding geographical range and

86 generate a map with average values for cells or regions. Although these phylogenetic metrics only

87 account for speciation events, macroecologists have used these maps as a proxy to test some

88 evolutionary-based hypothesis in macroecological research (Diniz-Filho *et al.*, 2013; Fritz *et al.*,

89 2013; see Table 2 for a compendium of these hypotheses).

90   The second approach used by macroecologists consists in the explicit estimation of

91 diversification parameters across geography (Goldberg et al. 2005, 2011, Ramiadantsoa et al.

92 2017). For instance, the geographic state speciation and extinction model –GeoSSE (Goldberg et

93 al. 2011; Table 1) allows estimating speciation, extinction and dispersal parameters across two

94 regions. It is possible to disentangle the relative role of each one of these processes on the

95 generation and maintenance of the geographical diversity gradients (Rolland et al. 2014, Pulido-

96 Santacruz and Weir 2016, Pinto-Ledezma et al. 2017). In addition, a recently developed Bayesian

97 approach (BAMM; Rabosky 2014, Rabosky et al. 2014) allows to infer the balance of speciation

98 and extinction in the generation of these biodiversity gradients (Rabosky et al. 2015, Sánchez-

99 Ramírez et al. 2015, Morinière et al. 2016, Pinto-Ledezma et al. 2017). The BAMM approach allows

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

101 regime; Rabosky 2014) and also get estimates of per-species diversification rates (i.e., as a

102 phylogenetic metric; Rabosky 2016) that can be mapped in a geographical domain. Although all

103 these methods aim to obtain a geographical picture of the diversification processes, it remains

104 unexplored if they can effectively capture these dynamics across regions.

105   In this paper, we conducted a review on macroecological literature to evaluate how

106 evolutionary and biogeographic processes contribute to shape geographical species richness

107 gradients. We review only those papers that make explicit use of phylogenetic metrics and/or

108 explicit diversification approaches (Table 1). We divided our review in three main sections. In the

109   first one, we discuss how studies use phylogenetic metric to test some evolutionary-based

110   hypotheses underlying geographical diversity gradients and we explore some limitations of these

111   metrics (see also Table 2). Also, we discuss to what extent these metrics are able to capture

112   macroevolutionary dynamics in a spatial explicit context. We illustrate these using three case

113   studies (Furnariides birds, Hylid frogs, and *Anolis* lizards; Figure 1) and explore how another

114   approaches (e.g., diversification modelling and biogeographical approaches) can complement our

115   inferences about diversification process across geography. In the second section, we discuss how

116   dispersal and extinction processes are limiting these diversification inferences and we propose

117   some research avenues to attempt to solve these problems. Using an explicit biogeographical

118   approach, we test the role of dispersal on the geographical species richness patterns of the three

119   case studies. Finally, in the third section, we call for the adoption of complementary approaches

120   (e.g., extensive simulations, parametric biogeographical methods) in macroecological research

121   with the aim to evaluate the relative role of speciation, extinction and dispersal process driving

122   geographical biodiversity gradients.

123

124   ***LITERATURE REVIEW***

125   We conducted a literature search in Web of Science for studies that explicitly have

126   addressed questions on how speciation, extinction and dispersal have shaped geographical

127   species richness gradients. We selected those papers that used either phylogenetic metrics (e.g.,

128   mean root distance -MRD-, phylogenetic diversity -PD-, phylogenetic species variability -PSV-;

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

130   GeoSSE, BAMM; Goldberg *et al.*, 2011; Rabosky 2014). We compiled a list of 44 papers (Table A1),

131   but we are aware that this likely is not an exhaustive search. The majority of papers reviewed are

132   testing historical process shaping latitudinal diversity gradients (LDG) in various taxa.

133

134   ***TESTING EVOLUTIONARY HYPOTHESIS USING PHYLOGENETIC METRICS AND EXPLICIT***

135   ***DIVERSIFICATION APPROACHES***

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

137   related to the generation and maintenance of geographical diversity. Several studies used the

138   mean root distance -MRD- metric to evaluate whether regional assemblages are composed of

139   "basal" or "derivate" linages. First, this terminology should be avoided because it provides an

140   incorrect interpretation of the phylogenetic trees (Baum et al. 2005, Crisp and Cook 2005,

141   Omland et al. 2008). Although this metric does not incorporate information from branch lengths

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

143   species in a given region from the root of the phylogeny (Kerr and Currie 1999). MRD therefore

144   provides information about the number of cladogenetic events (splits) that have occurred through

145   the history of co-occurring lineages in each region (Pinto-Ledezma et al. 2017, Velasco et al.

146   2018). Under this view, MRD should be interpreted as a metric of total diversification (Rabosky

147   2009), where high MRD values indicating regional assemblages dominated by extensive

148   cladogenesis and low MRD values indicating assemblages with few cladogenetic events. A main

149   concern with this metric concern with the fact that it does not provide any information about

150   what macroevolutionary dynamics have taken place in a region. For example, it is very hard to

151   establish whether MRD allows to distinguish between diversity-dependent (Rabosky 2009,

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

153   processes dominating regional diversity. Although the distinction between these two dynamics,

154   and its relationship with the origin and maintenance of regional diversity, is an intense topic in the

155   macroevolutionary literature (Rabosky 2009, 2013, Wiens 2011, Cornell 2013, Harmon and

156   Harrison 2015, Rabosky and Hurlbert 2015). However, more empirical and theoretical work is

157   necessary to establish what scenario plays a significant role in regional species richness assembly

158   (Rabosky 2012, Etienne et al. 2012, Valente et al. 2015, Graham et al. 2018). It might worth to

159   establish whether local ecological process scaling up to regional scales or emergent effects (i.e.,

160   the existence of a strong equilibrium process) governed the build-up of regional diversity (Cornell

161   2013, Harmon and Harrison 2015, Rabosky and Hurlbert 2015, Marshall and Quental 2016).

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

163   is directly proportional to the colonization time of its constituent clades (Stephens and Wiens

164   2003b; Table 2). However, many phylogenetic metrics used to test this hypothesis, did not

165   incorporate any age information (Fritz and Rahbek 2012, Qian et al. 2015). Qian et al. (2015) did

166   some additional predictions for the time effect hypothesis regarding the phylogenetic structure of

167   regional assemblages. We suggest that these predictions are not easily deduced from the original

168   statement of the time-for-speciation effect hypothesis (Stephens & Wiens 2003). For instance,

169   Qian et al. (2015, p. 7) predicted that regions with low species richness (e.g., extra-tropical

170   regions) should be composed of more closely related species than regions with high species

171   richness (e.g., tropical regions). This assumes that regions with low species richness were

172   colonized recently and therefore these lineages had little time for speciation. However, it is also

173   plausible consider that high extinction occurred in these poor species richness regions by

174   marginal climatic niche conditions preventing adaptive diversification (Wellborn and Langerhans

175   2015). By contrast, regions with high species richness might also be assembled by multiple

176   dispersals from nearby regions becoming to be a macroevolutionary sink (Goldberg et al. 2005). In

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

178   dispersal through time. To evaluate which of these scenarios is more plausible it is necessary to

179   adopt an approach that explicitly infer the number of the dispersal and cladogenetic events across

180   areas (Roy and Goldberg 2007, Dupin et al. 2017).

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

182   geographical diversity gradient for many groups (Kennedy et al. 2014, Pinto-Ledezma et al. 2017).

183   This hypothesis states (Table 2) that differences in net diversification rates between areas are the

184   main driver of differences in regional species richness between areas. Davies and Buckley (2011)

185   used the phylogenetic diversity controlled by species richness (i.e., residual PD –rPD-) to

186   distinguish areas with different evolutionary processes. These authors predicted that areas where

187   rapid speciation and low immigration events from other areas occurred, are dominated by large

188   adaptive radiations (e.g., large islands; Losos and Schluter 2000). By contrast, areas with slow

189   speciation and colonized by multiple lineages through time should have high values of residual

190   PD.

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

192   latitudinal diversity gradient is due to that the majority of lineages originated in the tropics and

193   then migrated to extratropical regions. Under this hypothesis, tropics harbour higher net

194   diversification rates (higher speciation and lower extinction) than extratropical regions and

195   dispersal rates are higher from the tropics to extratropical regions than the reverse (Jablonski et

196   al. 2006; Table 1). For instance, Rolland et al. (2014) used the GeoSSE model to test this

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

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

199   temperate regions and dispersal rates were higher from the tropics to temperate regions than the

200   reverse. Also, Pinto-Ledezma et al. (2017) used the GeoSSE model to test an analogue hypothesis

201   to OTT, as form of Out of the Forest hypothesis (OTF), using Furnariides birds as a clade model.

202   Their favoured a model where open areas have higher speciation, extinction and dispersal rates

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

204   metrics or explicit diversification approaches (e.g., the GeoSSE model) to evaluate a set of

205   evolutionary-based hypotheses as a main driver of geographical diversity gradients. However, we

206   show here (see below) that these approaches fail to capture the evolutionary and biogeographic

207   processes at spatial scales.

208

209   ***Are phylogenetic metrics capturing well the diversification process across geography?***

210   A deep understanding of evolutionary processes affecting regional species assemblages is

211   coming from the integration of molecular phylogenies and fossil record (Quental and Marshall

212   2010, Marshall 2017). From this integration of neontological and paleontological perspectives, it is

213   clear that both approaches are necessary to test evolutionary-based hypothesis in

214   macroecological research. Several hypotheses were proposed to explain geographical diversity

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

216   compilation of the main hypotheses reported in the literature). Although the ideal approach is to

217   generate robust conclusions from multiple lines of evidence (e.g., fossil record, molecular

218   phylogenies, biogeographical inference) it is clear that this information is scarce for many

219   taxonomic groups. Many macroecological studies have adopted either phylogenetic metrics or

220   explicit diversification approaches (e.g., the GeoSSE model) to evaluate the relative contribution

221   of speciation, extinction and dispersal on the resulting geographical diversity gradients (Table S1).

222   Phylogenetic metrics can be easily visualized in a geographical context and several

223   inferences about ecological (e.g., dispersal) and evolutionary (e.g., speciation) process can be

224   done. As these metrics provide a *per-species level diversification* metric for each species in a

225   phylogeny, it is possible to associate these values with the corresponding species' geographical

226   range and obtain a mean value for cells or regions in a given geographical domain (Table 1; Figure

227   2). By contrast, explicit diversification approaches (e.g., GeoSSE; BAMM; fitting models) provide a

228   *per-lineage level diversification* metric for a given clade or a regional assemblage (Rabosky 2016a).

229   However, in some cases, it is possible to generate a *per-species level diversification* metric with

230   these approaches. For instance, Pérez-Escobar et al. (2017) used the function GetTipsRates in

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

232   These two approaches (phylogenetic metrics and lineage diversification) potentially can

233   provide complementary pictures about how macroevolutionary dynamics have taken place in the

234   geography. One the one hand, it is possible to estimate diversification rates for a given clade

235   using the number of species, its age and a birth-death models (Magallón and Sanderson 2001,

236   Nee 2006, Sánchez-Reyes et al. 2017). These model-fitting approaches allow to whether diversity-

237   or time-dependent diversification process has taken place in a regional assemblage (Etienne et al.

238   2012, Rabosky 2014, Valente et al. 2015). On the other hand, per-species diversification rate

239   metrics allow establishing the potential of each individual species to generate more species (Jetz

240   et al. 2012, Rabosky 2014, 2016a). However, these approaches imply at least a different process,

241   which left a different signature on the geography. Phylogenetic metrics captures a total

242   diversification process (Rabosky 2009), whereas lineage diversification approaches (e.g., BAMM)

243   can potentially provide information about an individual diversification process (Rabosky 2013). In

244   addition, still is not clear whether phylogenetic metrics can provide an accurate description of the

245   diversification dynamics across geography.

246   The first step to clarify how well these phylogenetic metrics behave is to establish a

247   comparison within and between different taxonomic groups. To evaluate how different

248   phylogenetic metrics vary across geography and their relationship with species richness, we used

249   two empirical data sets from our own empirical work (furnariid birds and anole lizards; (Pinto-

250   Ledezma et al. 2017, Velasco et al. 2018) and a data set compiled from several sources (hylid

251   frogs; (Wiens et al. 2006, Algar et al. 2009, Pyron 2014a). We mapped across geography five

252   phylogenetic metrics (Table 1, Figure 2). We selected these three data sets because previous work

253   analysed how evolutionary-based hypotheses affected the present-day species richness gradient

254   (Wiens et al. 2006, Algar et al. 2009, Pinto-Ledezma et al. 2017, Velasco et al. 2018).

255   Figure 2 shows the geographical pattern of species richness and the five phylogenetic metrics

256   for *Anolis* lizards, hylid frogs and Furnariides birds. For all clades, there is a higher species

257   concentration near to the Ecuador. Higher species concentration for hylids and Furnariides can be

258   found in the Amazon and the Atlantic forest and for *Anolis* lizards in Central America and the

259   Caribe (Figure 2A-C; see also Algar et al. 2009, Pinto-Ledezma et al. 2017, and Velasco et al. 2018,

260   for a detailed description of the geographical species richness pattern for these clades,

261   respectively). In terms of the geographical pattern of each phylogenetic metric (Figure 2D-R), in

262   most of the cases cells with higher metric values are related to cells that contain high species

263   richness and vice versa (Figure 2D-R; Figure A1). However, the degree and the direction of this

264   relationship changes according to the phylogenetic metric used. For example, MRD, a metric of

265   species derivedness, shows a negative correlation with species richness (Figure 2J-L; Figure A1).

266   Importantly, the spatial relationships between species richness and phylogenetic metrics found in

267   our analysis could simply be the result of aggregated species-level attributes within cells or

268   assemblages (Hawkins et al. 2017). Hence, any conclusion derived from these relationships needs

269   to be considered carefully. In addition, there are different levels of correlation between

270   phylogenetic metrics (Figure A1). For example, MDR - MA present a high but negative correlation,

271   and rPD - PSV and MRD - MDR present a mid-high positive correlation (Figure A1). Although

272   there are few studies comparing correlations between metrics (Vellend et al. 2010, Miller et al.

273   2017), to our knowledge, none previous study compares the similarity of these diversification

274   metrics (Table 1). However, some of these metrics sharing mathematical assumptions, which

275   increase the likelihood of correlation between them. For example, for ultrametric trees, metrics as

276   MDR could be approximated by considering the mean root distance (i.e. MRD metric) from the

277   tips to the root (Freckleton et al. 2008), so further studies exploring the mathematical relation

278   between metrics are needed.

279   In order to assess if the cells/assemblages on average do not represent a random sampling

280   from the species pool, we applied a simple permutation test to explore the non-randomness in

281   each of the phylogenetic metrics. We applied a null model where the presence-absence matrix

282   (i.e., PAM) was randomly shuffled 1000 times, but maintaining the frequency of species

283   occurrence and observed richness in the cells/assemblages (Gotelli 2000). This kind of null model

284   is standard in studies at the community/assemblage level that use phylogenetic information

285   (Cavender-Bares et al. 2004, 2006). Interestingly, none of the phylogenetic metrics deviates from

286   the null expectation for the three clades (Figure 3). Also, very few cells/assemblages present p-

287   values below the 0.05 threshold, thus indicating that the cells/assemblages present random

288   association among species (Figure 3). These results should be supported by repeating analyses

289   with more clades at different spatial extents, but again, we stress that any result obtained with

290   the use of phylogenetic metrics need to be interpreted carefully.

291

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

293　**biogeographic approaches**

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

295　most used in macroecological research. We explored whether the geographical patterns of these

296　phylogenetic metrics in three empirical examples coincide with the macroevolutionary dynamics

297　inferred using explicit modelling diversification approaches. In particular, we implemented the

298　GeoSSE model to estimate the three parameters (speciation, extinction, and dispersal) between

299　two areas in each taxonomic group (Table 3 and 4). In addition, we used the BAMM approach to

300　generate the per-species level diversification metric implemented in the software BAMM 2.5.0

301　(Rabosky 2014). In the following section, we discuss each metric and we compare them with the

302　explicit diversification approaches.

303

304　*Residual Phylogenetic Diversity (rPD)*

305　　　In the case of furnariid birds, we show that forest areas tend to exhibit slightly higher

306　values of rPD in contrast with open areas (Figure 4; see also Figure 2). According to Davies and

307　Buckley's logic, these areas exhibit slow diversification and frequent dispersal from open areas.

308　Pinto-Ledezma et al. (2017) using GeoSSE and BAMM approaches indicated that open areas

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

310　tropical areas tend to exhibit higher rPD values than extratropical regions (Figure 5). However, by

311　adopting an explicit diversification approach (GeoSSE and BAMM), we found that net

312　diversification rates were similar in both regions (Table 3). In the case of *Anolis* lizards, the rPD

313　values were higher in the continent than in the island areas (Figure 6). However, using GeoSSE

314   and BAMM, we found that both rates were similar (Table 3). In a recent paper, Poe et al. (in press)

315   also found that macroevolutionary rates are similar between insular and mainland clades. All

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

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

318   differences between regions when a stationary diversification process is occurring across

319   geography. A potential solution might be rethinking the way in which we visualize rPD across

320   geography in contrast with the original meaning by Davies & Buckley (2011; see also Forest et al.

321   2007).

322

323   *Mean root distance (MRD)*

324   As we discussed, *MRD* captures a total diversification value portraying the number of

325   cladogenetic events co-occurring in a given region. In the case of furnariid birds, we found that

326   MRD values tend to be higher in open than forest areas (Figure 4). Accordingly, this metric

327   suggests that more cladogenetic events were accumulated in open areas (i.e., more total

328   diversification; Rabosky 2009). Therefore, this metric, for this bird clade, is consistent with results

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

330   differences in MRD values between extratropics and tropics areas (Figure 5). However, tropical

331   areas have some cells with very high values. Again, MRD provide an accurate description of the

332   total diversification pattern in this clade across the latitudinal gradient. In *Anolis* lizards, we found

333   that MDR values tend to be lower in islands in comparison with mainland areas (Figure 6). In this

334   case, MRD did not provide an accurate description of the evolutionary processes occurring

335   between the mainland and insular anole assemblages. However, there is also a high probability

336   that the high MRD values in the mainland are a direct reflect of an idiosyncratic evolutionary

337   trajectory of each one of the two clades that radiated there (i.e., *Draconura* and *Dactyloa* clade;

338   see Poe et al. 2017, Velasco et al. 2018). These two clades seems to exhibit differential

339   diversification dynamics across geography (Velasco et al. 2018) but further research might be

340   necessary to evaluate these differences.

341

342   *Phylogenetic species variability (PSV)*

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

344   regional assemblage. In hylid frogs, we found that tropical assemblages tend to be composed of

345   more related species than extratropical assemblages (Figure 5). Hylid assemblages in

346   extratropical areas are composed of multiple lineages that dispersed from tropical areas and then

347   diversified there. We found higher dispersal rates from tropical to temperate regions than vice

348   versa (Table 3 and 4). The same tendency is present in the case of furnariid birds where open

349   areas exhibit higher PSV values than forest areas (Figure 4) and dispersal rates were higher from

350   open to forest areas than the reverse (Table 3). By contrast, we did not find any evidence for

351   differences in PSV values between island and mainland *Anolis* assemblages (Figure 6). In addition,

352   the dispersal rates were very low between these two regions (Table 3; Poe et al. 2017). All these

353   results confirm that the PSV metric can provide some insights about how dispersal process have

354   shaped regional assemblages. We find evidence that low PSV values (i.e., phylogenetically over-

355   dispersed faunas) are influenced by multiple dispersals along its evolutionary history.

356

357   *Mean diversification rate (MDR)*

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

359   the branch length along the path from the root of a tree to each individual species. In furnariid

360   birds, we noted that MDR was slightly higher in open versus forest areas and the same pattern is

361   present using the BAMM approach (Pinto-Ledezma et al. 2017; Figure 5; Table 3). For hylid frogs,

362   extratropical regions tend to exhibit higher values than tropical regions (Figure 5). MDR seems to

363   capture well the differences in macroevolutionary diversification for these taxa along the

364   latitudinal diversity gradient. A similar pattern is present when the BAMM approach is used (Table

365   3). We consider that both metrics (MDR vs per-species diversification rate from BAMM) leave the

366   same signature in the geography. In *Anolis*, we found that insular assemblages tend to exhibit

367   higher MDR values than continental assemblages (Figure 6), However, there is no difference in

368   the macroevolutionary dynamic between these two areas for the *Anolis* lizards clade (Poe et al. in

369   press, Velasco et al. 2018).

370

371   *Mean ages (MA).*

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

373   about whether a region maintains older lineages than others (e.g., a museum) or a combination of

374   old and recent lineages (e.g., OTT hypothesis, Table 1). Although this metric does not provide any

375   inference of the ancestral area of the clade, it is possible to implement an explicit biogeographic

376   approach to test this (see below). For example, in hylid frogs, we found that extratropical areas

377   are composed of older lineages than tropical regions (Figure 5). The biogeographic parametric

378   approach infers this same area as ancestral for the entire lineage (Figure A2). In furnariid birds,

379   mean ages metric revealed that older lineages have accumulated more in forest than open areas

380   (Figure 4). In accordance, the ancestral area inferred with a parametric biogeographic method

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

382   composed of older lineages than continents. However, the ancestral area for the entire anole

383   clade is the mainland, particularly South America (Poe et al. 2017). The mainland *Anolis* radiation

384   is composed of two clades, one clade that originated in South America (the *Dactyloa* clade; Poe et

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

386   that originated in the Caribbean islands and then colonized back the mainland in Middle America

387   and then dispersed to South America. Therefore, the biogeographical history of the *Anolis*

388   radiation is complex and involves multiple dispersals between islands and mainland areas (Poe et

389   al. 2017; Figure A4). In general, mean ages does not provide enough information about the

390   biogeographic origin and maintenance of a clade. This happens because multiple dispersals and *in*

391   *situ* cladogenesis might erase any simplistic pattern elucidated for this metric, as found in the

392   case of the *Anolis* lizards.

393

394   ***HOW DISPERSAL AND EXTINCTION AFFECT INFERENCES OF GEOGRAPHICAL***

395   ***DIVERSIFICATION GRADIENTS?***

396   Dispersal is another key macroevolutionary process that ultimately determines the number of a

397   species in a region (Roy and Goldberg 2007, Eiserhardt et al. 2013, Rolland et al. 2014, Chazot et

398   al. 2016). However, few studies evaluated explicitly how the direction of dispersals between

399   region contributes to the generation of regional differences between areas (Chown and Gaston

400   2000, Goldberg et al. 2005, 2011, Jablonski et al. 2006). Roy and Goldberg (2007) showed with

401   simulations that dispersal asymmetry between areas had a strong impact in the regional species

402   richness and the average age of these lineages. Accordingly, phylogenetic metrics can be

403   sensitive to dispersal between areas because it is impossible to distinguish which lineages

404   originated by *in situ* speciation or simply due to dispersal from nearby areas. Goldberg et al. (2011)

405   developed the GeoSSE model to evaluate how range evolution affected diversification rates in a

406   phylogenetic comparative approach. The GeoSSE model only considers three states (A: endemic

407   species to a region; B: endemic species to another region; and AB for widespread species) and

408   makes a series of assumptions that can be problematic. The first assumption of the GeoSSE

409   model is that a time-dependent process dominates the diversification dynamic in each region

410   (Stephens and Wiens 2003, Wiens 2011). This assumption conflicts with a diversity-dependent

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

412   Harrison 2015, Rabosky and Hurlbert 2015). The second problematic assumption has to do with

413   the fact that the GeoSSE model consider dispersal rates as stable through time and lineages. In

414   other words, the dispersal ability and therefore the frequency of transitions between areas are

415   constant across the evolutionary history of a clade. There are many empirical evidence showing

416   that dispersal rates vary across time and space among lineages (McPeek and Holt 1992,

417   Sanmartín et al. 2008, Robledo-Arnuncio et al. 2014).

418   Regardless of these major assumptions, the GeoSSE model has been adopted to evaluate

419   relative contributions of speciation, extinction and dispersal to the generation of species richness

420   gradients (e.g., Rolland et al. 2014, Pyron 2014b, Staggemeier et al. 2015, Looney et al. 2016,

421   Morinière et al. 2016, Pulido-Santacruz and Weir 2016, Alves et al. 2017, Hutter et al. 2017, Pinto-

422   Ledezma et al. 2017). In a recent study, Rabosky and Goldberg (2015) found that state-dependent

423   diversification models tend to inflate excessively the false discovery rates (i.e., type I error rates).

424   In particular, Rabosky and Goldberg (2015) found that these models tend to find false associations

425   between trait shifts and shifts in macroevolutionary dynamics. Although the Rabosky and

426   Goldberg's study was not based on the GeoSSE model, it is clear that transitions between areas

427   (i.e., dispersal events) can be falsely associated with shifts in speciation and extinction rates

428   across the phylogeny. Alves et al. (2017) also found that geographical uncertainties in the

429   assignment of species to a given area affect the parameter estimates (i.e., speciation, extinction

430   and dispersal rates) in the GeoSSE model. Same authors also evaluated how incorrect

431   assignments of bat species to tropical or extra-tropical regions can generate erroneous

432   conclusions about the relative role of speciation, extinction and dispersal on a latitudinal diversity

433   gradient. From these studies, it is clear that dispersal is a major issue that needs to be evaluated

434   explicitly in macroecological studies.

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

436   effect of speciation, extinction and dispersal on the latitudinal bird diversity gradient. They found

437   that extinction was prevalent across all bird clades and therefore they suggest this as a main

438   driver of the geographical bird diversity gradient. Pyron (2014c), also using the GeoSSE model,

439   found that temperate diversity in reptiles is due to higher extinction in these areas. We consider

440   that extinction inferences from the GeoSSE model should be treated with caution. For the few

441   clades where fossil record is abundant (e.g., marine bivalves; Jablonski et al. 2006), studies point

442   out to conclude that extinction differences between regions should be treated with caution due to

443   the potential sampling bias (Jablonski et al. 2006, 2017). In addition, studies based on extensive

444   simulations found that extinction inferences based only in molecular phylogenies are not reliable

445   (Rabosky 2010a, 2016b, Quental and Marshall 2010), although extinction rates can be estimated

446   relatively well using medium to large phylogenies (Beaulieu & O'Meara 2015).

447   In a recent review, Sanmartín and Meseguer (2016) proposed that it is possible to detect the

448   extinction signature in molecular phylogenies using extensive simulations and lineage-through-

449   time –LTT- plots (see also Antonelli and Sanmartín 2011). These authors also found that many

450   birth-death models leave a similar phylogenetic imprint, which make indistinguishable some

451   scenarios. In addition, extinction events can affect substantially the ancestral range estimates,

452   and therefore dispersal and extinction parameters in several parametric biogeographic methods

453   (e.g., Dispersal-Vicariance –DIVA- and Dispersal-Extinction-Cladogenesis –DEC- models;

454   Ronquist 1997, Ree et al. 2005). Sanmartín and Meseguer (2016) finally proposed that the

455   adoption of a hierarchical Bayesian approach using continuous-time Markov Chain models will

456   allow a better estimation of extinction both in geography and in the phylogeny (Sanmartín et al.

457   2008, Sanmartin et al. 2010).

458   Recently, Rabosky and Goldberg (2017) developed a semi-parametric method (FiSSE) to

459   correct the statistical problems found in BiSSE models by themselves in a previous paper

460   (Rabosky and Goldberg 2015). However, the FiSSE method does not allow the evaluation of the

461   contribution of dispersal on regional species richness. In any case, the best suitable framework to

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

463   model (or parametric biogeographic models; e.g., Matzke 2014; see below), although it requires

464   the simulation of a series of null scenarios to evaluate the statistical power in each case (see Alves

465   et al. 2017, Pinto-Ledezma et al. 2017 for a few examples). For instance, Pinto-Ledezma et al.

466   (2017) developed a parametric bootstrapping approach simulating traits to evaluate whether

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

468   characters along a set of empirical phylogenies and using this new information repeated the same

469   procedure with empirical data (see Appendix S1 in Pinto-Ledezma et al. 2017 for details of the

470   bootstrapping approach). This bootstrapping procedure assumes no direct effect of the

471   geographic character states on the parameter estimations (Feldman et al. 2016, Pinto-Ledezma

472   et al. 2017).

473   Finally, it should be clear that more research would be necessary to establish how

474   extinction affect estimation parameters in state-dependent diversification approaches (e.g., the

475   GeoSSE model). For instance, the inclusion-exclusion of extinct species in simulated phylogenies

476   using birth-death models could substantially affect the geographical inferences of speciation,

477   extinction and dispersal parameters in the GeoSEE model. This kind of approach might provide

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

479   using the GeoSSE model or any other modeling approach.

480

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

482   The use of parametric biogeographic approaches is an optimal solution to estimate

483   dispersals across time and space (Matzke 2014, Dupin et al. 2017). These methods are promising

484   in identifying the relative roles of cladogenetic and anagenetic processes shaping regional species

485   richness. Recently, Dupin et al. (2017) developed a biogeographical stochastic mapping to infer

486   the number of dispersals, and other biogeographical events, in the evolutionary history of

487   Solanaceae plants across the world. This approach allows the inference from multiple process

488   including sympatric speciation, allopatric speciation, founder-event speciation, range expansion

489   (i.e., dispersal without speciation) and local extinction (i.e., range contractions) based on a time-

490   calibrated phylogenetic tree and the occurrence of species in geographical regions (see also

491   Matzke 2014 for more detailed description of the method). These explicit biogeographical

492   approaches are promising in macroecological studies since they allow to test simultaneously a set

493   of evolutionary process during the diversification of a clade in a region (Velasco 2018). In addition,

494   with these new approaches it is possible to differentiate effectively between macroevolutionary

495   sources and sink areas (Goldberg et al. 2005, Castroviejo-Fisher et al. 2014, Poe et al. 2017). For

496   instance, Poe et al. (2017) used a parametric biogeographical approach to estimate the number of

497   events among regions and distinguish those areas where many cladogenetic events occurred (i.e.,

498   *in situ* speciation) and areas where almost all its diversity was build-up from extensive

499   colonization of other regions.

500   The biogeographical stochastic mapping (BSM) method developed by Dupin et al. (2017)

501   is promising to estimate more accurately the number of dispersal events between regions based

502   on a better estimation of the ancestral area for a clade. We evaluated how dispersal rates

503   between regions can affect inferences drawn only from phylogenetic metrics in our three data

504   sets. We implemented GeoSSE and BSM approaches for each data set (Table 3 and 4). For the

505   case of hylid frogs, we counted the inferred number of dispersal events between tropical and

506   extra-tropical regions in the Americas (Table 3; see also (Wiens et al. 2006, Algar et al. 2009). For

507   furnariid birds, we counted the number of dispersal events between open and forest areas (Table

508   3; see also Pinto-Ledezma et al. 2017). Finally, for anole lizards, we counted the number of

509   dispersal events between insular and mainland areas (Table 3; see also Algar and Losos 2011, Poe

510   et al. 2017, Velasco et al. 2018).

511   Using biogeographical stochastic mapping –BSM-, we inferred the number of dispersal

512   events from one region to another for each one of the three taxonomic groups examined (Table

513   3). The BSM approach allows us to disentangle which dispersals were only range expansions and

514   which dispersals generated a speciation event (i.e., a founder-event speciation; (Barton and

515   Charlesworth 1984, Templeton 2008). For furnariid birds, we found that range expansions were

516   three times higher from forest areas to open areas than the reverse and founder events were

517   twice higher from forest to open areas than the opposite (Table 3). This result suggests that

518   differences in species richness between forest and open areas are due by recurrent dispersal

519   events along the furnariid diversification history (Pinto-Ledezma et al. 2017). Pinto-Ledezma et al.

520   (2017) found a similar result using the GeoSSE approach, but they conducted a parametric

521   simulation approach to evaluate whether there was a direct effect of the geographic location on

522   the parameter estimates. Their results show that the GeoSSE approach, in this case, had limited

523   power to detect a signature of geographic region on speciation, extinction and dispersal rates.

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

525   findings with improved statistical power. In the case of hylid frogs and the transitions between

526   tropical and extra-tropical areas, we found that the BSM approach inferred more dispersal events

527   from tropical to extra-tropical regions (Table 3 and 4). However, the number of founder events

528   was relatively low in comparison with range expansions (Table 3). These results suggest that few

529   dispersal events have occurred across the diversification of hylid frogs and corroborate that the

530   species richness in each region largely originated by *in situ* speciation modulated by climatic

531   factors (Wiens et al. 2006, Algar et al. 2009). Finally, for *Anolis* lizards, we found that dispersal

532   events between insular and mainland regions were relatively low (Table 3 and 4). We did not find

533   evidence of any expansion range events from mainland to island or vice versa. This also

534   corroborates previous findings that evolutionary radiation of anole in insular and mainland

535   settings is due to extensive *in situ* diversification (Poe et al. in press, 2017, Algar and Losos 2011).

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

537   when we are interested in testing the role of anagenetic and cladogenetic events on the resulting

538   geographical species richness gradients. Although parametric biogeographic approaches are still

539   in their infancy (Sanmartín 2012, Matzke 2014, Dupin et al. 2017), these methods allow us to

540   evaluate macroevolutionary dynamics (i.e., speciation and extinction) in an explicit geographical

541   context. These methods are statistical powerful and make use of a series of explicit geographic

542   range evolution models (Velasco 2018).

543

TOWARD AN INTEGRATION OF BIOGEOGRAPHICAL AND SPECIES DIVERSIFICATION APPROACHES IN MACROECOLOGICAL STUDIES.

546   Although different parametric biogeographic methods have been developing at least for

547   the last 20 years (Ronquist 1997, Ree et al. 2005, Landis et al. 2013, Matzke 2014, Dupin et al.

548   2017), the adoption of these methods to test evolutionary-based hypotheses underlying

549   geographical diversity gradient has been rare. For instance, few studies examined here tested

550   the effect of dispersal events in the generation of regional species richness assemblages. It should

551   clear that the current paradigm in biogeography makes a call for an evaluation of the relative

552   frequency of cladogenetic and anagenetic process during the biogeographical history of lineages.

553   The adoption of parametric approaches in future macroecological studies will contribute to an

554   improvement of the estimation of speciation, extinction and dispersal processes as drivers of the

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

556   macroevolutionary dynamics govern regional assemblages. Phylogenetic approaches based on

557   fitting diversification models help to test whether regional species richness is due to diversity

558   dependence (i.e., ecological limits), time dependence, or environmental factors (Rabosky and

559   Lovette 2008, Etienne et al. 2012, Etienne and Haegeman 2012, Condamine et al. 2013). We also

560   stress that the adoption of many approaches providing multiple lines of evidence will help to

561   disentangle the evolutionary and ecological causes of biodiversity gradients. Some recent studies

562   have pointed toward this strategy and have begun to provide evidence from many lines to

563   understand how evolutionary processes underlying species richness gradients works (Hutter et al.

564   2017, Pinto-Ledezma et al. 2017).

565

566   *Conclusions and recommendations*

567   The resulting geographical pattern of several phylogenetic metrics did not provide any

568   robust evidence of a spatially explicit diversification dynamic. As we have shown, these resulting

569   geographical patterns did not differ from that generated by a simple null model. It is hard to

570   untangle causal mechanisms (i.e., speciation, extinction, and dispersal) from only the

571   geographical signature that these metrics attempt to capture. We recommend that phylogenetic

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

573   residual PD; MDR), phylogenetic structure (e.g., PSV), or mean ages of co-distributed species

574   (e.g., MA) (Table 1). We suggest that conclusions about the role of evolutionary processes in the

575   generation and maintenance of species richness gradients based only in these phylogenetic

576   metrics should be avoided and additional approaches always should be used.

577   Some explicit diversification approaches (e.g., model fitting approaches; (Etienne et al.

578   2012, Rabosky 2014, Valente et al. 2015) are useful to establish the macroevolutionary dynamics

579   operating at regional scales. Although some approaches (e.g, the GeoSSE model) allow us to

580   evaluate the relative role of the ultimate process that modify the regional species diversity, its

581   statistical power (e.g., high Type I errors) has been challenged by simulation and empirical

582   studies. Furthermore, the extinction and dispersal estimates inferred by the GeoSSE model tend

583   to be unbiased. Parametric biogeographic approaches are becoming a standard tool to evaluate

584   how evolutionary processes can explain the geographical distribution of extant taxa. These

585   approaches are promising and should be extensively used because allow us to estimate the

586   relative frequency of cladogenetic and anagenetic process shaping the regional species richness.

587   It is necessary that macroecological studies use a combination of explicit diversification

588   approaches and parameter biogeographic methods with the aim to clarify how evolutionary

589   process have shaped regional species richness assemblages. As Jablonski et al. (2017) have

590   outlined, one of the main obstacles to generate an appropriate understanding of the causal

591   mechanisms underlying geographical diversity gradients has been that many studies have tested

592   a single hypothesis, either evolutionary or ecological, as an explanatory factor. We suggest that

593   ecological and evolutionary hypotheses should be tested simultaneously to explain the relative

594   contribution of each process to the regional diversity. As shown by our empirical comparison of

595   phylogenetic metrics, explicit diversification models, and historical biogeographic methods have

596   showed, it is necessary to obtain evidence of different approaches to guarantee sound

597   conclusions about the evolutionary causes of these biodiversity gradients.

598

599   **Acknowledgments**

606

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860

861 Table 1: Phylogenetic metrics and explicit diversification approaches used in macroecological
862 studies to address evolutionary questions related with the 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

863 Table 2. Description of some evolutionary hypothesis tested in macroecological studies as causal mechanisms of 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).

864   Table 3. Parameter estimates from the GeoSSE model for three taxonomic groups (Furnariides birds,
865   hylid frogs, and *Anolis* lizards) across two regions. Areas for each taxonomic group as follows:
866   Furnariides birds: A: Forest; B: Open areas; Hylid frogs: A: Extra tropics; B: Tropics; *Anolis* lizards: A:
867   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	-

868

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

873

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

874

875

876   FIGURE LEGENDS

877   Figure 1. Diagram illustrating how differences in speciation, extinction, and dispersal rates between
878   regions can generate a geographical species richness gradient. The phylogenetic trees below illustrate
879   how the differences in speciation and extinction rates between two regional assemblages can shape a
880   gradient of species richness (degraded blue colour).

881

882   Figure 2. Geographical patterns of some phylogenetic metrics used in macroecological studies to
883   explore evolutionary process underlying geographical diversity gradients (see also Table 1 for a detailed
884   explanation). Left column *Anolis* lizards; Middle column: Hylid frogs; Right column: Furnariides birds.
885   (A-C) observed richness patterns; (D-F) rPD: residual phylogenetic diversity (i.e., after controlling for
886   species richness); (G-I) PSV: phylogenetic species variability; (J-L) MRD: mean root distance; (M-O)
887   MDR: mean diversification rate; (P-R) Mean ages: average ages of species.

888

889   Figure 3. P-values distribution for each phylogenetic metric obtained through the null model (see main
890   text for details). The vertical red lines represent the empirical 0.05 cut-off. Note that for all cases very
891   few cells are below the 0.05 cut-off. (A-C) rPD: residual phylogenetic diversity (i.e., after controlling for
892   species richness); (D-F) PSV: phylogenetic species variability; (G-I) MRD: mean root distance; (J-L)
893   MDR: mean diversification rate; (M-O) Mean ages: average ages of species.

894

895   Figure 4. Variation of phylogenetic metric values for Furnariides birds in forest and open areas. rPD:
896   residual phylogenetic diversity (i.e., after controlling for species richness); PSV: phylogenetic species
897   variability; MRD: mean root distance; MDR: mean diversification rate; Mean ages: average ages of
898   species.

899

900   Figure 5. Variation of phylogenetic metric values for Hylid frogs in tropics and extra-tropics regions.
901   rPD: residual phylogenetic diversity (i.e., after controlling for species richness); PSV: phylogenetic
902   species variability; MRD: mean root distance; MDR: mean diversification rate; Mean ages: average ages
903   of species.

904

905   Figure 6. Variation of phylogenetic metric values for *Anolis* lizards in continental and insular areas. rPD:
906   residual phylogenetic diversity (i.e., after controlling for species richness); PSV: phylogenetic species
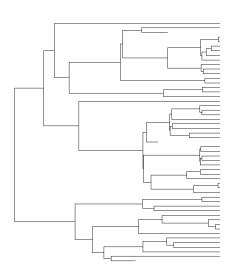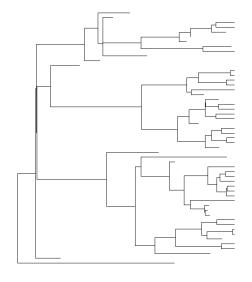907   variability; MRD: mean root distance; MDR: mean diversification rate; Mean ages: average ages of
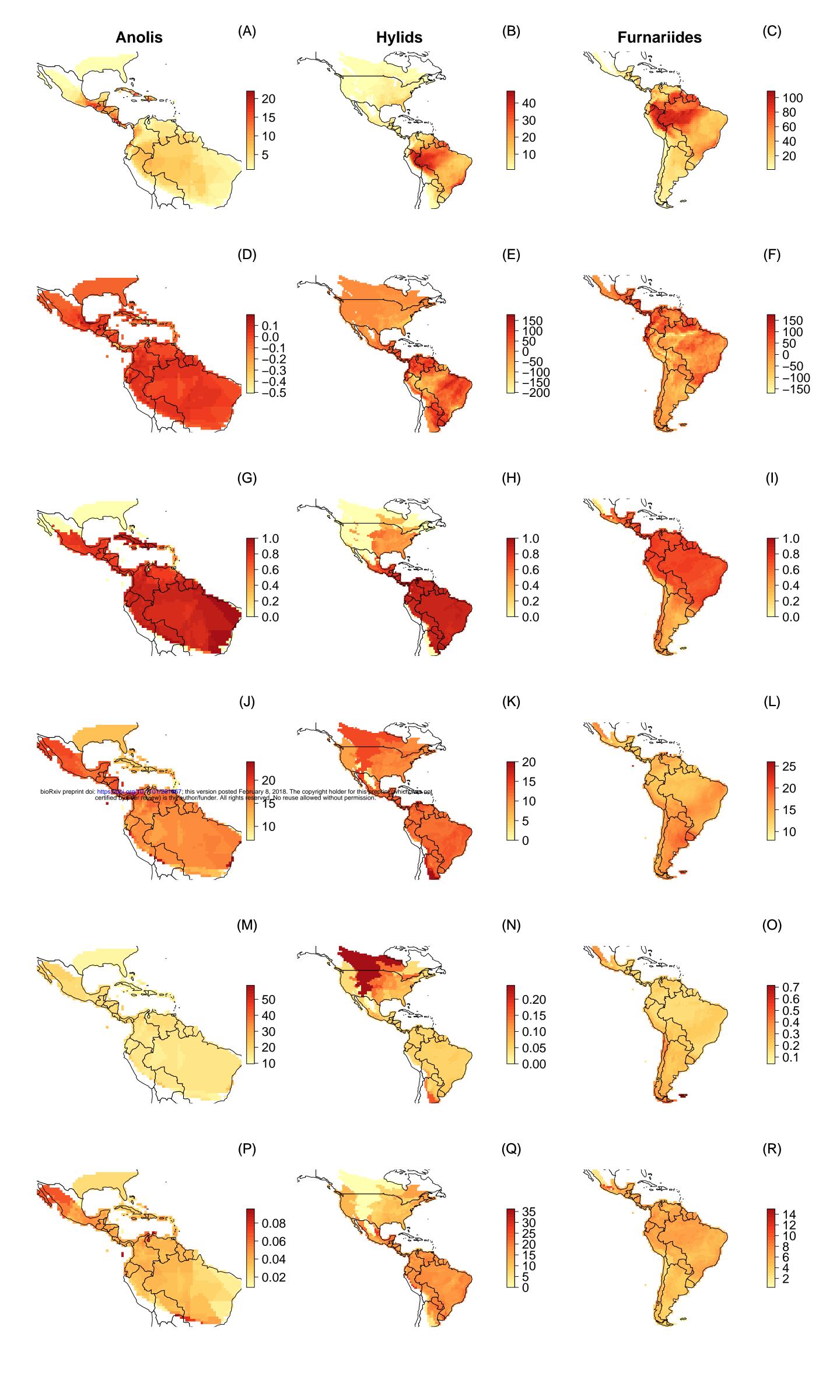908   species.

909

DIVERSITY GRADIENTS

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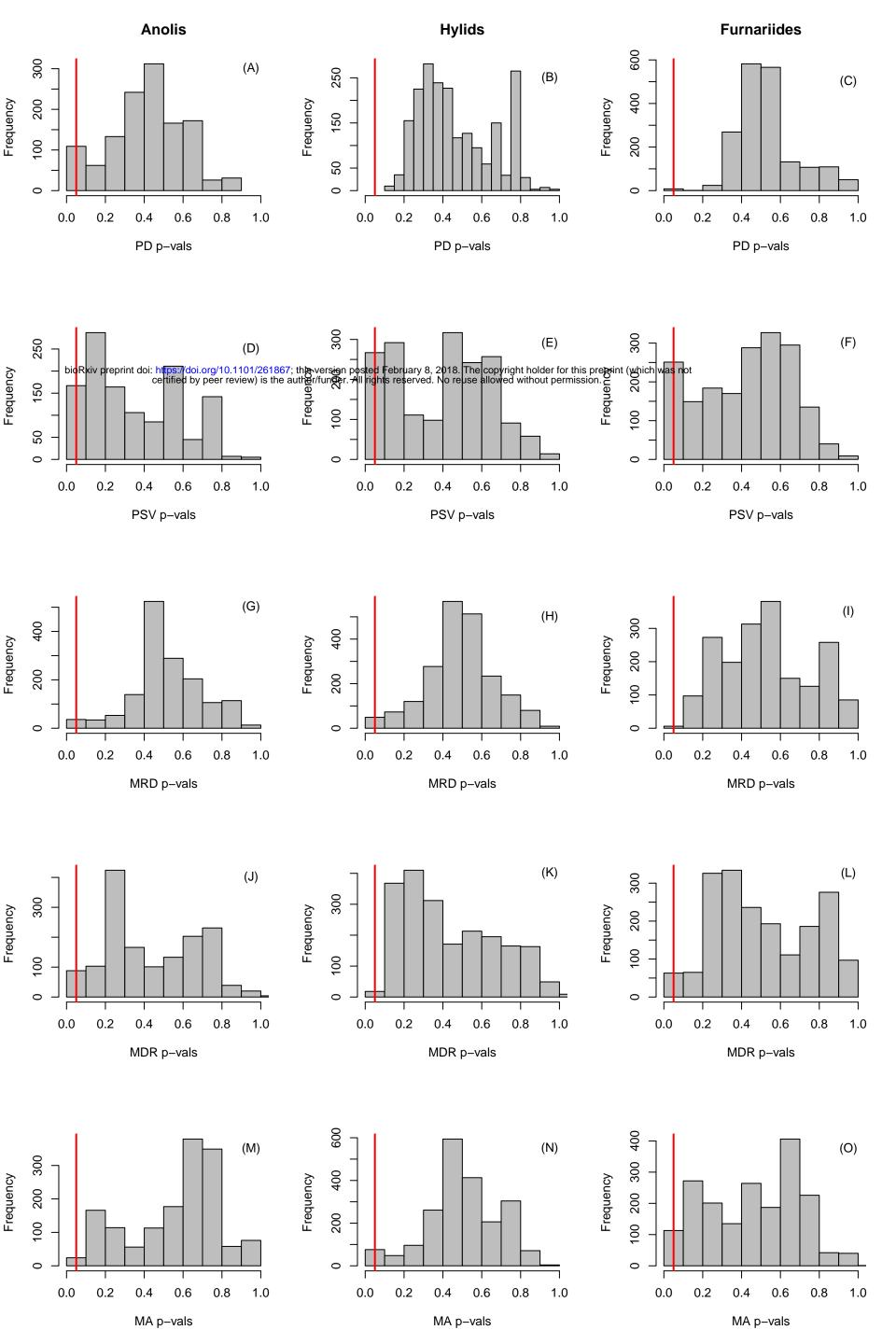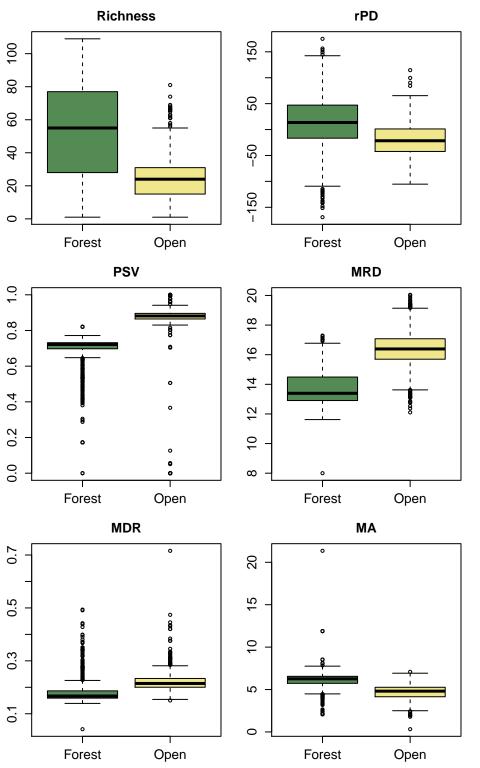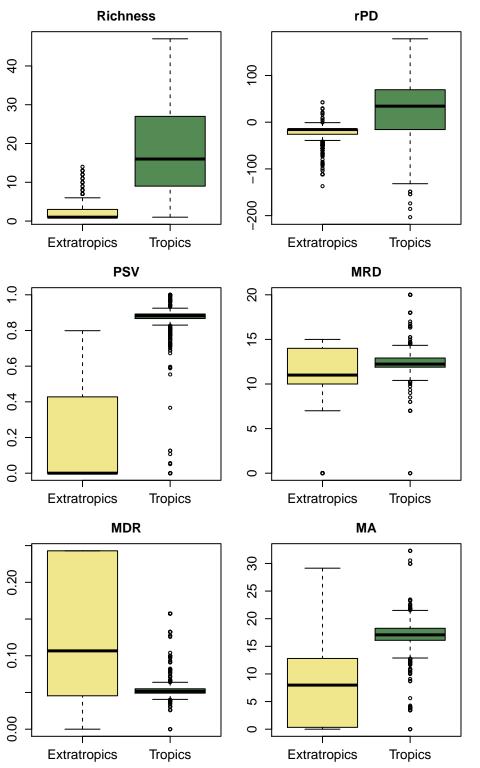
Lower speciation
Higher extinction
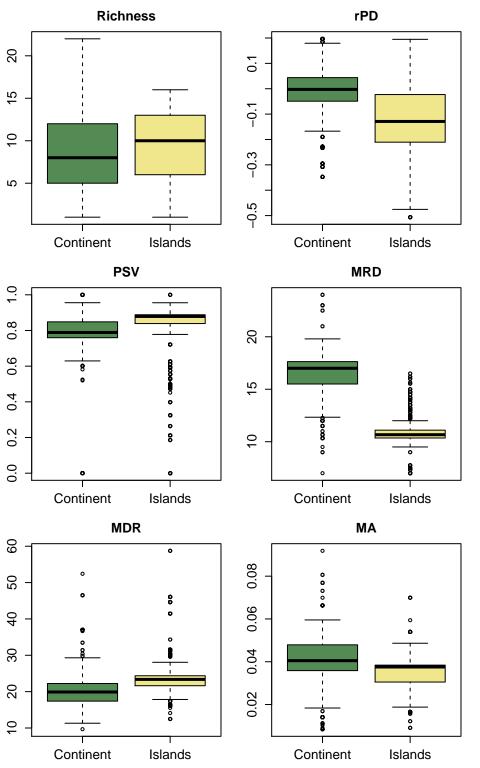Dispersal (in)

Speciation = 0.5; Extinction = 0.05

Speciation = 0.3; Extinction = 0.15

Anolis (A)

Hylids (B)

Furnariides (C)

(D) (E) (F)

(G) (H) (I)

(J) (K) (L)

(M) (N) (O)

(P) (Q) (R)

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

Hyla_walkeri
Smilisca_puma
Smilisca_phaeota
Smilisca_cyanosticta
Smilisca_fodiens
Smilisca_sila
Smilisca_sordida
Smilisca_baudinii
Triprion_petasatus
Anotheca_spinosa
Isthmohyla_pseudopum
Isthmohyla_zeteki
Isthmohyla_rivularis
Isthmohyla_tica
Tlalocohyla_loquax
Tlalocohyla_godmani
Tlalocohyla_picta
Tlalocohyla_smithii
Charadrahyla_taeniopus
Charadrahyla_nephila
Megastomatohyla_mixe
Ptychohyla_leonhardscl
Ptychohyla_zophodes
Ptychohyla_euthysanota
Ptychohyla_hypomykter
Ptychohyla_dendrophas
Ptychohyla_spinipollex
Duellmanohyla_rufioculi
Duellmanohyla_soralia
Bromeliohyla_bromeliac
Ecnomiohyla_minera
Ecnomiohyla_miliaria
Ecnomiohyla_micrympa
Plectrohyla_penthter
Plectrohyla_calthula
Plectrohyla_bistincta
Plectrohyla_ameibothal
Plectrohyla_arborescan
Plectrohyla_cyclada
Plectrohyla_siopela
Plectrohyla_matudai
Plectrohyla_guatemaler
Plectrohyla_chrysopleu
Plectrohyla_glandulosa
Exerodonta_smaragdina
Exerodonta_xera
Exerodonta_melanomm
Exerodonta_sumichrast
Exerodonta_perkinsi
Exerodonta_abdivita
Pseudacris_triseriata
Pseudacris_feriarum
Pseudacris_maculata
Pseudacris_clarkii
Pseudacris_fouquettei
Pseudacris_kalmi
Pseudacris_nigrita
Pseudacris_brimleyi
Pseudacris_brachyphor
Pseudacris_ocularis
Pseudacris_crucifer
Pseudacris_streckeri
Pseudacris_ornata
Pseudacris_cadaverina
Pseudacris_regilla
Acris_crepitans
Acris_gryllus
Osteocephalus_deriden
Osteocephalus_fuscifac
Osteocephalus_leprieur
Osteocephalus_taurinus
Osteocephalus_oophag
Osteocephalus_yasuni
Osteocephalus_buckley
Osteocephalus_vertcip
Osteocephalus_cabrera
Osteocephalus_mutabo
Osteocephalus_albopunt
Tepuihyla_rodriguezi
Tepuihyla_talbergae
Tepuihyla_edelcae
Phyllodytes_luteolus
Trachycephalus_hadroc
Trachycephalus_resinific
Trachycephalus_nigrom
Trachycephalus_imitatri
Trachycephalus_coriace
Trachycephalus_mesop
Trachycephalus_jordani
Argenteohyla_siemersi
Nyctimantis_rugiceps
Corythomantis_greenin
Aparasphenodon_brunc
Itapotihyla_langsdorffii
Dendropsophus_minusc
Dendropsophus_juliani
Dendropsophus_sanbor
Dendropsophus_rubicu
Dendropsophus_branne
Dendropsophus_tritaeni
Dendropsophus_walford
Dendropsophus_nanus
Dendropsophus_reichle
Dendropsophus_riveroi
Dendropsophus_bertha
Dendropsophus_gauch
Dendropsophus_bipunc
Dendropsophus_sartori
Dendropsophus_robertt
Dendropsophus_microc
Dendropsophus_rhodop
Dendropsophus_leali
Dendropsophus_minutu
Dendropsophus_leucop
Dendropsophus_triangu
Dendropsophus_saraya
Dendropsophus_bifurcu
Dendropsophus_ebracc
Dendropsophus_elegan
Dendropsophus_miyata
Dendropsophus_aperor
Dendropsophus_ancepc
Dendropsophus_schuba
Dendropsophus_pelidna
Dendropsophus_labialis
Dendropsophus_carnife
Dendropsophus_giesler
Dendropsophus_parvice
Dendropsophus_brevifr
Dendropsophus_koechl
Dendropsophus_melan
Dendropsophus_melano
Dendropsophus_senicu
Dendropsophus_allenor
Xenohyla_truncata
Pseudis_tocantins
Pseudis_fusca
Pseudis_paradoxa
Pseudis_bolbodactyla
Pseudis_cardosoi
Pseudis_minuta
Scarthyla_goinorum
Scinax_ruber
Scinax_x–signatus
Scinax_nasicus
Scinax_chiquitanus
Scinax_fuscovarius
Scinax_cuentommus
Scinax_boesemani
Scinax_stauffeli
Scinax_parkeri
Scinax_squalirostris
Scinax_cruspedospilus
Scinax_proboscideus
Scinax_garbei
Scinax_jolyi
Scinax_rostratus
Scinax_boulengeri
Scinax_sugillatus
Scinax_nebulosus
Scinax_acuminatus
Scinax_uruguayus
Scinax_berthae
Scinax_catharinae
Scinax_peixotoi
Scinax_faivovichi
Scinax_perpusillus
Sphaenorhynchus_doris
Sphaenorhynchus_lacte
Sphaenorhynchus_orop
Hypsiboas_cordobae
Hypsiboas_pulchellus
Hypsiboas_prasinus
Hypsiboas_caingua
Hypsiboas_marginatus
Hypsiboas_bischoffi
Hypsiboas_guentheri
Hypsiboas_balzani
Hypsiboas_marianitae
Hypsiboas_riojanus
Hypsiboas_latistriatus
Hypsiboas_polytaenius
Hypsiboas_leptolineatus
Hypsiboas_semiguttatus
Hypsiboas_joaquini
Hypsiboas_melanopleur
Hypsiboas_ericae
Hypsiboas_lundii
Hypsiboas_pardalis
Hypsiboas_rosenbergi
Hypsiboas_crepitans
Hypsiboas_punctatus
Hypsiboas_albomargina
Hypsiboas_faber
Hypsiboas_rufitelus
Hypsiboas_multifasciat
Hypsiboas_albopunctat
Hypsiboas_lanciformis
Hypsiboas_calcaratus
Hypsiboas_fasciatus
Hypsiboas_dentei
Hypsiboas_picturatus
Hypsiboas_raniceps
Hypsiboas_lemai
Hypsiboas_ornatissimus
Hypsiboas_microderma
Hypsiboas_nympha
Hypsiboas_roraima
Hypsiboas_semilineatus
Hypsiboas_geographicu
Hypsiboas_boans
Hypsiboas_sibleszi
Hypsiboas_cinerascens
Aplastodiscus_leucopyg
Aplastodiscus_cavicola
Aplastodiscus_callipygi
Aplastodiscus_albosign
Aplastodiscus_cochrana
Aplastodiscus_perviridi
Aplastodiscus_weygoldt
Aplastodiscus_arildae
Aplastodiscus_eugenioi
Aplastodiscus_albofren
Bokermannohyla_hylax
Bokermannohyla_circur
Bokermannohyla_astart
Bokermannohyla_martin
Hyloscirtus_pacha
Hyloscirtus_staufferor
Hyloscirtus_psarolaimu
Hyloscirtus_ptychodacty
Hyloscirtus_pantostictu
Hyloscirtus_lindae
Hyloscirtus_tapichalaca
Hyloscirtus_armatus
Hyloscirtus_simmonsi
Hyloscirtus_alytolylax
Hyloscirtus_colymba
Hyloscirtus_phylogmath
Hyloscirtus_lascinius
Hyloscirtus_palmeri
Myersiohyla_inparquesi
Myersiohyla_kanaima

70   60   50   40   30   20   10   0
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