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Back to the Future: Conserving Functional and Phylogenetic Diversity in the Amphibian-Climate Refuges

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21

22 **Abstract** Climate refuges have been used by several species over historical climate change. Ectothermic species

23 often display good models for climate change studies because they are highly sensitive to temperature. Analysis

24 of species loss with ecosystem and evolutionary values helps to understand environmental processes and climate

25 consequences. Here, we associate the functional and phylogenetic diversity of amphibians in the Atlantic Forest

26 hotspot, using multiple models for the present and future conditions. Through a novel approach, we predict

27 species' threat status by 2080, following the IUCN's criterion B1. Our results estimate a drastic reduction in

28 species richness, ecosystem functioning and evolutionary history at low latitudes and altitudes. We show that

29 species will tend to disperse to the areas with milder temperatures (i.e., high latitudes/altitudes). Some of these

30 areas are the same climate refuges that have been suggested for the Late Pleistocene. We highlight that 60% of

31 amphibians can become threatened under future conditions. This work advances the knowledge on climate

32 refuges for amphibian ecology and evolution, supporting complementary tools for conservation strategies.

33

34 **Keywords:** Anthropocene, Climate change, Atlantic Forest, Anura, Gymnophiona

35

44

Introduction

Over millions of years, the Earth has undergone several climatic transformations that seem to appear to be cyclical (Raup and Sepkoski 1982). During these changes, most species had to take refuge in areas with milder environments and better resource availability (Haffer 1969; Mayr and O'Hara 1986; Bush 1994; Bush and Oliveira 2006; Carnaval et al. 2009; Bush et al. 2011). However, these cyclical events lead to five massive extinctions (Raup and Sepkoski 1982; Jablouski 1994; Bambach 2006; Barnorsky et al. 2011). The current Anthropocene Age is directing toward the sixth mass extinction of the biodiversity (Wake and Vredenburg 2008; Barnosky et al. 2011; Dirzo et al. 2014).

Anticipating climate consequences on biogeographic patterns are key to address changes on functional and phylogenetic diversity relations to organism-mediated ecosystem goods and services (Montoya and Raffaelli 2010; Cardinale et al. 2011; Prather et al. 2012), as well as evolutionary processes (Thuiller et al. 2011; Pio et al. 2014). In this context, studies available about climate change should be evaluated integrating functional and phylogenetic diversity (Sobral and Ciacianruso 2012; Campos et al. 2017). Functional diversity is the value and variation of species and their characteristics that influence the functioning of communities (Tilman 2001) and the phylogenetic diversity is a measure of the diversity of a community that incorporates the phylogenetic relationships of species (Magurran 2004). Thus, it is possible to associate ecological and evolutionary approaches into spatial decision-making for conservation. The assumption that closely phylogenetic species have the same ecosystem roles is still an uncertain issue (Webb et al. 2002). Phylogenetic structure of communities depends on how the ecological characteristics evolved (Sobral and Cianciaruso 2012). Therefore, ecosystem functioning and stability are often correlated with changes in evolutionary process, producing several implications for ecological and human well-being on short-time scales (Alberti 2015).

Climate change is one of the main threats to global biodiversity (Thomas et al. 2004; Pereira et al. 2010), continuously promoting variations in physiological and ecological processes that directly affect the distribution and persistence of species (Stenseth et al. 2002; MacDonald et al. 2004; Huey et al. 2009). Some studies have addressed how climate change affects individual performances (Huang et al. 2013; Holt and Jorgensen 2015), demographic dynamics (Lukoscheck et al. 2013; Pomara et al. 2014), and species richness (Lemes and Loyola 2013; Ferro et al. 2014). Predictive outcomes have included adaptation to novel conditions (Quintero and Wiens 2013), expansion or retraction of species' extent of occurrence (Ferro et al. 2014; Lemes et al. 2014), isolation to climate refuges (Puschendorf et al. 2009), and in the worst cases, species extinctions

74 (Thomas et al. 2004). Such climate change effects are the reasons there is a growing consensus that management

75 decisions for biodiversity conservation must take into account this phenomenon (Araújo and Rahbek 2007).

76   Ecological niche models (ENMs), also referred to as species distribution models (SDMs) (Peterson et

77 al. 2011; Rangel and Loyola 2012), have been used increasingly to estimate species ranges for future scenarios

78 of climate change (Peterson et al. 2011). These models can be used to evaluate the current and future hotspots of

79 functional and phylogenetic diversity (Thuiller et al. 2011; Loyola et al. 2013; Pio et al. 2014), working as

80 efficient conservation tools (Del Toro et al. 2015). Ectothermic animals are highly susceptible to climate change

81 (Pounds et al. 2006; Sinervo et al. 2010) due to the due to the interdependence of their behavioral-physiological

82 functions in relation to the external environment (Ribeiro et al. 2012). More specifically, amphibians are very

83 sensitive to environmental changes (Lourenço-de-Moraes et al. 2014) due to their metabolic features (Duellman

84 and Trueb 1994), at high temperatures amphibians lose water to the atmosphere (Wells 2007) and may have

85 local extinctions (Becker et al. 2007). Therefore, using ENMs may be an effective tool in predicting dispersion

86 driven by climate change for amphibian species (Pie et al. 2013; Ribeiro et al. 2015), and may help to conserve

87 these species.

88   The consequences of human activities go further than the loss of species and various studies reported

89 losses of both evolutionary history and functional diversity at different landscapes (Purvis et al. 2000; Flynn et

90 al. 2009; Mayfield et al. 2010). The Anthropocene is characterized by drastic climate change (especially warmer

91 temperature), causing a massive defaunation (Dirzo et al. 2014). Facing this scenario, many species may be

92 underestimated for their threat status (e.g., Ocampo-Peñuela et al. 2016). Carnaval et al. (2009) found three

93 points of refuge during the Pleistocene, included areas of altitude in the mountain range of southeastern and

94 northeastern in Atlantic Forest. Recent studies have suggested that areas of high altitude may be important

95 refuges for vertebrates during the Anthropocene (Loyola et al. 2013; Lemes et al. 2014; Campos et al. 2017). In

96 this context, we tested the hypothesis that the high elevation areas are refuges for amphibians and may maintain

97 their contribution to ecosystem services and evolutionary potential. To address this hypothesis, we analysed the

98 present and future distribution of taxonomic, functional and phylogenetic diversity of Atlantic Forest amphibian

99 species. We correlated this diversity with altitude in both periods and analysed the retraction of species in the

100 direction to higher areas. We also projected the potential species conservation status for 2080 based on the IUCN

101 criteria.

102

103 **Materials and Methods**

104 *Study area*

105 We focused our analyses on the Atlantic Forest Biodiversity Hotspot (Myers et al. 2000), which originally

106 covered around 150 million ha with heterogeneous environmental conditions provided by a wide range of

107 climatic belts and vegetation formations (Tabarelli et al. 2005; Ribeiro et al. 2009). This biome has an altitudinal

108 range from sea level to the mountain chains of Serra do Mar and Serra da Mantiqueira (Cavarzere and Silveira

109 2012). This region has a longitudinal range with different forest compositions due to a diminishing gradient in

110 rainfall from the coast to the interior, and a latitudinal range extending into tropical and subtropical environments

111 (Ribeiro et al. 2009) (Fig. 1).

112

113 *Spatial species data*

114   We obtained spatial data of amphibian species through six steps: 1. We built a dataset with all the

115 species distributed in the Atlantic Forest according to Haddad et al. (2013); 2. We included the species

116 occurrences records available through the Global Biodiversity Information Facility (GBIF: http://www.gbif.org);

117 3. We added maps of geographical ranges for each species from the IUCN Red List of Threatened Species

118 (IUCN 2017); 4. We filtered out species that only occur in forested environments overlapping the spatial species

119 data by the Atlantic Forest remnant map (SOS Mata Atlântica and INPE 2015), excluding all urban areas from

120 the species distribution data; 5. We conducted complementary fieldwork in the major Atlantic Forest remnants of

121 Brazil to supplement the dataset with observed functional traits, such as body size, reproductive mode, habitat,

122 activity, poison patterns, habit and calling site (see Supplementary material Appendix 1, Fig. A1); and 6. We

123 modelled the potential present and future distribution of species using ecological niche modelling.

124   We used the "Spatial Join" ArcGIS toolbox to transform species' spatial occurrences in matrices,

125 matching rows from the join features to the target features based on their relative spatial locations. Then, we

126 combined vector files based on expert knowledge of the species' ranges and forest remnant polygons into an

127 overall coverage for species distribution modelling. We only considered spatial occurrences by those species

128 where the distribution data intersected at least a grid cell (i.e. ~ 10 km2). We used forest remnant data to meet

129 the habitat patch requirements based on visual interpretation at a scale of 1:50,000, delimiting more than 260,000

130 forest remnants with a minimum mapping area of 0.3 km2. Therefore, we considered a species present in a cell if

131 its spatial range intersected more than 0.3 km2. We also used the "Count Overlapping Polygons" ArcGIS

132   toolbox to obtain the species richness at the spatial resolution assessed, removing all duplicate records from the

133   analyses (i.e. repeated records of a species at a single locality).

134

135   *Ecological niche modelling, species richness and turnover*

136   We used ArcGIS 10 software (ESRI 2010) to build presence/absence matrices from the species

137   distribution data by superimposing a grid system with cells of 0.1 latitude/longitude degrees, creating a network

138   with 10,359 grid cells. In total, we assessed the geographical ranges of 453 amphibian species (five

139   Gymnophionas and 448 Anurans) covered by our grid system. We only considered a grid cell occupied by those

140   species where the centre of the grid cell intersected with the species ranges. We also used the "Count

141   Overlapping Polygons" ArcGIS toolbox to obtain species richness at the spatial resolution assessed, removing all

142   duplicate records from the analyses (i.e. repeated records of a species at a single locality).

143   Considering that species occurrence patterns are determined at large-scales by responses of organisms

144   to different environmental conditions (reflecting the Grinellian component of the ecological niche, *sensu*

145   Soberón 2007), we used ecological niche models (ENMs) to predict the distribution area of amphibian species in

146   the Atlantic Forest. For this, we used the species occurrence matrix and the layers of climatic-environmental

147   variables, resulting in a suitability matrix, which we used to model and map the potential distribution of each

148   species evaluated.

149   We used the following bioclimatic variables in the modelling process: 1. annual mean temperature; 2.

150   annual temperature range; 3. precipitation of the wettest month; 4. precipitation of the driest month; and 5.

151   precipitation of the warmest quarter. We obtained these variables for the present and future (mean of simulations

152   for 2080-2100) from CMIP5 – Coupled Models Intercomparison Project Phase 5 (http://cmip-

153   pcmdi.llnl.gov/cmip5/; and also at http://ecoclimate.org, see Lima-Ribeiro 2015), and downscaled to the

154   resolution of 0.1 degrees. We also used altitude as predictor of richness and dispersion from the dataset available

155   at WorldClim Global Climate Data (www.worldclim.org). We assumed altitude will remain constant through

156   time, these permit to perform future predictions. For the future, we used the greenhouse gas concentration

157   trajectory corresponded to the Representative Concentration Pathway (RCP) 4.5, which represents a moderated

158   emission scenario within an optimistic context. This moderate scenario (RCP4.5) incorporates historical

159   emissions pathways and land cover information to meet potential climate policies (Thomson et al. 2011). We

160   choose this scenario believing to present better information than extreme scenarios (pessimistic RCP 8.5 or

161   optimistic RCP 3). In the context, we used simulations provided by four Atmosphere-Ocean General Circulation

162   Models (AOGCMs): CCSM, CNRM, MIROC and MRI, which were obtained from CMIP5 (Coupled Model

163   Intercomparison Project – Phase 5) for the consensus model. Original data resolution varied from 1º to 2.8º (in

164   longitude and latitude) and both present and future climate variables were re-scaled to fit our grid resolution.

165   We performed four conceptually and statistically different ENMs based on presence data (i.e. only

166   occurrences are known, absences are unknown) using the algorithms: 1. Bioclim (BIO, Busby 1991) based on

167   bioclimatic envelope logic; 2. Gower Distance and Euclidean Distance (GD, EUD, Carpenter et al. 1993) based

168   on environmental distance approach; 3. Maximum Entropy (ME, Phillips et al. 2006) and random forest (RF,

169   Breiman 2001) based on machine learning technique; and 4. Ecological Niche Factor Analysis (ENFA, Hirzel et

170   al. 2002) based on multivariate analysis, and Genetic Algorithm for Rule set Production (GARP, Stockwell and

171   Noble 1992). Given the particularities of each model, they provided different predictions, generating

172   uncertainties about which model is more appropriate to represent the geographical distribution of species (Diniz-

173   Filho et al. 2009). To overcome this uncertainty and minimize errors, we employed the ensemble forecasting

174   approach, which offers a consensus of multiple models (Araújo and New 2006). The main idea of ensemble

175   forecasting is that different sources of errors will affect each niche model in different ways and, by obtaining a

176   consensus result of these models, errors will tend to cancel each other out and produce a more trustworthy and

177   conservative solution (Diniz-Filho et al. 2010). Assuming that the richness consensus model (CONS) reduces

178   uncertainty and error associated with alternative ENMs, we interpreted only the range sizes from the CONS

179   model.

180   We randomly partitioned presence and absence (pseudo-absence in the case of Maxent) data of each

181   species into 75% for calibration (or training) and 25% for evaluation (or test); repeating this process 10 times by

182   cross-validation for all models. For each ENM, we converted the continuous predictions of suitability into a

183   binary vector of 1/0 (presence and absence in each cell), finding the threshold that maximizes sensitivity and

184   specificity values in the receiver operating characteristic (ROC). The ROC curve is generated by plotting the

185   fraction of true positives vs. the fraction of false positives at various threshold settings. The distribution areas

186   were estimated obtaining 280 predictions (7 models x 10 randomizations x 4 AOGCMs) for each species and

187   time-period of climatic conditions (i.e. present and future). This allowed us to generate a frequency of

188   projections in the ensemble. Then, we generated the frequency of projections weighted by the total sum of

189   squares (TSS) statistics for the present and future (the best models according to this metric have more weight in

190   our consensus projections). The TSS range from -1 to +1, where values equal to +1 is a perfect prediction and

191   values equal to or less than zero is a prediction no better than random (Allouche et al. 2006; Eskildsen et al.

192 2013). We considered the species present only in cells where at least 50% of models retained in the ensemble

193 point out the species as present. In our analyses, we obtained the CONS for each AOGCM and time period

194 (present and 2080). Thus, we obtained the final maps of richness for present, future and turnover through the

195 average of values projected by CONS for each grid cell – considering the different GCMs. We ran all models

196 using the computational platform Bioensembles (Diniz-Filho et al. 2009), and mapped results using the software

197 SAM v.4.0 (Rangel et al. 2010). To determine the species patterns of amphibians of the Atlantic Forest, we

198 employed the modelling strategy at the community level of "predict first, assemble later" (*sensu* Overton et al.

199 2002), where the ranges of individual species are modelled one at a time as a function of environmental

200 predictors and then overlapped to obtain the species richness.

201 We calculated species turnover between present and future species distributions in each cell according

202 to formula 100*((G+L)/(S+G)). (Thuiller 2005), where ''G'' refers to the number of species gained, ''L'' the

203 number of species lost and ''S'' the species richness (contemporary) found in the cell.

204

205 *Functional and Phylogenetic Diversity*

206 We used the following functional traits according to Haddad et al. (2013), and supplemented with data

207 from our fieldwork: 1. body size; 2. appendices (apodal and tetrapod); 3. activity (nocturnal, diurnal, and both);

208 4. toxicity (toxic, nontoxic, unpalatable, or bad odour); 5. habitat (forested area, open area, and both); 6. habit

209 (arboreal, phytotelmate, terrestrial, cryptozoic, fossorial, rheophilic, semi-aquatic, and aquatic); 7. calling site

210 (bamboo grove, swamp or lake, bromeliad, forest floor, tree canopy, caves or burrows, rock wall, backwater

211 river, stream, river, shrubs, grasslands and not sings); and 8. reproductive mode (1 to 39 modes; see Haddad and

212 Prado 2005; see Supplementary Material Appendix 1, Table A1 for traits details). Each functional trait

213 contributes to ecosystem supporting services through direct and indirect changes on the ecosystem functions and

214 their processes (Hocking and Babbitt 2014). For further details of specific functions and ecosystem supporting

215 services of each one of the functional traits assessed, see Supplementary Material Appendix 1, Table A2.

216 We followed the protocol proposed by Petchey and Gaston (2006) to calculate functional diversity

217 (FD): 1. construction of a species-trait matrix; 2. conversion of species-trait matrix into a distance matrix; 3.

218 clustering distance matrix into a dendrogram (UPGMA); and 4. calculating functional diversity by summing

219 dendrogram branch lengths of species community. To create the distance matrices, we used the method Gower

220 distance proposed by Pavoine et al. (2009).

221 We used the phylogenetic diversity index (Faith 1992) to quantify the phylogenetic diversity (PD),

222   which comprises the sum of the branches lengths of the phylogenetic tree of all species assessed and is often

223   used in the assessment of phylogenetic diversity of con-current species (e.g., Rodrigues and Gaston 2002; Safi et

224   al. 2011; Trindade-Filho et al. 2012). The PD index has appropriate ways of accounting for relatedness between

225   taxa and evolutionary history in a conservation context (Pio et al. 2011).

226   We based the phylogenetic distance through 207 species nucleotide sequences obtained from GenBank

227   (Benson et al. 2013) and provided by the National Center for Biotechnology Information (NCBI) (See

228   Supplementary Material Appendix 1, Table A3). Following the protocol proposed by Pyron and Wiens (2011) in

229   an extant amphibian phylogeny, we used 12 genes to produce a novel estimate phylogeny for the Atlantic Forest

230   amphibians (i.e. 11,906 bp for each species), though three mitochondrial genes were included: cytochromeb (cyt-

231   b), and the large and small sub-units of the mitochondrial ribosome genes (12S/16S); and nine nuclear genes: C-

232   X-C chemokine receptor type 4 (CXCR4), histone 3a (H3A), sodium–calcium exchanger (NCX1), pro-

233   opiomelanocortin (POMC), recombination-activating gene 1 (RAG1), rhodopsin (RHOD), seventh-in-absentia

234   (SIA), solute-carrier family 8 (SLC8A3), and tyrosinase (TYR). For the length-variable regions, we performed

235   multiple pairwise comparisons by the online version of MAFFT v.6.8 and the G-INS-i algorithm (Katoh and Toh

236   2008). After, we put together alignments of all genes in the same alignment using the software SequenceMatrix

237   1.7.7 (Vaidya et al. 2011) to concatenate the supermatrix previously produced.

238   We analysed the phylogenetic relationships with Bayesian analyses in software BEAST 1.8 (Drummond

239   and Rambaut 2007). We generated the phylogeny based on the combined data matrix using a HKY model of

240   sequence evolution for one partition for all genes, under a Yule speciation process as the tree prior and an

241   uncorrelated relaxed clock. After removal of the burn-in, we run the Yule process for 100 million generations,

242   ensuring that the number of generations after convergence were sufficient assessed with Tracer v1.6 (Drummond

243   and Rambaut 2007), combining the results with the use of Logcombiner 1.8 and Treeanotator 1.8 (Drummond

244   and Rambaut 2007). We considered the nodes strongly supported if they received probability (pp) support values

245   ≥ 0.95. Thus, we reconstructed a new phylogenetic tree using the Mesquite software version 3.0 (Maddison and

246   Maddison 2015).

247   To verify whether functional diversity (FD) and phylogenetic diversity (PD) was influenced by species

248   richness (Devictor et al. 2010), we used independent swap null models (Gotelli and Entsminger 2001), according

249   to the protocol proposed by Swenson (2014). The values provided by such models are more sensitive to

250   preserving both site diversity and species frequency of occurrence while randomizing the pairs of species/sites,

251   which ensure that patterns of trait assembly do not simply reflect differential occurrence of particular species

252 (Ackerly et al. 2006; Swenson 2014) for present and future times. The null model is totally independent of the

253 species richness of an assemblage (Swenson 2014), which provides expected values at different species richness

254 levels (Mouchet et al. 2010). Hence, we tested if the functional and phylogenetic diversity were higher, equal or

255 lower than expected by chance for each grid cell (random or non-random pattern), assuming a random

256 distribution in which every species could occupy any grid cell in the biome. For each pruning event (present and

257 future), we computed 1,000 replicates of random remaining PD and FD, allowing us to obtain a P-value of

258 predicted PD and FD as compared to the distribution of the random replicates. All analyses were performed

259 using the packages "ade4", "picante", "FD" and "vegan" through the R software (R Development Core Team

260 2017).

261

262 *Species Richness, and Functional and Phylogenetic Diversity vs. Topography and Spatial References*

263 We used correlation matrices to compare the topographic patterns and spatial references (altitude and

264 latitude) to the values obtained by the richness consensus model for CONS, Turnover, FD and PD in each grid

265 cell for present and future time (2080). Thus, we correlated the values obtained for CONS, FD and PD with

266 altitude, and the turnover values with altitude and latitude using simple linear regression models.

267 We used correlation matrices to compare the topographic patterns and bioclimatic variables (altitude vs

268 bioclimatic variables) to the values in each grid cell for present and future conditions. Using multiple linear

269 regression models for the correlation matrices, we compared the following bioclimatic variables: 1. annual mean

270 temperature; 2. annual temperature range; 3. precipitation of the wettest month; 4. precipitation of the driest

271 month; and 5. precipitation of the warmest quarter.

272

273 *Threat status of species facing climate change*

274 From the individual range sizes (i.e. number of occupied cells) of each species in present and future, we

275 estimated the threat status of amphibian species by 2080, fitting the species' extent of occurrence under the

276 IUCN's criterion B1 (IUCN, 2015). We considered the following threat categories: 1. Extinct (EX) = 0 km^2, 2.

277 Critically Endangered (CR) = occurrence < 100 km^2; 3. Endangered (EN) = occurrence < 5,000 km^2; 4.

278 Vulnerable (VU) = occurrence < 20,000 km^2; and 5. Nonthreatened (NT) = occurrence > 20,000 km^2.

279 We also evaluated the percentage of range loss for the future. We considered the following categories:

280 1. species with total loss 100%; 2. species whose loss is estimated at 80% for the projected time interval; 3. the

281 species whose loss is estimated at 50% for the projected time interval; 4. the species whose loss is estimated at

282   30% for the projected time interval; and 5. the species whose loss is estimated at below 30% for the projected

283   time interval.

284   .

285   **Results**

286   The results from the total sum of squares (TSS) for most species presented average and standard deviation of

287   0.61 ± 0.11, indicating relatively high fit model. The overlap of individual species ranges generated by the

288   CONS model suggested that the highest species richness values were restricted almost entirely to the eastern-

289   central portion of the Atlantic Forest in the present times (Fig. 2, 3 and 4). Species richness pattern showed no

290   significant relationships with the altitude ($r^2 = 0.000$, $P = 0.182$, Fig. 4c). The future predictions produced by

291   CONS from different AOGCMs pointed out the losses of climatically suitable areas in this region by 2080, with

292   the species richness directed to the east-central portion of the Atlantic Forest. In this case, species richness

293   increased toward higher altitude ($r^2 = 0.132$, $P < 0.001$ Fig. 3d). In general, CCSM and MRI showed two distinct

294   species-rich areas and CNRM and MIROC produced more homogeneous results, with the latter being more

295   restrictive (Fig. 2a-d). By combining the results of the AOGCMs in a full ensemble model, we found that in the

296   future the species richness peaks are likely to be restricted to a reduced portion of the central-eastern region of

297   the biome in locations closer to the mountain regions of the Atlantic Forest (Fig. 3).

298   Temporal turnover was high after the results of AOGCMs were combined in a full ensemble model.

299   Changes in species composition are predicted to be greater on the western edge and on the northeastern edge of

300   the biome. Higher turnover rates were found at lower latitudes ($r^2 = 0.308$, $P < 0.001$) and lower altitudes ($r^2 =$

301   0.307, $P < 0.001$) (see Fig. 4a-c).

302   Our results showed high Functional Diversity (FD) in the regions of the eastern Atlantic Forest with the

303   highest rates in the east-central region rising to the northeast in the present time (Fig. 5a, c). In 2080, these

304   values will decrease from 17.30 to 15.53 at its maximum value (Fig. 5b), and will have a significant higher loss

305   in areas of lower altitudes (Fig. 5b, d). High rates of FD were found mainly in the south of Bahia to the south of

306   São Paulo states. High values of FD were correlated with high altitude for both the present ($r^2 = 0.004$, $P <$

307   0.001, Fig. 5c) and future ($r^2 = 0.101$, $P < 0.001$, Fig. 5d).

308   The highest values of Phylogenetic Diversity (PD) in the present time are distributed in the east-central

309   region, mainly in the region of Serra do Mar rising to the Central Corridor and in a small part of Pernambuco (in

310   high altitude areas) (Fig. 6a, c). For 2080, these values will decrease from 5.65 to 5.44 at its maximum value

311   (Fig. 6b), which will dramatically decrease in the south and north of Bahia, increasing towards the south of the

312   Serra do Mar mountain chain. Higher-altitude regions will be replaced by significant values in the future ($P <$

313   0.001, Fig. 6d). Built null models for FD and PD in present and future times showed different values than

314   expected by chance ($P < 0.001$), indicating a non-random pattern of FD and PD. FD and PD were highly

315   correlated (present $r^2 = 0.91$, $P< 0.001$; future $r^2 = 0.94$, $P< 0.001$), based on comparison of the CONS consensus

316   model (present FD – $r^2= 0.87$, $P< 0.001$, PD – $r^2 = 0.89$, $P< 0.001$; future FD - $r^2 = 0.86$, $P< 0.001$, PD – $r^2=$

317   0.84, $P< 0.001$). Therefore, the loss of species richness in the future may be accompanied by the loss of FD and

318   PD (Fig. 7).

319   The bioclimatic variable correlation with altitude was correlated (present $r^2= 0.60$, $P<0.001$; future $r^2=$

320   0.60, $P<0.001$), but the only bioclimatic variable with positively relation was the precipitation of the wettest

321   month (Table 1). The change of bioclimatic variables in high altitude areas can be lower in the future than in the

322   low altitude areas. It may leave the higher altitudes more favourable to amphibians in the future.

323   The prediction of massive habitat suitability losses under climate change will negatively affect most

324   (60%) amphibians of the Atlantic Forest and most will be subjected to some level of threat by 2080 (Fig. 8).

325   According to our estimations under the IUCN's criterion B1, 40% (n= 181 spp.) of the species will be not

326   threatened. However, 15% (n= 62 spp.) of the species will experience less than 30% reduction from the original

327   distribution area by considering the projections for a moderate carbon emission scenario. Our results also

328   indicated that 21.6 % (n= 97 spp.) of the species are expected to be extinct from the biome by 2080. The

329   summary of the impacts of future climatic alterations on each individual species is given in Supplementary

330   Material Appendix 1, Table A4. Our results showed that the functional traits can have losses of 30% on average.

331   The trait habit was that most show reduction and species with the subtrait phytotelmata cannot occur (Fig. 9).

332

333   **Discussion**

334   Our data showed a dramatic reduction of species range (CONS, PD and FD) for 2080. High rates of turnover in

335   the lower latitudes and lower rates in the high altitudes strengthen the mountains of Atlantic Forest as climatic

336   refuges (Randin et al. 2009; Araújo et al. 2011). The persistence of the species in their original ranges depend on

337   their degree of physiological and phenotypic plasticity, antipredator mechanisms, reproductive mode, and

338   evolutionary adaptation to environmental change (Holt 1990; Visser 2008; Toledo et al. 2012; Urban et al. 2014;

339   Ferreira et al. 2016; Lourenço-de-Moraes et al. 2016, 2018). As result, some species have increased their ranges,

340   but with low range in the future. For instance, opportunistic species adapted to warmer and drier environments

341   had a spatial range expansion (e.g., *Rhinella crucifer, Dendropsophus branneri, Leptodactylus troglodytes* and

342   *Siphonops annulatus*). Species that live in high altitudes and high latitudes had their ranges little affected, due to

343   the low temperature increase and high rainfall in these localities. *Brachycephalus brunneus,* a species that due to

344   its morphology and great dependence on abiotic factors (i.e., temperature and rainfall – 1,300 m a.s.l.; Ribeiro et

345   al. 2005), had low range changes in our model, which enable it to remain in the future. However, species of this

346   same genus that occur in the north portion of the Atlantic Forest, such as *B. pulex* (Napoli et al. 2011), also can

347   become extinct according to the same model.

348   Our results showed that FD and PD have high correlation among themselves and a non-random pattern

349   of species composition for both present and future times. This pattern suggests that environmental factors may

350   act as a filter that does not allow the co-existence of similar species (Diamond 1975; Weiher and Keddy 1999).

351   In addition, historical factors provided biogeographic barriers acting to determine the regional bank of some

352   species assemblages (Ricklefs and Schluter 1993). We revealed three major areas of FD and PD for the present

353   time, which are located in the mountains of the Serra do Mar, the Central Corridor of the Atlantic Forest and the

354   high altitude areas of Pernambuco state. Carnaval et al. (2009) pointed out three climatic refuges for amphibians

355   during the Pleistocene: 1. Southern Bahia state (located in the Central Corridor of the Atlantic Forest); 2.

356   Pernambuco state; 3. East-north region of São Paulo (i.e., Serra do Mar). We showed higher rates of PD and FD

357   in these areas, supporting Carnaval et al. (2009) hypothesis. Our results also suggested climatic refuges in the

358   Espírito Santo state, the Serra da Mantiqueira region that corresponds to the South of Minas Gerais state, and the

359   South of Serra do Mar that corresponds to the east of Paraná state. In the future (i.e., 2080), these same areas will

360   continue as climatic refuges, mainly in higher altitudes. Our model showed that species may have suitable

361   habitat in higher latitudes and altitudes (see Fig. 3 and 4). Species with access to mountainous regions may

362   migrate to higher altitude areas, which have lower temperatures (Colwell et al. 2008), and in the case of the

363   Atlantic Forest, should retain greater humidity due to better-preserved forests cover (Ribeiro et al. 2009). Our

364   data showed that altitude areas are positively correlated with increased rainfall mainly in the drier months. In

365   addition, we suggested that areas of higher altitude will have lower temperature under climate change, making

366   these areas suitable for species survival. Therefore, high altitude areas can be associated to amphibian-friendly

367   climatic variables using forecast scenarios.

368   Loyola et al. (2013) indicated high values of PD for amphibians in the Atlantic Forest in both the

369   present and future (i.e., 2080). Our findings contradict these values, indicating low PD values and significant

370   correlations may result in the loss of richness consensus model (CONS) for the future. However, our results

371   corroborate the data obtained by Thuiller et al. (2011), which showed that the loss of species richness may be

372 accompanied by the loss of PD. Furthermore, we also found that the loss of species richness in the future will

373 result in the loss of FD.

374   The historical loss and their relationships do not reflect the actual proportion of loss in relation to the

375 conservation of species. FD reflected better the loss of ecological functions and evolutionary perspectives,

376 because similar species from similar phylogenetic clades may not coexist due to possible competitive exclusion

377 (Arnam et al. 2016). However, closely phylogenetic species may have different roles on the ecosystem

378 functioning (Webb et al. 2002; Gomez et al. 2010). In these cases, the loss of phylogenetically similar species

379 may coexist and may have greater losses in processes and ecosystem services (Webb et al. 2002). By framing

380 evolutionary ecology into conservation science, we revealed that phylogenetic metrics can be relevant tools for

381 functional landscape planning for threatened amphibian species.

382   According to our results, 60% of the studied species will be threatened or extinct by 2080. It is highly

383 concerning that 92% of the species of our study are not included in any threatened status by the Brazilian Red

384 list (Supplementary material Appendix 1, Table A4). Moreover, amphibian species from Atlantic Forest

385 protected areas are more threatened by extinction than in other Brazilian protected networks (Campos et al.

386 2016). The Atlantic Forest was destroyed severely and fragmented, resulting in only 9-12% of its original

387 formation remaining (Ribeiro et al. 2009). The current distributions of species provided by IUCN do not undergo

388 any type of biological filter (e.g., urban and rural areas). The proximity of the protected areas to urban

389 environmental, also negatively affect the local species richness (Lourenço-de-Moraes et al. 2018). Because of

390 this, the analysed data can lead to overestimations, and the results for the future may be even more alarming.

391   Many biotic and abiotic factors can influence the richness and composition of species in an ecosystem

392 (Diamond 1975). Amphibians are particularly sensitive to environmental changes, and depending on the species,

393 dispersion may be difficult because of its specializations and diminutive size (Crump 2010; Early and Sax 2011;

394 Lourenço-de-Moraes et al. 2012, 2014). The main reason behind our choice by the consensus modelling

395 approach was to look for a straightforward combination of environmental predictors that best explains the

396 presence-only species distribution across forest remnants. Given that temperature and humidity are the main

397 climate components that directly affect the biology of amphibians (Carey and Alexander 2003), we selected

398 these variables along altitudinal gradients to provide a reasonably good representation of the species present in

399 the forest remnants.

400   The use of various algorithms to reach a better consensus model have been demonstrated as an effective

401 strategy to reach outcomes closer to reality, and it is one of the keys to understanding how communities can

402 respond to climate change (Araújo and New 2006; Marmion et al. 2009). Therefore, our consensus model

403 showed useful results to plan conservation actions in relation to spatial and temporal patterns in ecology and

404 evolution. We introduced a new conservation framework that has sought to understand the functioning of

405 ecosystems from the amphibian-climate refuges in an age of extinction.

406 Studies in the Atlantic Forest have been warning about the need to invest in protected areas at high

407 altitudes (Lemes et al. 2013; Loyola et al. 2013), mainly in the areas of Serra do Mar and south of Bahia

408 (Carnaval et al. 2009; Campos et al. 2017; Campos and Lourenço-de-Moraes 2017). Considering the dramatic

409 evolutionary and ecological loss showed in this study, we suggest four large areas as priority for conservation in

410 the Atlantic Forest: the Serra do Mar, the Serra da Mantiqueira, the Central Corridor and areas of high altitude in

411 the Pernambuco state.

412 Amphibians are very sensitive to climate change mainly due to their metabolic characteristics. Dispersal

413 across disturbed areas may be unfeasible for most species. The management of the already conserved areas,

414 inserted in the points of climatic refuges, as well as areas of connections to these refuges is indispensable for the

415 conservation of the amphibians. Knowing the first climatic refuges facilitates the decision making to conserve

416 the amphibians during the climatic changes avoiding mass extinctions.

417

418 **References**

419 Ackerly DD, Schwilk DW, Webb CO (2006) Niche evolution and adaptive radiation: testing the order of trait

420   divergence. Ecology 87:50–61

421 Alberti M (2015) Eco-evolutionary dynamics in an urbanizing planet. Trends Ecol. Evol. 30:114–126

422 Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence,

423   kappa and the true skill statistic (TSS). J App Ecol 43:1223–1232 doi:10.1111/j.1365-

424   2664.2006.01214.x

425 Arnan X, Cerdá X, Retana J (2016) Relationships among taxonomic, functional, and phylogenetic ant diversity

426   across the biogeographic regions of Europe. Ecography 39:001–010

427 Araújo MB, Cabeza M, Thuiller W, Hannah L, Williams PH (2004) Would climate change drive species out of

428   reserves? An assessment of existing reserve-selection methods. Glob Change Biol 10:1618–1626

429   doi:10.1111/j.1365-2486.2004.00828.x

430 Araújo MB, New M (2006) Ensemble forecasting of species distributions. Trends Ecol Evol 22:43–47

431   doi:10.1016/j.tree.2006.09.010

432   Araújo MB, Rahbek C (2007) Conserving biodiversity in a world of conflicts. J Biog 34:199–200

433   doi:10.1111/j.1365-2699.2006.01687.x

434   Araújo MB, Alagador D, Cabeza M, Nogués-Bravo D, Thuiller W (2011) Climate change threatens European

435   conservation areas. Ecol Letters 14:484–492

436   Bambach RK (2006) Phanerozoic biodiversity mass extinctions. Annu Rev Earth Planet Sci 34:127–155

437   Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB Marshall C, McGuire JL, Lindsey EL,

438   Maguire KC, Mersey B, Ferrer EA (2011) Has the Earth's sixth mass extinction already arrived? Nature

439   471:51–57

440   Benson DA, Cavanaugh M, Clark K, Karsch-Mizrachi I, Lipman DJ, Ostell J, Sayers EW (2013) GenBank Nuc

441   Aci Res 41:36–42

442   Becker CG, Fonseca CR, Haddad CFB, Batista RF, Prado PI (2007) Habitat split and the global decline of

443   amphibians. Science 318:1775–1777

444   Busby Jr (1991) BIOCLIM - A bioclimate analysis and prediction system. In: Nature Conservation: Cost

445   Effective Biological Surveys and Data Analysis. Margules, C. R. and Austin, M. P. (eds.) Melbourne:

446   CSIRO, pp. 64–68

447   Bush MB (1994) Amazonian speciation: a necessarily complex model. J Biog 21:5–17 doi: 10.2307/2845600

448   Bush MB, Oliveira PE (2006) The rise and fall of the refugial hypothesis of of Amazonian speciation: a

449   paleoecological perspective. Biot Neot 6: http://dx.doi.org/ 10.1590/S1676-06032006000100002.

450   Bush MB, Gosling WD, Colinvaux PA (2011) Climate and vegetation change in the lowlands of the Amazon

451   Basin. In: Tropical Rainforest Responses to Climatic Change, 2º Edition. Bush, M., Flenley, J. and

452   Gosling, W. (eds). Springer-Praxis Books, New York, New York, pp. 61–84

453   Breiman L (2001) Random Forests. Mach Lear 45:5–32 http://dx.doi.org/10.1023/A:1010933404324

454   Campos FS, Llorente GA, Rincón L, Lourenço-de-Moraes R, Solé M (2016) Protected areas network and

455   conservation efforts concerning threatened amphibians in the Brazilian Atlantic Forest. W Ecol 16:9–12

456   Campos FS, Lourenço-de-Moraes R (2017) Amphibians from the mountains of the Serra do Mar Coastal Forest,

457   Brazil. Herpetol Notes 10:547–560

458   Campos FS, Lourenço-de-Moraes R, Llorente GA, Sole M (2017) Cost-effective conservation of amphibian

459   ecology and evolution. Science Adv 3(6):e1602929 doi: 10.1126/sciadv.1602929.

460   Carey C, Alexander MA (2003) Climate change and amphibian declines: is there a link? Div Dist 9:111–121

461 Carnaval AC, Hickerson MJ, Haddad CFB, Rodrigues MT, Moritz C (2009) Stability predicts genetic diversity

462   in the Brazilian Atlantic forest hotspot. Science 323:785–789

463 Carpenter G, Gillison AN, Winter J (1993) DOMAIN : a flexible modelling procedure for mapping potential

464   distributions of plants and animals. Biodivers Conserv 2:667–680

465 Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, Balvanera P, O'Connor MI, Gonzalez

466   A (2011) The functional role of producer diversity in ecosystems. Am J Bot 98:572–592

467 Cavarzere V, Silveira LF (2012) Bird species diversity in the Atlantic Forest of Brazil is not explained by the

468   Mid-domain Effect. Zoologia 29:285–292 doi:10.1590/S1984-46702012000400001

469 Colwell RK, Brehm G, Cardelús C, Gilman A, Longino JT (2008) Global warming, elevational range shifts, and

470   lowland biotic attrition in the wet tropics. Science 322:258–261

471 Crump ML (2010) Amphibian diversity and life history. In: Amphibian Ecology and Conservation A handbook

472   of techniques. Dodd Jr., C. K. (ed.) Oxford: Oxford University Press, pp. 1–19

473 Del Toro I, Silva RR, Ellison AM (2015) Predicted impacts of climatic change on ant functional diversity and

474   distributions in eastern North American forests. Div Dist 21:781–791

475 Devictor V, Mouillot D, Meynard C, Jiguet F, Thuiller W, Mouquet N (2010) Spatial mismatch and congruence

476   between taxonomic, phylogenetic and functional diversity: the need for integrative conservation

477   strategies in a changing world. Ecol Lett 13:1030–1040

478 Diamond JM (1975) Assembly of species communities. In: Ecology and evolution of communities. Cody, M. L.

479   and Diamond, J. (eds.). Cambridge: Harvard University Press, pp. 342–444

480 Diniz-Filho JAF, Bini ML, Rangel TF, Loyola RD, Hof C, Nogués-Bravo D, Araújo MB (2009) Partitioning and

481   mapping uncertainties in ensembles of forecasts of species turnover under climate change. Ecography

482   32:897–906 doi:10.1111/j.1600-0587.2009.06196.x

483 Diniz Filho JAF, Ferro VG, Santos T, Nabout JC, Dobrovolski R, De Marco Jr, P (2010) The three phases of the

484   ensemble forecasting of niche models : geographic range and shifts in climatically suitable areas of

485   *Utetheisa ornatrix.* Rev Bras Ent 54:339–349

486 Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B (2014) Defaunation in the Anthropocene.

487   Science 345:401–406 DOI:10.1126/science.1251817

488 Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. Evol Biol 7:214

489   DOI**:** 10.1186/1471-2148-7-214

490 Duellman WE, Trueb L (1994) Biology of Amphibians. McGraw Hill, New York.

491 Early R, Sax DF (2011) Analysis of climate paths reveals potential limitations on species range shifts. Ecol Lett
492   14:1125–1133

493 Environmental Systems Research Institute ESRI (2011) Arcgis Software: Version10.1. ESRI, Redlands, CA

494 Eskildsen A, Le Roux PC, Heikkinen RK, Hoye TT, Kissling WD, Poyry J, Wisz MS, Luoto M (2013) Testing
495   species distribution models across space and time: high latitude butterflies and recent warming. Global
496   Ecol Biogeogr 22:1293–1303

497 Faith DP (1992) Conservation evaluation and phylogenetic diversity. Biol Cons 61:1–10

498 Ferreira RB, Beard KH, Crump ML (2016) Breeding guild determines frog distributions in response to edge
499   effects and habitat conversion in the Brazil's Atlantic Forest. PLoS One 11:e0156781
500   doi:10.1371/journal.pone.0156781

501 Ferro VG, Lemes P, Melo AS, Loyola R (2014) The reduced effectiveness of protected areas under climate
502   change threatens atlantic forest tiger moths. PLoS One 9:e107792 doi:10.1371/journal.pone.0107792

503 Flynn DF, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, Simpson N, Mayfield
504   MM, DeClerck F (2009) Loss of functional diversity under land-use intensification across multiple taxa.
505   Ecol Lett 12:22–33

506 Gómez JP, Bravo GA, Brumfield RT, Tello JG, Cadena CDA (2010) A phylogenetic approach to disentangling
507   the role of competition and habitat filtering in community assembly of Neotropical forest birds. J Anim
508   Ecol 79:1181–1192

509 Gotelli NJ, Entsminger GL (2001) Swap and fill algorithms in null model analysis: rethinking the knight's tour.
510   Oecologia 129:281–291 DOI 10.1007/s004420100717

511 Haddad CFB, Prado CPA (2005) Reproductive modes in frogs and their unexpected diversity in the Atlantic
512   forest of Brazil. Bioscience 55:207–217

513 Haddad CFB, Toledo LF, Prado CPA, Loebmann D, Gasparini JL, Sazima I (2013) Guia dos anfíbios da Mata
514   Atlântica: diversidade e biologia. Anolis Books, São Paulo

515 Haffer J (1969) Speciation in Amazon forest birds. Science 165:131–137

516 Hirzel AH, Hausser J, Chessel D, Perrin N (2002) Ecological-niche factor analysis: how to compute habitat-
517   suitability maps without absence data? Ecology 83:2027–2036

518 Huey RB, Deutsch CA, Tewksbury JJ, Vitt LJ, Hertz PE, Alvarez-Pérez HJ, Garland TJr (2009) Why tropical
519   forest lizards are vulnerable to climate warming. Proc R Soc B Biol Sci 276:1939–1948
520   doi:10.1098/rspb.2008.1957

521   Holt RD (1990) The microevolutionary consequences of climate change. Trends Ecol Evol 5:311–315

522   Holt RE, Jørgensen C (2015) Climate change in fish : effects of respiratory constraints on optimal life history

523   and behavior. Biol Lett 11:20141032 doi:http://dx.doi.org/10.1098/rsbl.2014.1032

524   Hocking DJ, Babbitt KJ (2014) Amphibian contributions to ecosystem services Herpet Cons Biol 9:1–17

525   Huang S-P, Chiou C-R, Lin T-E, Tu M-C, Lin C-C, Porter WP (2013) Future advantages in energetics, activity

526   time, and habitats predicted in a high-altitude pit viper with climate warming. Funct Ecol 27:446–458

527   doi:10.1111/1365-2435.12040

528   Katoh K, Toh H (2008) Recent developments in the MAFFT multiple sequence alignment program. Brief

529   Bioinform 9:286–298

530   International Union for Conservation of Nature (2015) IUCN Red List of Threatened Species: Version 2015.4,

531   <ww.iucnredlist.org/technical-documents/spatial-data>.

532   Jablonski D (1994) Extinctions in the fossil record. Phil Trans R Soc Lond Ser B 344:11–17

533   Lima-Ribeiro MS, Varela S, González-Hernández J, Oliveira G, Diniz-Filho JAF, Terribile LC (2015)

534   Ecoclimate: a Database of climate data from multiple models for past, present, and future for

535   macroecologists and biogeographers. Biodivers Inform 10:1–21. doi:10.17161/bi.v10i0.4955

536   Lemes P, Loyola RD (2013) Accommodating species climate-forced dispersal and uncertainties in spatial

537   conservation planning. PLoS One 8:e54323 doi:10.1371/journal.pone.0054323

538   Lemes P, Melo AS, Loyola RD (2014) Climate change threatens protected areas of the Atlantic Forest. Biodiver

539   Conserv 23:357–368 doi:10.1007/s10531-013-0605-2

540   Loyola RD, Lemes P, Nabout JC, Trindade-Filho J, Sagnori MD, Dobrovolski R, Diniz-Filho JAF (2013) A

541   straightforward conceptual approach for evaluating spatial conservation priorities under climate change.

542   Biodiver Conserv 22:483–495 doi:10.1007/s10531-012-0424-x

543   Lourenço-de-Moraes R, Sole M, Toledo LF (2012) A new species of *Adelophryne* Hoogmoed and Lescure 1984

544   (Amphibia: Anura: Eleutherodactylidae) from the Atlantic forest of southern Bahia, Brazil. Zootaxa

545   3441:59–68

546   Lourenço-de-Moraes R, Ferreira RB, Fouquet A, Bastos RP (2014) A new diminutive frog species of

547   *Adelophryne* (Amphibia: Anura: Eleutherodactylidae) from the Atlantic Forest, southeastern Brazil.

548   Zootaxa 3846:348–360

549   Lourenço-de-Moraes R, Ferreira RB, Mira-Mendes CCV, Zocca CZ, Medeiros T, Ruas DS, Rebouças R, Toledo

550   LF, Brodie Jr ED, Solé M (2016) Escalated antipredator mechanisms of two neotropical marsupial

551   treefrogs. Herpetol J 26:237–244

552   Lourenço-de-Moraes R, Malagoli LR, Guerra VB, Ferreira RB, Affonso IP, Haddad CFB, Sawaya RJ, Bastos

553   RP (2018) Nesting patterns between Neotropical species assemblages: Can reserves in urban areas be

554   failing to protect anurans? Urban Ecosyst https://doi.org/10.1007/s11252-018-0767-5

555   Lukoschek V, Beger M, Ceccarelli D, Richards Z, Pratchett M (2013) Enigmatic declines of Australia's sea

556   snakes from a biodiversity hotspot. Biol Cons 166:191–202 doi:10.1016/j.biocon.2013.07.004

557   McDonald PG, Olsen PD, Cockburn A (2004) Weather dictates reproductive success and survival in the

558   Australian brown falcon *Falco berigora*. J Anim Ecol 73:683–692

559   Maddison WP, Maddison DR (2015) Mesquite: a modular system for evolutionary analysis: Version 3.04.

560   Mesquite Project Team < http://mesquiteproject.org.>

561   Magurran AE (2004) Measuring biological diversity. Blackwell, Oxford.

562   Mayfield MM, Bonser SP, Morgan JW, Aubin I, McNamara S, Vesk PA (2010) What does species richness tell

563   us about functional diversity? Predictions and evidence for responses of species and trait diversity to

564   land use change. Global Ecol Biogeogr 19:423–431

565   Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W (2009) Evaluation of consensus methods in

566   predictive species distribution modelling. Divers Distrib 15:59–69

567   Mayr E, O'hara RJ (1986) The biogeographic evidence supporting the Pleistocene forest refuge hypothesis.

568   Evolution 40:55–67 doi: 10.2307/2408603

569   Myers N, Mittermeier RA, Mittermeier CG, Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation

570   priorities. Nature 403:853–858

571   Montoya J M, Raffaelli D (2010) Climate change, biotic interactions and ecosystem services. Phil Trans R Soc

572   Ser B 365:2013–2018 doi:10.1098/rstb.2010.0114

573   Mouchet M, Villéger S, Mason NWH, Mouillo D (2010) Functional diversity measures: an overview of their

574   redundancy and their ability to discriminate community assembly rules. Funct Ecol 24:867–876

575   Napoli MF, Caramaschi U, Cruz CAG, Dias IR (2011) A new species of flea-toad, genus

576   *Brachycephalus* Fitzinger (Amphibia: Anura: Brachycephalidae), from the Atlantic rainforest of

577   southern Bahia, Brazil. Zootaxa 2739:33–40

578 Ocampo-Peñuela N, Jenkins CN, Vijay V, Li BV, Pimm SL (2016) Incorporating explicit geospatial data shows

579   more species at risk of extinction than the current Red List. Science Advanc 2:e1601367 doi:

580   10.1126/sciadv.1601367

581 Overton JM, Stephens RTT, Leathwick JR, Lehmann A (2002) Information pyramids for informed biodiversity

582   conservation. Biodivers Conserv 11:2093–2116 doi:10.1023/A:1021386426790

583 Paradis E, Claude J, Strimmer K (2004) APE: Analyses of phylogenetics and evolution in R language.

584   Bioinformatics 20:289–290

585 Pavoine S, Vallet J, Dufour AB, Gachet S, Daniel H (2009) On the challenge of treating various types of

586   variables: application for improving the measurement of functional diversity. Oikos 118:391–402

587   doi:10.1111/j.1600-0706.2008.16668.x.

588 Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JP, Fernandez-Manjarrés JF, Araújo

589   MB, Balvanera P, Biggs R, Cheung WW, Chini L, Cooper HD, Gilman EL, Guénette S, Hurtt

590   GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila

591   UR, Walpole M (2010) Scenarios for global biodiversity in the 21st century. Science 330:1496–1501

592   doi:10.1126/science.1196624

593 Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9:741–758

594 Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011)

595   Ecological niches and geographical distributions. Princeton, New Jersey: Princeton University Press.

596 Pie MR, Meyer ALS, Firkowski CR, Ribeiro LF, Bornschein MR (2013) Understanding the mechanisms

597   underlying the distribution of microendemic montane frogs (*Brachycephalus* spp, Terrarana:

598   Brachycephalidae) in the Brazilian Atlantic Rainforest Ecol Model 250:165–176

599 Pio DV, Broennimann O, Barraclough TG, Reeves G, Rebelo AG, Thuiller W, Guisan A, Salamin N (2011)

600   Spatial predictions of phylogenetic diversity in conservation decision making. Cons Biol 25:1229–1239

601   PMid:22070274 http://dx.doi. org/10.1111/j.1523-1739.2011.01773.x

602 Pio D, Engler R, Linder H, Monadjem A, Cotterill F, Taylor P, Schoeman C, Price B, Villet M, Eick G, Salamin

603   N, Guisan A (2014) Climate change effects on animal and plant phylogenetic diversity in southern

604   Africa. Glob Change Biol 20:1538–1549

605 Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions.

606   Ecol Model 190:231–259 doi:10.1016/j.ecolmodel.2005.03.026

607   Pyron A, Wiens JJ (2011) A large-scale phylogeny of Amphibia including over 2800 species, and a revised

608   classification of extant frogs, salamanders, and caecilians. Mol Phyl Evol 61:543–583

609   Pomara LY, Ledee OE, Matin KJ, Zuckerberg B (2014) Demographic consequences of climate change and land

610   cover help explain a history of extirpations and range contraction in a declining snake species. Glob

611   Change Biol 20:2087–2099 doi:10.1111/gcb.12510

612   Pounds JA, Bustamante MR, Coloma LA, Consuegra JA, Fogden MP, Foster PN, La Marca E, Masters

613   KL, Merino-Viteri A, Puschendorf R, Ron SR, Sánchez-Azofeifa GA, Still CJ, Young BE (2006)

614   Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439:161–

615   167 doi:10.1038/nature04246

616   Purvis A, Agapow PM, Gittleman JL, Mace GM (2000) Non-random extinction and the loss of evolutionary

617   history. Science 288:328–330

618   Puschendorf R, Carnaval AC, VanDerwal J, Zumbado-Ulate H, Chaves G, Bolaños F, Alford RA (2009)

619   Distribution models for the amphibian chytrid *Batrachochytrium dendrobatidis* in Costa Rica:

620   proposing climatic refuges as a conservation tool. Divers Distrib 15:401–408 doi:10.1111/j.1472-

621   4642.2008.00548.x

622   Prather MJ, Holmes CD, Hsu J (2012) Reactive greenhouse gas scenarios: Systematic exploration of

623   uncertainties and the role of atmospheric chemistry. Geophys Res Lett 39:L09803

624   doi:10.1029/2012GL051440

625   Quintero I, Wiens JJ (2013) Rates of projected climate change dramatically exceed past rates of climatic niche

626   evolution among vertebrate species. Ecol Lett 16:1095–1103 doi:10.1111/ele.12144

627   R Development Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation

628   for Statistical Computing, Vienna, Austria.

629   Randin CF, Engler, R, Normand S, Zappa M, Zimmermann NE, Pearman PB, Vittoz P, Thuiller W, Guisan A

630   (2009) Climate change and plant distribution: local models predict high-elevation persistence. Glob

631   Change Biol 15:1557–1569

632   Rangel TF, Diniz-filho JAF, Bini LM(2009) SAM : a comprehensive application for Spatial Analysis in

633   Macroecology. Ecography 33:46–50. doi:10.1111/j.1600-0587.2009.06299.x

634   Rangel TF, Loyola RD (2012) Labeling ecological niche models Nat Conserv 10:119–126

635   doi:10.4322/natcon.2012.030

636   Raup DM, Sepkoski JJ (1982) Mass extinctions in the marine fossil record. Science 215: 1501–1503

637 Ribeiro LF, Alves ACR, Haddad CFB, Reis SF (2005) Two new species of *Brachycephalus* Günther, 1858 from

638   the state of Paraná Southern Brazil. Bol Mus Nac Nov Ser Zool 519:10–18

639 Ribeiro LF, Bornschein MR, Belmonte-Lopes R, Firkowski CR, Morato SAA, Pie MR (2015) Seven new

640   microendemic species of *Brachycephalus* (Anura: Brachycephalidae) from southern Brazil. PeerJ

641   3**:**e1011https://doi.org/10.7717/peerj.1011

642 Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: How

643   much is left, and how is the remaining forest distributed? Implications for conservation. Biol Cons

644   142:1141–1153

645 Ribeiro PL, Camacho A, Navas CA (2012) Considerations for assessing maximum critical temperatures in small

646   ectothermic animals: Insights from leaf-cutting ants. PLoS One 7: e32083.

647   doi:10.1371/journal.pone.0032083

648 Ricklefs RE, Schluter D (1993) Species diversity in ecological communities: historical and geographical

649   perspectives. Chicago: University of Chicago Press.

650 Rodrigues ASL, Gaston KJ (2002) Maximising phylogenetic diversity in the selection of networks of

651   conservation areas. Biol Cons 105:103–111

652 Safi K, Cianciaruso MV, Loyola RD, Brito D, Armour-Marshall K, Diniz-Filho JAF (2011) Understanding

653   global patterns of mammalian functional and phylogenetic diversity. Phil Trans R Soc Ser B 366: 2536–

654   2544 doi:10.1098/rstb.2011.0024)10.1098/rstb.2011.0024

655 Sinervo B, Méndez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagrán-Santa C, Lara-Resendiz R,

656   Martínez-Méndez N, Calderón-Espinosa ML, Meza-Lázaro RN, Gadsden H, Avila LJ, Morando M,

657   De la Riva IJ, Sepulveda PV, Rocha CFD, Ibargüengoytía N, Puntriano CA, Massot M, Lepetz V,

658   Oksanen TA, Chapple DG, Bauer AM, Branch WR, Clobert J, Sites JW (2010) Erosion of lizard

659   diversity by climate change and altered thermal niches. Science 328: 894–899

660   doi:10.1126/science.1184695

661 Sobral FL, Cianciaruso MV (2012) Estrutura filogenética e funcional de assembleias: (re)montando a Ecologia

662   de Comunidades em diferentes escalas espaciais. Biosc J 28:617–631

663 Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of species. Ecol Lett 10:1115–

664   1123 doi:10.1111/j.1461-0248.2007.01107.x

665 SOS Mata Atlântica, INPE (2015) Atlas dos Remanescentes Florestais da Mata Atlântica Período 2013-2014.

666   https://www.sosma.org.br/projeto/atlas-da-mata-atlantica/dados-mais-recentes/

667   Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan K, Lima M (2002) Ecological effects of climate

668   fluctuations. Science 297:1292–1297

669   Stockwell DRB, Noble IR (1992) Induction of sets of rules from animal distribution data: a robust and

670   informative method of data analysis. Math Comp Sim 33:385–390

671   Swenson NG (2014) Functional and Phylogenetic Ecology in R. – Springer, New York, NY.

672   Tabarelli M, Pinto LP, Silva JMC, Hirota M, Bede L (2005) Challenges and opportunities for biodiversity

673   conservation in the brazilian Atlantic Forest. Conserv Biol 19:695–700

674   Tilman D (2001) Functional diversity. In Encyclopedia of Biodiversity (S.A. Levin, ed.). Academic Press, San

675   Diego, p. 109-120

676   Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Siqueira MF,

677   Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta

678   MA, Townsend PA, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature

679   427:145–148 doi:10.1038/nature02121

680   Thomson AM., Calvin KV, Smith SJ, Kyle GP, Volke A, Patel P, Delgado-Arias S, Bond-Lamberty B, Wise

681   MA, Clarke LE, Edmonds JA (2011) RCP4. 5: a pathway for stabilization of radiative forcing by 2100.

682   Climat Chang 109:77 https://doi.org/10.1007/s10584-011-0151-4

683   Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in

684   Europe. Proc Nat Acad Sci 102:8245–8250 doi:10.1073/pnas.0409902102

685   Thuiller W, Lavergne S, Roquet C, Boulangeat I, Araújo MB (2011) Consequences of climate change on the

686   Tree of Life in Europe. Nature 448:550–552

687   Trindade-Filho J, Carvalho RA, Brito D, Loyola RD (2012) How does the inclusion of Data Deficient species

688   change conservation priorities for amphibians in the Atlantic Forest? Biodivers Conserv 21:2709–2718

689   Urban MC, Richardson JL, Freidenfelds NA (2014) Plasticity and genetic adaptation mediate amphibian and

690   reptile responses to climate change. Evol Appl 7: 88–103

691   Wake DB, Vredenburg VT (2008) Are we in the midst of the sixth mass extinction? A view from the world of

692   amphibians. Proc Nat Aca Sci 105:11466–11473 doi: 10.1073/pnas.0801921105.

693   Webb CO, Ackerly DD, Mcpeek MA, Donoghue MJ (2002) Phylogenies and community ecology. Ann Rev

694   Ecol Syst 33: 475–505

695   Wells KD (2007) The ecology and behavior of amphibians. University of Chicago Press.

696   Weiher E, Keddy PA (1999) Ecological Assembly Rules - Perspectives, advances, retreats. Cambridge:

697   Cambridge University Press.

698   Vaidya G, Lohman DJ, Meier R (2011) Sequence Matrix: concatenation software for the fast assembly of multi-

699   gene datasets with character set and codon information. Cladistics 27:171–180

700   Visser ME (2008) Keeping up with a warming world: assessing the rate of adaptation to climate change. Proc R

701   Soc Lond B 275: 649–659

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704 **Caption to Tables and Figures**

705 Table 1. Multiple linear regressions on altitude vs bioclimatic variables to present and future.

	Stimated Std.	Error	t value	P
	Present/Future	Present/Future	Present/Future	Present/Future
(Intercept)	3821.527/4566.084	85.25597/82.31261	44.82/55.47	<0.001
Annual Mean Temperature	-152.191/-168.309	2.35075/2.33988	-64.74/-71.93	<0.001
Temperature Annual Range	-16.7108/-7.51973	0.90175/0.72161	-18.53/-10.42	<0.001
Precipitation of Wettest Month	2.52711/2.32013	0.11515/0.09978	21.95/23.25	<0.001
Precipitation of Driest Month	-7.93307/-12.0148	0.28229/0.22446	-28.10/-53.53	<0.001
Precipitation of Warmest Quarter	-0.42978/-0.51133	0.03805/0.03226	-11.29/-15.85	<0.001
R-squared		0.60/0.59		<0.001
F-statistic		3122/3091		

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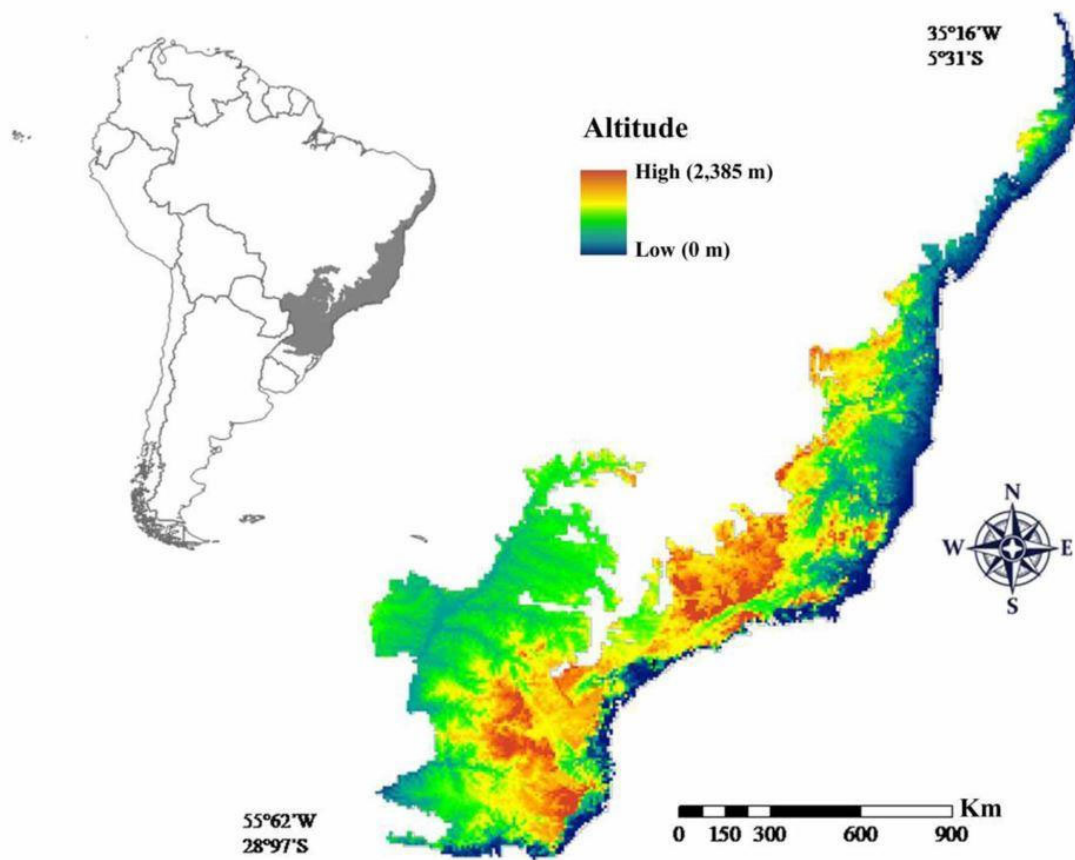
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709 **Fig. 1.** Map of the study area of Brazilian Atlantic Forest hotspot.

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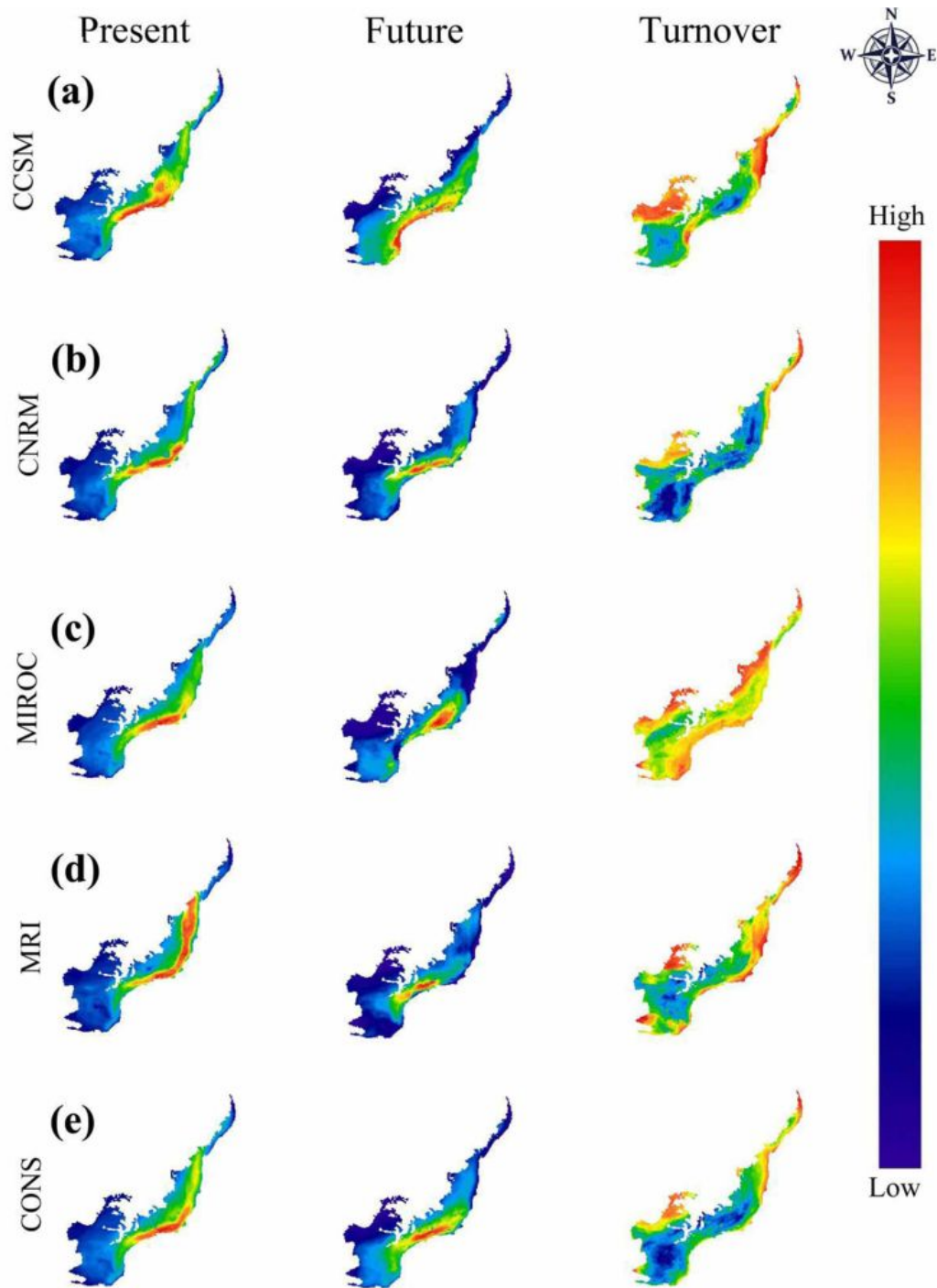
Fig. 2. Species richness and turnover derived from different Global Circulation Models (a) CCSM, CNRM (b), MIROC (c), MRI (d) and Richness Consensual Model-CONS (e) for amphibian species in the present time and for 2080.
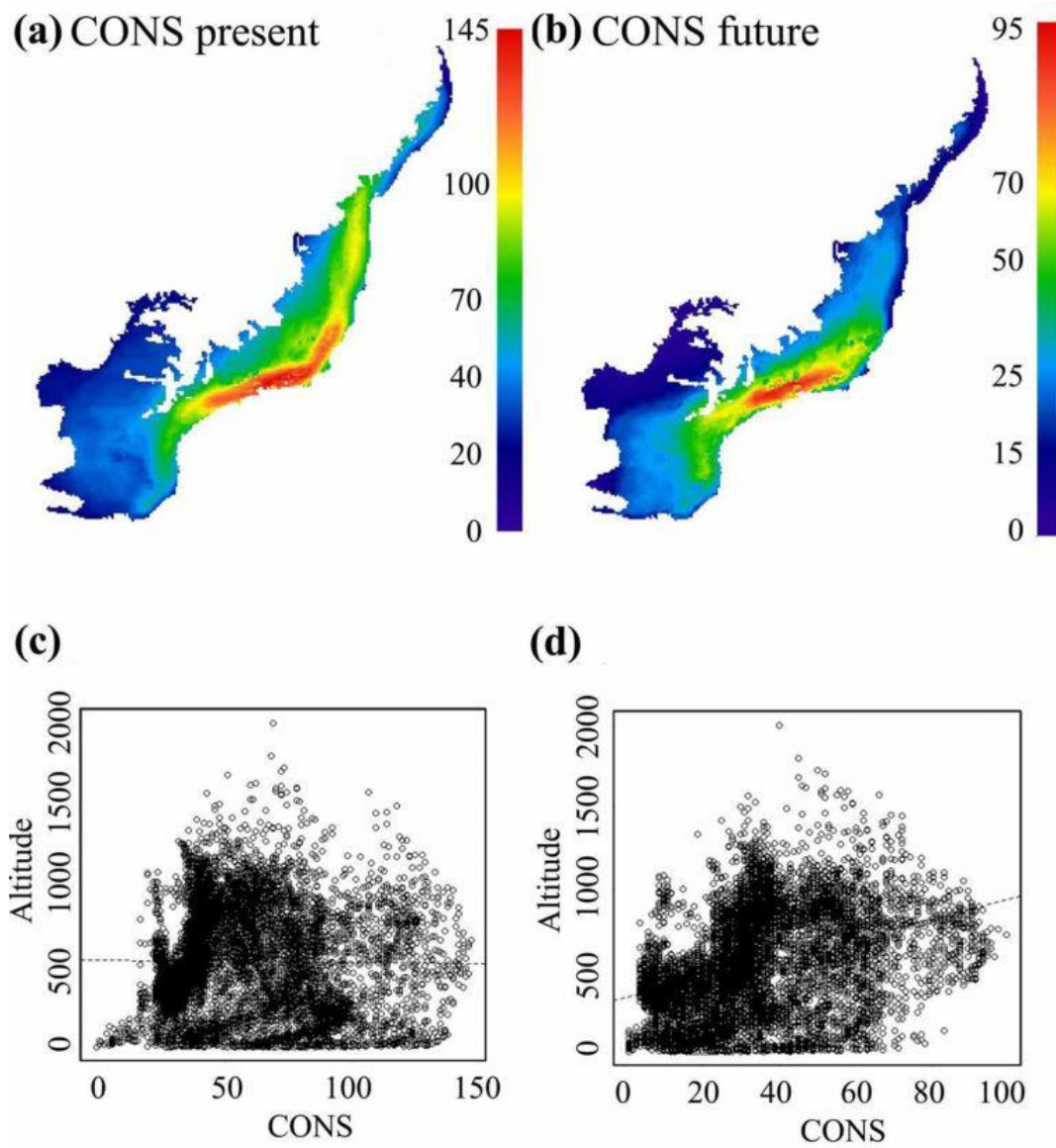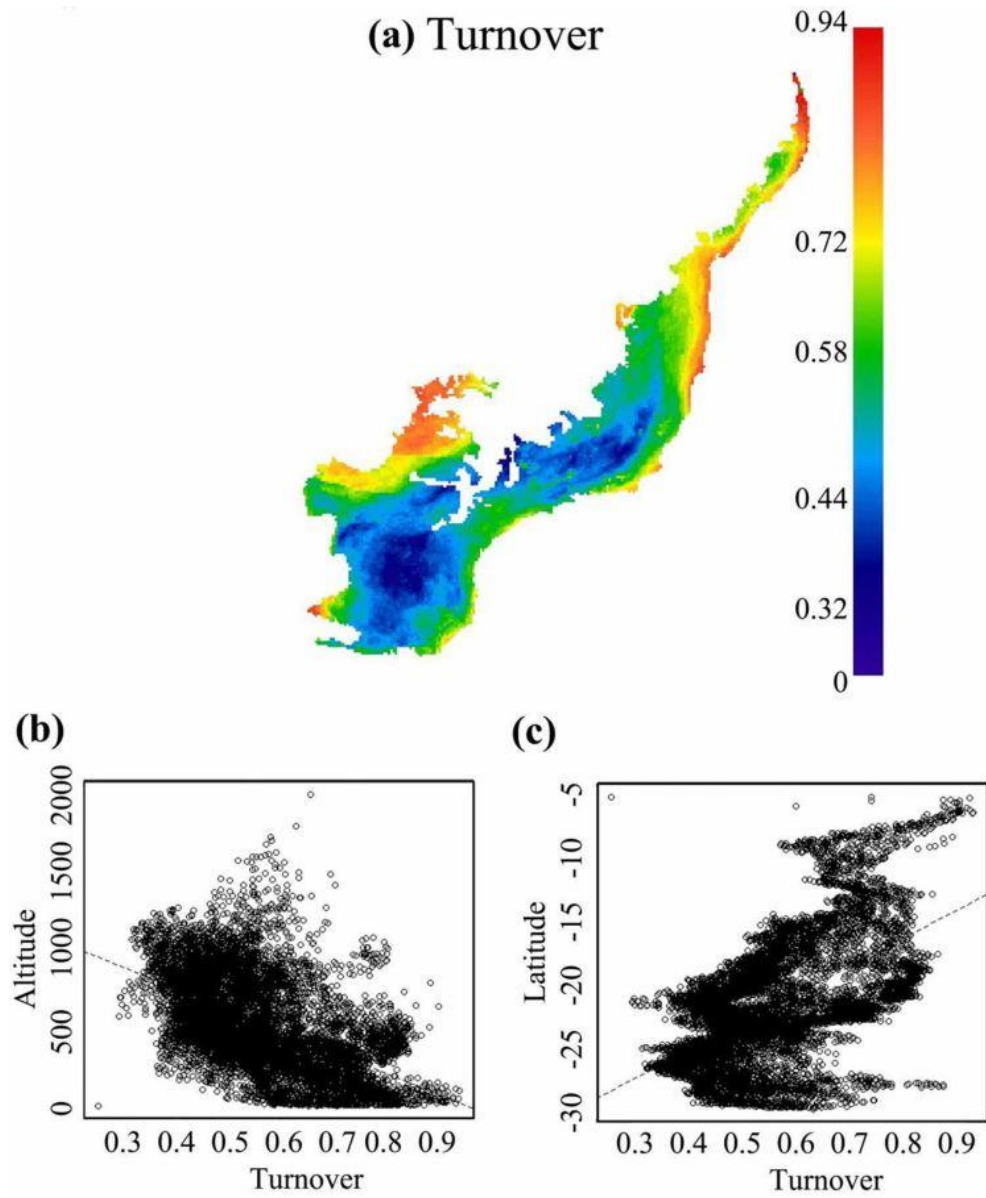
Fig. 3. Species richness derived from consensus model map for present time (a) and for 2080 (b). Relation between amphibian species richness consensual model (CONS) and altitude (in meters) for present time (c) and for 2080 (d).

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Fig. 4. Turnover derived from consensus model map (a). Relation between turnover consensus model with

altitude (in meters) (b), and latitude (c) for amphibian species.

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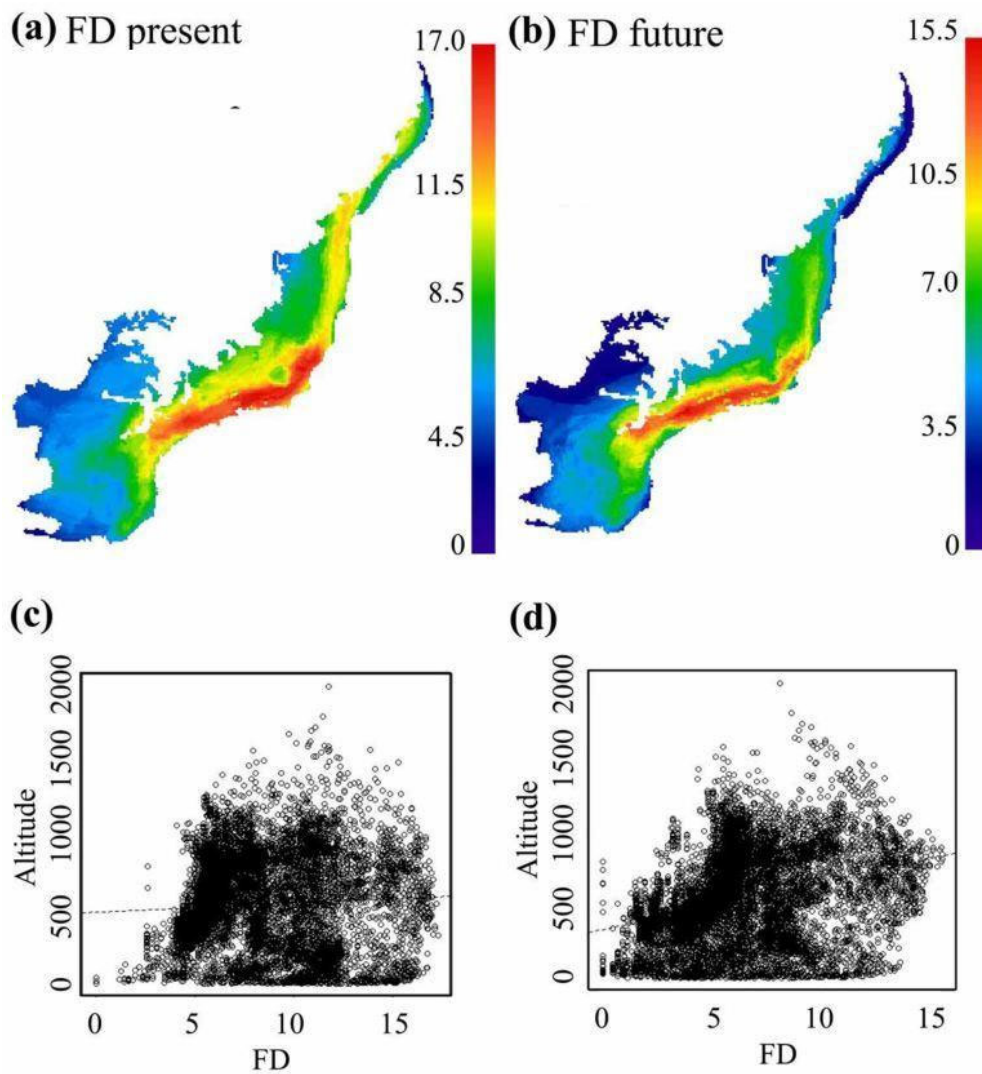
Fig. 5. Spatial distribution of Functional diversity (FD) derived from amphibian species richness consensus

model map for present time (a) and for 2080 (b). Relation between Functional diversity (FD) consensus model

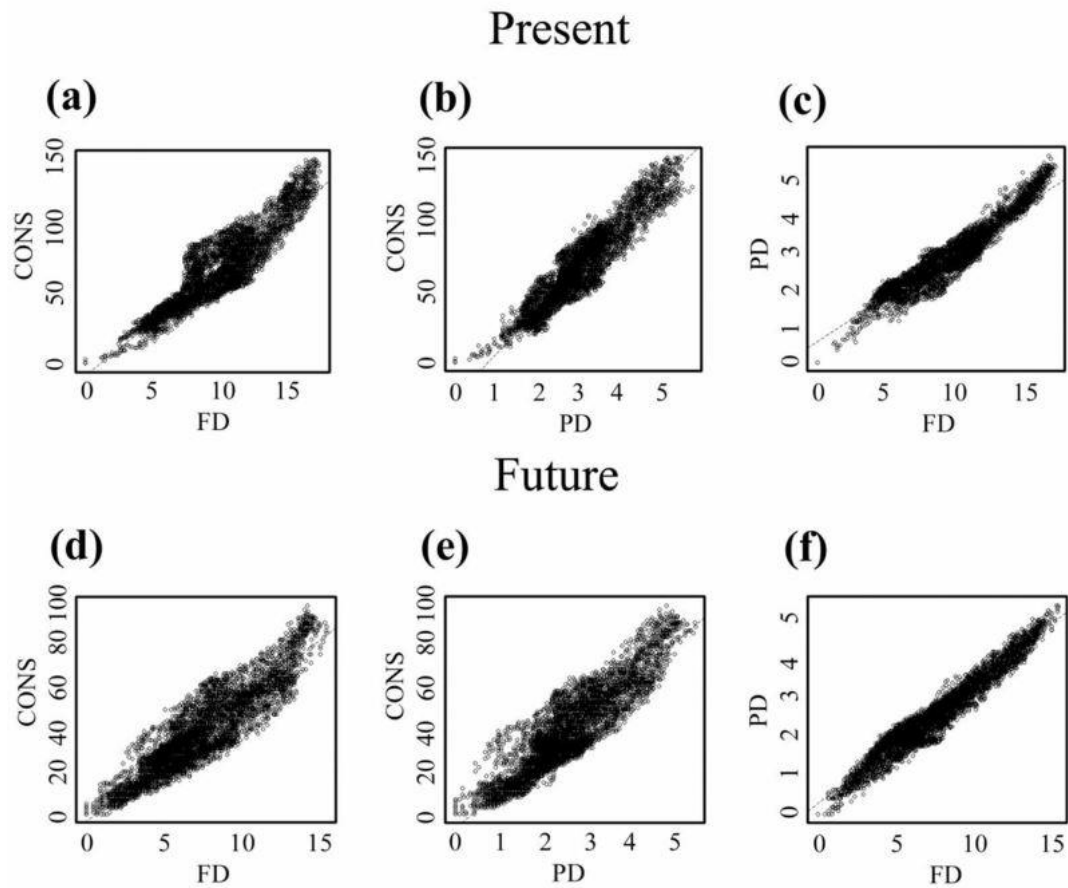and altitude (in meters) for present time (c) and for 2080 (d).
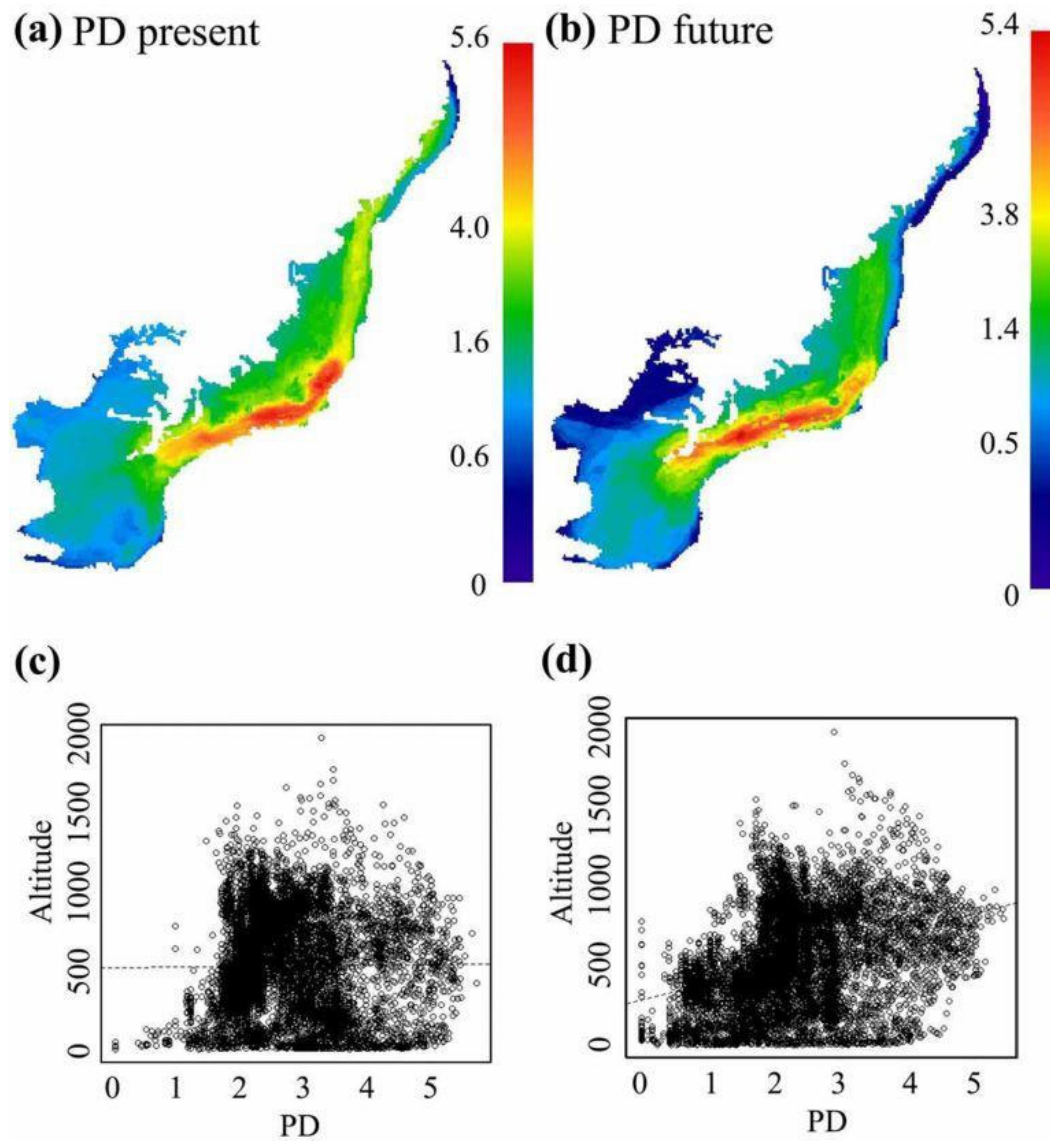
Fig. 6. Spatial distribution of Phylogenetic diversity (PD) derived from amphibian species richness consensus model map for present time (a) and for 2080 (b). Relation between Phylogenetic diversity (PD) consensus model and altitude (in meters) for present time (c) and for 2080 (d).
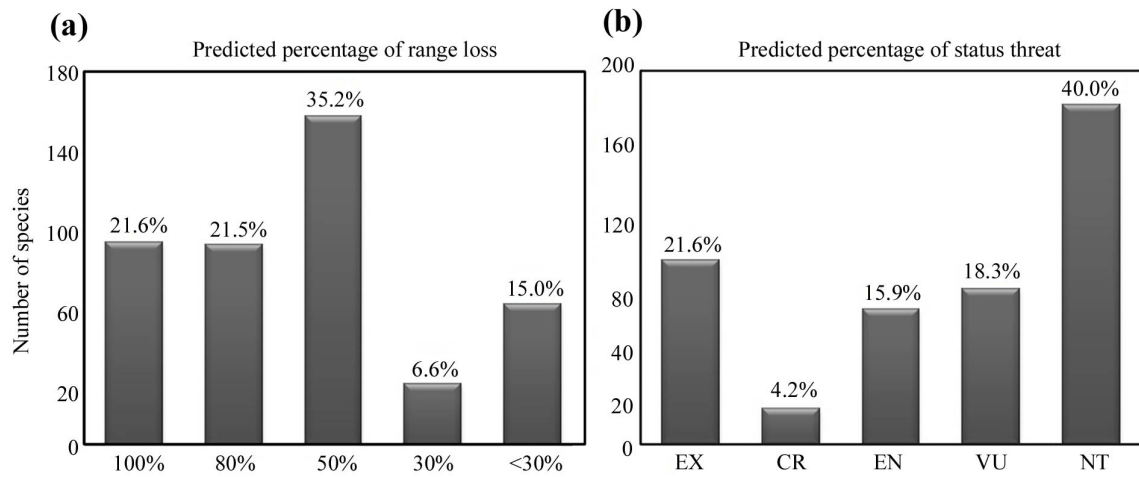
Present

Future

Fig. 7. Relationships between species richness consensual model (CONS), Functional diversity (FD),

Phylogenetic diversity (PD) of amphibians in the Brazilian Atlantic Forest. Present time: CONS vs FD (a),

CONS vs PD (b) and FD vs. PD (c); Future time: CONS vs FD (d), CONS vs PD (e) and FD vs PD (f).

Fig. 8. Status of threat projection to 2080 in the face of climate change for amphibians of Atlantic Forest hotspot. In the top of bars is the percentage of species number. (a) percentage of lost species range; (b) status of species: Extinct (EX) 0 km^2, Critically Endangered (CR) <100 km^2, Endangered (EN) <5,000 km^2, Vulnerable (VU) < 20,000 km^2, and Nonthreatened (NT) > 20,000 km^2.
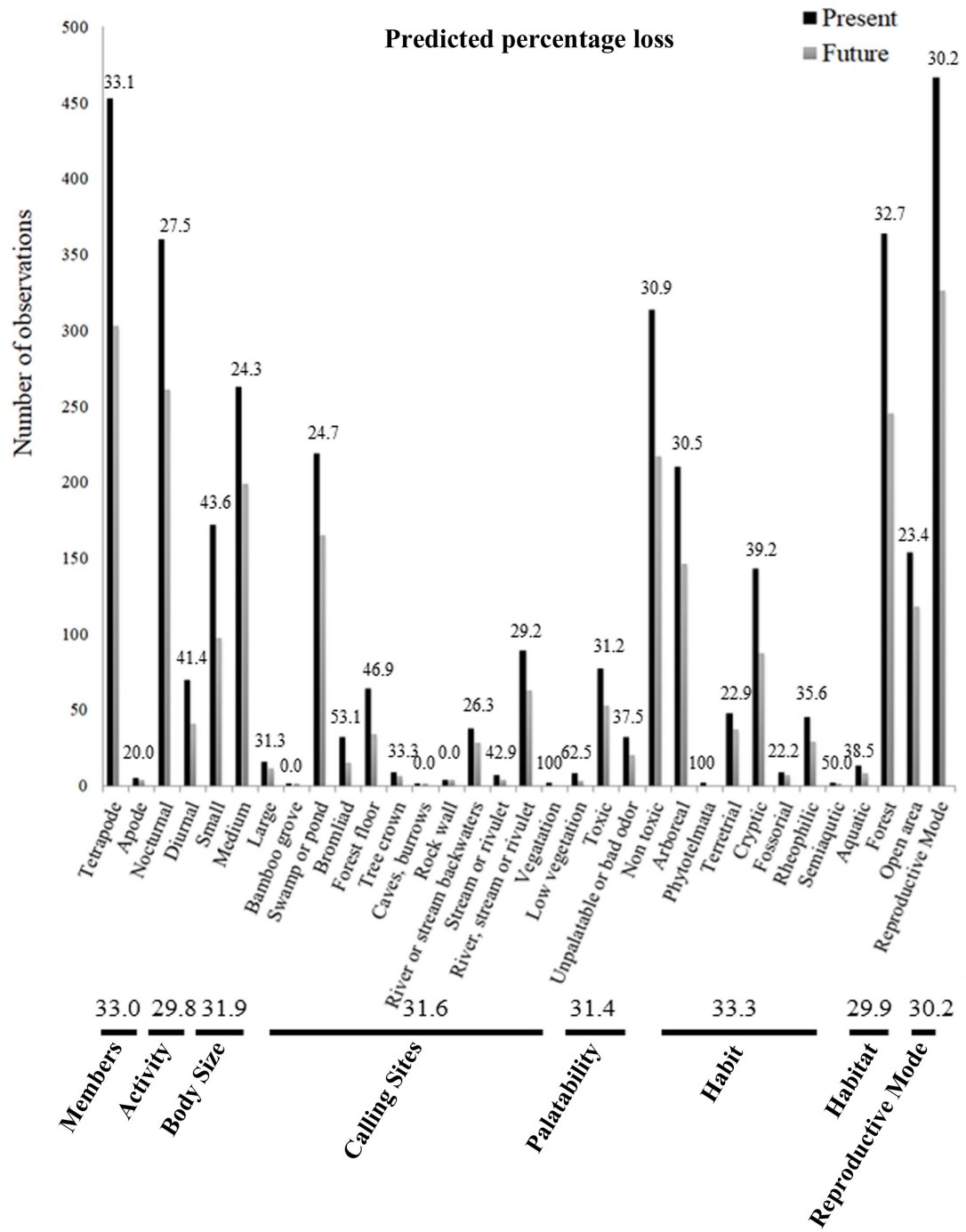
Fig. 9. Predicted percentage loss of functional traits and subtraits to 2080 in the face of climate change for amphibians of Atlantic Forest hotspot.