Searching for Networks: Ecological Connectivity for Amphibians Under Climate Change

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2 **change**

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34   **Abstract**

35   Ecological connectivity depends on key elements within the landscape, which can

36   support ecological fluxes, species richness and long-term viability of a biological

37   community. Landscape planning requires clear aims and quantitative approaches to

38   identify which key elements can reinforce the spatial coherence of protected areas

39   design. We aim to explore the probability of the ecological connectivity of forest

40   remnants and amphibian species distributions for current and future climate scenarios

41   across the Central Corridor of the Brazilian Atlantic Forest. Integrating amphibian

42   conservation, climate change and ecological corridors, we design a landscape ranking

43   based on graph and circuit theories. To identify the sensitivity of connected areas to

44   climate-dependent changes, we use the Model for Interdisciplinary Research on Climate

45   by means of simulations for 2080-2100, representing a moderated emission scenario

46   within an optimistic context. Our findings indicate that more than 70% of forest

47   connectivity loss by climate change may drastically reduce amphibian dispersal in this

48   region. We show that high amphibian turnover rates tend to be greater in the north-

49   eastern edges of the corridor across ensembles of forecasts. Our spatial analysis reveals

50   a general pattern of low-conductance areas in landscape surface, yet with some well-

51 connected patches suggesting potential ecological corridors. Atlantic Forest reserves are

52 expected to be less effective in a near future. For improved conservation outcomes, we

53 recommend some landscape paths with low resistance values across space and time. We

54 highlight the importance of maintaining forest remnants in the southern Bahia region by

55 drafting a blueprint for functional biodiversity corridors.

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59

60 **Introduction**

61

62 The implementation of Protected Areas (PAs) is among the most effective methods for

63 long-term biodiversity conservation plans (Rodrigues et al. 2004), working as a key

64 strategic tool in the development of environmental policies and efforts to sustain natural

65 ecosystem processes (Le Saout et al. 2013; Laurance et al. 2014). The selection of PAs

66 is often aimed to preserve either species of different taxonomic groups, conservation

67 target species (e.g., threatened and/or endemics), or combinations of different abiotic

68 conditions favourable to local ecosystems that will likely protect a wide range of

69 biodiversity (Lawler and White 2008). Given that habitat loss is the most important

70 threat to species survival (Haddad et al. 2015), the protected sites chosen by decision-

71 makers can determine which species will be able to survive in the area (Jenkins et al.

72 2015). The effectiveness of these selected sites in reaching conservation goals depends

73 on how many of the target species are represented in a given area (Dietz et al. 2015).

74 Although generally unseen, amphibians are the most abundant land vertebrates in humid

75 tropical forests (Stebbins and Cohen 1995). Globally, they include over 7,000 species

76   of frogs (Anura), 700 species of salamanders (Caudata) and 200 species of caecilians

77   (Gymnophiona) (Frost, 2019). However, amphibian conservation actions have

78   overlooked the biodiversity patterns in an effective conservation policy (Campos et al.

79   2017).

80   Among all vertebrates, amphibians are the group with the most species (24%)

81   whose geographical ranges are unprotected and not included in PAs (Nori et al. 2015).

82   More than 2,000 amphibian species are listed as threatened by extinction, which makes

83   them the most threatened vertebrate group worldwide (Stuart et al. 2004; IUCN 2018).

84   Many reductions and extinctions of amphibians have occurred due to the habitat loss

85   (Stuart et al. 2004; Becker et al. 2007; Ferreira et al. 2016), mainly in the Neotropical

86   region, which harbours a significant amount of the global amphibian diversity (Young

87   et al. 2004; Silvano and Segalla 2005; Becker et al. 2007). Amphibian conservation in

88   fragmented landscapes is directly related to the establishment of protected areas and

89   requires special management tools such as habitat restoration and management of forest

90   patches, ensuring habitat quality and, hopefully, the permanence of the species (Ochoa-

91   Ochoa et al. 2009; Lourenço-de-Moraes et al. 2018). Therefore, compiling data about

92   species distribution ranges is key to planning conservation actions (Verdade et al. 2012;

93   Morais et al. 2013; Campos et al. 2017).

94   Conservation strategies aimed at protecting threatened amphibians were

95   proposed by previous studies that highlighted parts of the Brazilian Atlantic Forest as

96   high priority areas (e.g., Loyola et al. 2008; Campos et al. 2013; Lemes and Loyola

97   2013; Dias et al. 2014). In addition, some taxonomic groups of amphibians from small

98   areas within the Atlantic Forest were identified as potential surrogates of biodiversity in

99   Brazil (Campos et al. 2014). Species with access to mountainous regions may migrate to

100   higher altitude areas with lower temperatures (Colwell et al. 2008), which in the case of

101 the Atlantic Forest, should retain greater humidity due to better-preserved forest cover

102 (Ribeiro et al. 2009). However, the survival of threatened amphibians in fragmented

103 tropical landscapes is dependent on the integrity and persistence of their PAs(Urbina-

104 Cardona 2008; Ochoa-Ochoa et al. 2009; Lourenço-de-Moraes et al. 2019).

105   The economic growth policy in Brazil is widely based on the expansion of

106 agricultural frontiers (Ribeiro et al. 2009), directly affecting the availability and the

107 distribution of forest remnants in scattered private lands, which are gradually becoming

108 crop and pasture production areas (Tabarelli et al. 2004). Forest isolation can affect

109 many species' distributions by habitat loss, leading to long-term changes in the structure

110 of the remaining fragments (Metzger 2009; Lourenço-de-Moraes et al. 2018). This

111 factor means that the use of ecological connectivity metrics can be good indicators for

112 measuring the isolation of PAs and their ecosystem functions (Gurrutxaga et al. 2011).

113 Assessing ecological connectivity among PAs is becoming a relevant subject of

114 growing international effort in relation to nature conservation policies (Bennett and

115 Mulongoy 2006; Worboys et al. 2006). By using connectivity in planning, managers

116 attempt to avoid functional isolation of PAs (Carroll et al. 2004; Liang et al. 2018) and

117 mitigate the effects of climate change on the population structure of endemic species by

118 allowing for range shifts (Bennett and Mulongoy 2006; Triviño et al. 2018). Thus, an

119 understanding of future climate conditions is essential for predicting the effects of

120 habitat isolation and species range shifts. In an attempt to understand these effects,

121 modelling species responses to different climatic scenarios of environmental conditions

122 has proven to be an effective tool (Carnaval and Moritz 2008; Diniz-Filho et al. 2009;

123 Austin and Van Niel 2011; Araújo and Peterson 2012). Researchers are combining

124 environmental spatial data with ecological and evolutionary processes to predict how

125 species will shift their ranges in the future (Elith et al. 2010; Kearney et al. 2010;

126 Martensen et al. 2017; Triviño et al. 2018; Lourenço-de-Moraes et al. 2019). Ecological

127 niche models (ENMs), also referred to as species distribution models (SDMs) (Peterson

128 et al. 2011; Rangel and Loyola 2012), have been increasingly used to estimate the

129 spatial ranges of species for future scenarios of climate change (Peterson et al. 2011).

130 These predictions may provide useful contributions to decision-making regarding

131 biodiversity conservation (Loyola et al. 2014).

132   Ecological implications of species tolerances to climate change are increasing

133 and contributing to a better understanding of how spatiotemporal connectivity

134 information can be incorporated into dispersal patterns (Bled et al. 2013). Climatic

135 change may alter species distributions (Pearson and Dawson 2003; Raxworthy et al.

136 2008), as well as significant species turnovers (Peterson et al. 2012). In this context,

137 ecological connectivity of forest landscapes is of paramount importance to ensure the

138 flow of species among potential climate refuges (Pearson and Dawson 2005).

139 Considering that climate change can aggravate environmental stresses from habitat loss

140 and fragmentation, there is high interest in maintaining ecological connectivity in

141 changing climates (Hamilton et al. 2016). However, only a few studies considered the

142 potential impact of climate change on the fragmentation of populations (Duan et al.

143 2016).

144   Ecological connectivity strategies depend not only on the existence of structural

145 connections between habitat patches but also on habitat suitability, stepping stones,

146 matrix permeability and the target organisms' responses to these elements (Tischendorf

147 and Fahrig 2000; Baum et al. 2004). Complex agroforestry systems are often used as

148 suitable habitats for different species across fragmented landscapes, also improving

149 dispersal pathways and connecting local species assemblages (Faria et al. 2007).

150 Advances in conservation biogeography have addressed many interactions between

151   habitat suitability and species response, varying in complexity, realism and data

152   requirements (Franklin 2010). Graph and circuit theories are complementary methods

153   that have been used to provide efficient approaches for identifying biodiversity

154   corridors (McRae et al. 2008; Spear et al. 2010). While circuit theory models outline

155   high-conductance areas between patches (McRae et al. 2008), graph-based models

156   determine the optimal least-cost routes pairwise landscape distances (Urban and Keitt

157   2001). However, efficient ecological corridors must facilitate dispersal movements and

158   consider species life-history requirements (Rosenberg et al. 1997). In this context,

159   amphibians have been cited as highly appropriate species for examining landscape

160   effects on community structure, due to their relatively limited mobility, sensitivity to

161   dispersal barriers and strong microhabitat associations (Austin et al. 2002; Spear et al.

162   2005; Lee-Yaw et al. 2009).

163   To answer where the amphibian species could disperse in the face of climate

164   change, we assess how changing climate might affect the protected network

165   effectiveness for amphibian distributions. Here, we explore the probability of the

166   ecological connectivity of forest remnants and amphibian species for current and future

167   climate scenarios. Specifically, we aim at modelling the ecological connectivity to

168   represent forest remnants that most contribute to upholding amphibian connectivity in

169   the Central Corridor of the Brazilian Atlantic Forest, estimating the species turnover

170   between current and future amphibian species distributions. We evaluate if the PAs

171   network of this corridor safeguards amphibian species that occur in this region, testing

172   if this network can work as an effective biodiversity corridor for amphibians. Then, we

173   show the relationship between environmental variables and amphibian species

174   distributions across the protected network. We highlight the importance of maintaining

175   forest remnants in the main Atlantic Forest biodiversity corridor (i.e., the Central

176 Corridor), suggesting implications for amphibian conservation planning and providing

177 new approaches on ecological connectivity in different climatic conditions. These

178 results may be useful as a tool for designing conservation strategies that incorporate the

179 effects of climate change and habitat fragmentation in a landscape planning approach.

180

181 **Materials and Methods**

182

183 **Study area**

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185 The Atlantic Forest represents one of the five most important biodiversity hotspots on

186 Earth (Mittermeier et al. 2011). Originally, it covered around 1,500,000 km^2, of which

187 only about 12% (i.e., 194 524 km^2) still remains in Brazil, Paraguay and Argentina

188 (Ribeiro et al. 2009), corresponding to about 100,000 km^2 of Brazilian forest remnants

189 (Tabarelli et al. 2005). Despite having high rates of habitat loss (Teixeira et al. 2009),

190 which is one of the main factors driving amphibians to extinction (Stuart et al. 2004;

191 Becker et al. 2007), the Atlantic Forest is the leader biome in amphibian diversity in

192 Brazil (Haddad et al. 2013), accounting more than 50% of all Brazilian amphibian

193 species (Haddad et al. 2013).

194   We focused our study on the Central Corridor of the Brazilian Atlantic Forest,

195 which comprises about 8% of the total biome area (i.e., 7,913.42 km^2), covering 14% of

196 forest remnants (SOS Mata Atlântica and INPE 2015). Here, we used the term Brazilian

197 Atlantic Forest to refer to the forest remnants map provided by SOS Mata Atlântica and

198 INPE (2015).

199

200 **Protected networks**

201

We examined all the PAs covered by the Central Corridor of the Brazilian Atlantic

Forest, providing information on the political categories and the sizes of each PA, as

well as their associated amphibian species richness and local environmental data. We

separated the PAs into two categories according to the IUCN criteria (IUCN 2018):

strict protection (IUCN categories I–II) and sustainable use (IUCN categories III–VI),

identifying the relative differences in the allocation of protection by each category. We

used national, state and municipal PAs spatial data through the Brazilian Ministry of the

Environment database (MMA 2015).

We assessed the relationships between species richness and their environmental

predictors (i.e., altitude, temperature, precipitation, and forest cover) to evaluate the

effect of environmental variables on the representation of species within the PAs

categories. For this, we performed a permutational multivariate analysis of variance

(PERMANOVA) using 1,000 permutations based on a Euclidean distance matrix,

through the "adonis" function in the R package "vegan" (Oksanen et al. 2013; R Core

Team 2016).

Species distribution data

We obtained spatial data of amphibian species through four steps: Firstly, we built a

dataset with all the species distributed in the Atlantic Forest according to Haddad et al.

(2013). Secondly, we included the species occurrences records available through the

Global Biodiversity Information Facility (GBIF: http://www.gbif.org). Thirdly, we

added spatial data for the mapping of species using the IUCN Red List of Threatened

Species database (IUCN 2018). Finally, we selected and filtered out the species that

9

226 only occur in the forest remnants within the limits of distribution of the Central Corridor

227 of the Brazilian Atlantic Forest, excluding all urban and non-forested areas (SOS Mata

228 Atlântica and INPE 2015). Hence, we combined vector files based on expert knowledge

229 of the species' ranges and forest remnant polygons into an overall coverage for species

230 distribution modelling, through both sources of species presences (Fourcade 2016).

231   We used ArcGIS 10 software (ESRI 2011) to build presence/absence matrices

232 from the species distribution data by overlapping a grid system with cells of 0.1

233 latitude/longitude degrees, creating a matrix with 838 grid cells. A total of 146

234 amphibian species were spatially represented in this grid system after using the "Spatial

235 Join" tool available in ArcGIS. We only considered spatial occurrences by those species

236 in which the distribution data intersected at least one grid cell (i.e., ~ 10 km^2). We used

237 forest remnant data to meet the habitat patch requirements based on visual interpretation

238 at a scale of 1:50,000, delimiting more than 260,000 forest remnants with a minimum

239 mapping area of 0.3 km^2. Therefore, we considered a species present in a cell if its

240 spatial range intersected more than 0.3 km^2. To improve coarse species distribution

241 data, the "Count Overlapping Polygons" ArcGIS toolbox was used to obtain the species

242 richness at the spatial resolution assessed, removing all duplicate records from the

243 analyses (i.e., repeated records of a species at the same location).

244

245 **Climate models and environmental data**

246

247 Given that species occurrence patterns are determined at large-scales by responses of

248 organisms to different climatic conditions (reflecting the ecological niche; see Soberón

249 2007; Booth et al. 2014), we used ecological niche models (ENMs) to predict the

250 distribution area of amphibian species. We used the species occurrence matrix and the

251   layers of climatic variables, resulting in a suitability matrix, which we used to model

252   and map the potential distribution of each species evaluated (Loyola et al. 2014).

253   We used current and future climate data according to the Coupled Model

254   Intercomparison Project Phase 5 – CMIP5 (http://cmip-pcmdi.llnl.gov), from coupled

255   Atmosphere-Ocean Global Climate Models (AOGCMs) to develop the spatial range

256   models. These simulations show a high sensibility to detect potential impacts of land

257   use changes on climate in human-induced landscapes (Dirmeyer et al. 2010). We

258   implemented the Model for Interdisciplinary Research on Climate (MIROC5) by 2080

259   (mean of simulations for 2080-2100), which represents a moderated emission scenario

260   within an optimistic context (Representative Concentration Pathway – RCP 4.5; Taylor

261   et al. 2012). This moderate scenario (RCP4.5) incorporates historical emissions

262   pathways and land cover information to meet potential climate policies (Thomson et al.

263   2011). We based the model projections on seven independent climatic variables tested

264   by stepwise multiple regression analyses, using a confidence interval of 95%: 1) annual

265   mean temperature, 2) temperature seasonality, 3) mean temperature of the warmest and

266   4) coldest quarters, 5) annual precipitation, and 6) precipitation of the driest and 7)

267   wettest quarters. We obtained these climatic data through the EcoClimate database

268   (Lima-Ribeiro et al. 2015) and downscaled them from 0.5 to 0.1 latitude/longitude

269   degrees for fitting our spatial scale. We also used altitude as an environmental filter to

270   predict the species richness from the dataset available at WorldClim Global Climate

271   Data (Hijmans et al. 2005). Given that temperature and humidity are the main climate

272   components that directly affect the biology of amphibians (Carey and Alexander 2003),

273   we compared these variables along altitudinal gradients to evaluate which

274   environmental features are the best predictors of amphibian richness.

275   We employed the maximum entropy method implemented in the MaxEnt

276   software (Phillips et al. 2006) to develop the potential distribution map for the forest

277   remnants associated with all the climatic variables adopted in the future predictions by

278   2080 (i.e., mean of simulations for 2080-2100). We randomly partitioned presence and

279   pseudo-absence data for each species into 75% of calibration (i.e., training) and 25% of

280   evaluation (i.e., tests), repeating this process ten times by cross-validation to avoid over-

281   fitting biases in the least-suitable environmental conditions. We converted the

282   continuous predictions of suitability into a binary vector of 1/0, finding the threshold

283   that maximizes sensitivity and specificity values in the receiver-operating characteristic

284   curves (Phillips et al. 2017) to build each ecological niche model. These curves are

285   generated by plotting values of the relative frequency of true positive records predicted

286   by a given model against the values of the relative frequency of pseudo-absence records,

287   generating the Area Under the Curve (AUC). For this purpose, one-third of the

288   occurrence records are set aside from modelling as test points (Phillips et al. 2006).

289   Values of AUC range from 0.5 (i.e., random) for models with no predictive ability to

290   1.0 for models giving perfect predictions. According to the Swets (1988) classification,

291   AUC values above 0.9 describe "very good", 0.8 "good", and 0.7 "useful"

292   discrimination abilities.

293   The main reason behind our choice of the MaxEnt modelling approach was to

294   look for a straightforward combination of environmental predictors that best explains

295   the presence-only species distribution across forest remnants. Using presence-only data,

296   MaxEnt is considered one of the most efficient methods for habitat suitability modelling

297   in terms of predictive performance (Elith and Graham 2009; Phillips et al. 2017; Duflot

298   et al. 2018). This predictive modelling approach has a high analytical power to combine

299   continuous and categorical environmental variables (Phillips et al. 2006), accounting for

300   potential interactions among them (Phillips and Dudik 2008). MaxEnt also has been

301   considered as less sensitive to sample sizes and layer resolutions when compared with

302   other habitat suitability models (Merow and Silander 2014; Wisz et al. 2008). In

303   addition, this multi-attribute approach works in free, user-friendly software that

304   provides input and output files totally compatible with geographic information system

305   tools (Phillips et al. 2006).

306   We assessed the potential current and future distributions of the forest cover

307   according to the current vegetation remnants map of the Brazilian Atlantic Forest (SOS

308   Mata Atlântica and INPE 2015), of which we excluded all the areas where there are

309   currently agriculture, urban zones or settlements, only representing forest remnants

310   without overlaps on the land use/cover changes.

311

312   **Species turnover**

313

314   We also applied the maximum entropy method implemented in the MaxEnt software

315   (Phillips et al. 2006), to determine the species geographic distributions patterns,

316   following the same climatic variables adopted in the modelling process for the forest

317   remnants assessed. However, in this case, we employed the modelling strategy at the

318   community level of "predict first, assemble later" (Overton et al. 2002), where the

319   ranges of individual species are modelled one at a time as a function of environmental

320   predictors and then overlapped for obtaining the species richness. We calculated the

321   species turnover between current and future amphibian species distributions according

322   to the equation proposed by Thuiller et al. (2005) (1):

323

324     $$Species\ Turnover = 100*((G+L)/(S+G)) \quad (1)$$

325

326 where "*G*" refers to the number of species gained, "*L*" the number of species lost and

327 "*S*" the contemporary species richness found in the forest remnants assessed. We

328 obtained the final maps of species richness for the current and future times, as well as

329 the species turnover rates through the average of values projected by the MaxEnt model

330 for each grid cell assessed (i.e., 0.1 latitude/longitude degrees of spatial resolution).

331

332 **Probability of connectivity**

333

334 We assessed the forest remnants through the probability of connectivity (PC) index

335 (Saura and Rubio 2010), calculated for the patches of the Central Corridor of the

336 Brazilian Atlantic Forest under two environmental scenarios (i.e., current and future),

337 using Conefor 2.6 software (Saura and Torné 2009). The PC is a graph-based habitat

338 availability metric that quantifies functional connectivity (Saura and Rubio 2010). It is

339 defined as the probability that two points randomly placed within the landscape fall into

340 habitat areas that are reachable from each other (interconnected) given a set of "n"

341 habitat patches and the links (direct connections) among them (Saura and Pascual-

342 Hortal 2007) (2).

343

344 $$PC = (\sum_{i=0}^{n} \sum_{i=0}^{n} a_1 \ x \ a_j \ x \ p_{ij}^*)/A_{L^2} \ = \ PCnum/A_{L^2} \quad (2)$$

345

346 where *ai* and *aj* are the attributes of patches *i* and *j* (i.e., ID and area). AL is the

347 maximum landscape attribute, which corresponds to the total landscape area (i.e., area

348 of the study region, comprising both habitat and non-habitat patches). The product

349 probability of a path is the product of all the values of the probability of direct dispersal

350 (*Pij*) for all the links in that path. Thus, *Pij* is the maximum product probability of all of

351 the possible paths between patches *i* and *j*, including direct dispersal between the two

352 patches.

353 　　We performed a prioritization ranking of the landscape elements (i.e., patches)

354 by their contribution to overall habitat availability and connectivity from the percentage

355 of the variation in PC (dPC_k), achieved by the removal of each patch from the overall

356 landscape (see Saura and Pascual-Hortal 2007; Saura and Rubio 2010). The dPC_k is a

357 relative measure of the increase in the PC value that resulted from the improvement in

358 the strength of that link after the implementation of the defragmentation measures

359 (Saura and Rubio 2010) (3).

360

361 $$dPC_k = 100 \; x \; (PC - PC_{remove.k})/PC = 100 \; x \; (dPC_k/PC) \quad (3)$$

362

363 where $PC_{remove.k}$ is the index value after removal of the landscape element (i.e., after a

364 certain habitat patch loss). This measure corresponds to the "link change" analysis mode

365 implemented in the Conefor 2.6 software (Saura and Torné 2009). For all the

366 connectivity analyses, we used a mean dispersal distance for amphibians according to

367 the review conducted by Smith and Green (2005), where an estimative average distance

368 of 400 m for amphibians, in general, was proposed. Whereas some amphibians can

369 disperse over distances greater than 400 m (Smith and Green 2005), we also assessed

370 scenarios with a greater potential for dispersal, using distances of 600 and 800 m. To

371 assess the ecological connectivity results for the future scenario, we considered only the

372 areas with an assessed likelihood greater than 50%, considering the potential

373 distribution areas with a minimum favourable condition for the forest persistence under

374 the climate change predictions used.

375

Landscape resistance models

377

378   We performed a landscape resistance approach to calculate the functional connectivity

379   between the forest remnants expressed as least-cost paths. To compare the sensitivity of

380   dPC models within the landscape, we used a resistance surface based on the landscape

381   heterogeneity with isolation-by-resistance (IBR), following the model proposed by

382   McRae (2006). We also assessed null models through isolation by Euclidean distance

383   (IBD), and isolation by Euclidean 3D distance with elevation data (IB3D), both of which

384   did not consider the influence of landscape heterogeneity. IBD and IB3D represent

385   landscape-free models and consider a maximum conductance for different land use types,

386   while IBR is strongly based on landscape heterogeneity. We estimated the resistance

387   values on the potential amphibian dispersal across the land use types within the landscape

388   matrix, according to a systematic mapping of land use at a 1:250,000 scale, provided by

389   the Brazilian Institute of Geography and Statistics (IBGE 2014).

390   We considered a conceptual framework for scoring the matrix permeability (cost

391   surface) associated with landscape features based on empirical data and expert opinion

392   (e.g., Ray et al. 2002; Joly et al. 2003; Semlitsch et al. 2008; Janin et al. 2009; Popescu

393   and Hunter 2011) to determine the resistance values assigned to each land use type.

394   Thus, we followed a rank-based criterion to reflect the relative order of landscape

395   conductance for amphibian ecological connectivity (e.g., Gibbs et al. 2005; Grant 2005;

396   Patrick 2006; Semlitsch et al. 2008; Popescu and Hunter 2011; Decout et al. 2012). We

397   used 27 detailed land use classes to generate our land cover input file, assuming

398   different resistance values to each land use type (Table S1). We estimated null

399   conductance values to each land use type for evaluating the extent to which the results

400   were influenced by the magnitude of these values, where a low conductance value

401   indicates a high resistance to dispersal. Considering the current landscape heterogeneity,

402   we examined the relationship between landscape resistance distances (IBD, IB3D and

403   IBR) and ecological connectivity under present and future climate conditions (dPC

404   present and dPC future). For this, we used Mantel tests to account for statistical

405   significance in pairwise comparisons. We performed the Mantel tests through 200,000

406   permutations in the PASSaGE 2 software (Rosenberg and Anderson 2011). We used

407   Circuitscape 2.2 software (McRae 2006) to generate the pairwise matrices of landscape

408   resistance and to produce the cumulative land conductance maps based on circuit

409   theory.

410

411   **Spatial prioritization framework**

412

413   Finally, we selected the most suitable habitats defining different representation targets

414   based on four methodological steps (i.e. forest modelling, species modelling, probability

415   of connectivity and landscape resistance models) (Fig. 1). Combining these targets into

416   a landscape modelling approach, we designed a spatial representation to select priority

417   areas for conservation, which might work as a suitability surface for ecological

418   connectivity in the Central Corridor of the Brazilian Atlantic Forest. Therefore, this

419   approach favoured the selection of habitats less disturbed by human-induced actions for

420   improved conservation outcomes.

421

422   **Results**

423

424   We showed that 110 PAs are covered by the Central Corridor of the Brazilian Atlantic

425   Forest (i.e. 70% of sustainable use and 30% of strict protection), which comprise to

426   6,607.98 km^2 and correspond to only 8% of the total corridor area (Fig. 2a).

427   Considering the 146 amphibian species distributed in the forest remnants assessed (Fig.

428   2b), only 20% are distributed within the current PAs network. According to the

429   PERMANOVA, when we compared species richness and PA categories with all the

430   environmental variables together, we found direct relations with precipitation,

431   temperature, evapotranspiration and forest cover (Table 1), where precipitation was the

432   variable most associated with the amphibian species richness in the Central Corridor of

433   the Brazilian Atlantic Forest. According to the stepwise multiple regression analyses,

434   there was no correlation among any of the climate variables ($R^2 = 0.26$; $F = 92.57$; $P =$

435   0.078). The potential distribution of the forest remnants for the future scenario showed

436   an average AUC value of 0.86, which indicated a good predictive ability by the dataset

437   provided (Fig. 3a). The climate change models predicted a reduction of 75% in the

438   probability of occurrence of the Atlantic Forest remnants in the central region of the

439   Central Corridor. The northern and southern edges of the Central Corridor, as well as

440   high altitude areas, showed the higher probability of forest occurrence. On the species

441   distribution models under climate change, we predicted a high amphibian turnover rate,

442   given that more than 50% of the grid cells had species turnover ratios greater than 0.7

443   (Fig. 3b). However, these expected changes in species composition tend to be greater on

444   the northern edge than the southern edge of the Central Corridor.

445   Considering a dispersal distance of 400 m, our analyses of connectivity showed

446   that the Central Corridor of the Brazilian Atlantic Forest does not guarantee good

447   connectivity among the fragments, with an average dPC value of 8.43. When we

448   assessed the dispersal distances of 600 and 800 m, the average dPC was the same than

449 that observed with a 400 m distance. However, our results showed higher connectivity

450 areas in the northeastern region of the Central Corridor of the Brazilian Atlantic Forest,

451 mainly in the southern Bahia region (Fig. 4). We found that 95% of the values pointed

452 out by the connectivity index were directed to the sustainable use areas, only of which

453 5% are classified as integral protection areas (Table S2)

454   For the current scenario, we only found 10 PAs with high connectivity (dPC >

455 60.0), although 71 had very low values (dPC < 1.0). This situation can be aggravated

456 considering the climate model results for the future (2080-2100), which showed a high

457 probability of forest remnants retraction in the evaluated region. This represents 74% of

458 connectivity loss in a total of 4,889.90 km^2 of Atlantic Forest areas (Fig. 4). According

459 to these future predictions, we estimated that 83 PAs would be without any ecological

460 connectivity by the years 2080-2100 (dPC < 0.0), while only six PAs will remain with

461 dPC higher than 1.0, which correspond to a plausible conservation attribute in terms of

462 interpatch connectivity and habitat suitability. RPPN Renascer, RPPN Refúgio do

463 Guigó I and II, and RPPN Boa União, in the Bahia state, and RPPN Mata da Serra, APA

464 Serra da Vargem Alegre, and Parque Estadual do Forno Grande, in the Espírito Santo

465 state represented the PAs with a better expected connectivity under climate change.

466   Circuit theory current flow maps predicted a high likelihood of connectivity in

467 the central portion of our study area (i.e., in southern Bahia) for the current scenario

468 (Fig. 5). The landscape surface was represented by a general pattern of low-conductance

469 areas (i.e., low potential for amphibian dispersal), yet with some well-connected areas

470 showing low resistance for species moving between patches. These well-connected

471 areas (i.e., with high-conductance) can be potential amphibian biodiversity corridors,

472 which would connect the Monte Pascoal, Pau Brasil and Serra das Lontras PAs, located

473 in the southern Bahia region. Landscape resistance models that incorporated absolute

474   dispersal barriers resulted in significant correlations when compared with those based

475   on landscape-free models (i.e., null resistances). The Mantel tests showed significantly

476   different relationships between dPC values (present and future) and resistance distances

477   (IBD, IB3D and IBR) (Table 2), indicating the sensitivity of the functional connectivity

478   models within the landscape.

479

480   **Discussion**

481

482   **Habitat suitability assessment**

483

484   Considering the effectiveness of habitat suitability models of our landscape planning,

485   we highlight the southern Bahia region and the Espírito Santo state with the best

486   ecological distances between forest remnants (i.e., high-conductance areas with low

487   resistance values). The use of resistance surfaces in landscape ecology incorporate

488   multiple pathways that rely on the habitat quality for identifying important landscape

489   elements connecting suitable environments for conservation (McRae et al. 2008; Zeller

490   et al. 2012). Interactions between habitat suitability and species dispersal movements

491   can be crucial for functional connectivity strategies in landscape change (Hodgson et al.

492   2009; Doerr et al. 2011). Therefore, given the landscape resistance surface and the

493   connectivity metrics used as an aid for our amphibian conservation approach, we

494   suggest some potential ecological corridors under current and future conditions.

495   Based on shifts in geographic ranges and climatically suitable habitats, our

496   results reveal that the areas with high turnover rates are not the same areas with high

497   occurrence probability of forest remnants under climate change. The selection of critical

498   habitats for amphibian conservation under climate change is important for making

499   effective management decisions (Guisan et al. 2013). Forecasting approaches in spatial

500   planning suggest that regions with high species turnover rates are expected to have more

501   restricted-range species than regions with low species turnover rates (Diniz-Filho et al.

502   2009). Areas with high turnover rates can be associated to areas with low species

503   richness under the current climate (Duan et al. 2016), which in the case of the Atlantic

504   Forest may be represented by higher altitude areas. Moreover, low turnover rates in high

505   altitude areas can strengthen mountainous regions as potential climatic refuges

506   (Carnaval et al. 2009; Randin et al. 2009; Araújo et al. 2011; Lourenço-de-Moraes et al.

507   2019).

508   The use of MaxEnt as a single modelling algorithm for ecological approaches

509   also has some concerns regarding data acquisition and analysis, which should include

510   the full environmental range of the species (Elith et al. 2011). One of the main

511   limitations of this presence-only modelling seems to be a biased approach for species–

512   habitat relationships, given the unknown sampling effort intensity (Elith et al. 2011).

513   Addressing possible sampling limitations by combining local field records with

514   environmental layers is a promising strategy to improve the relevancy of habitat

515   suitability models for effective landscape planning (Maréchaux et al. 2017). Possible

516   solutions to avoid this sample selection bias can be corrected by adding a mask as an

517   explanatory variable or by discarding some of the presence points in oversampled areas

518   (Phillips et al. 2009; Radosavljevic and Anderson 2014; Stevenson-Holt et al. 2014).

519   Another limitation of our habitat suitability models is that climate datasets needed for

520   this modelling approach are not always available, and some of them need to be

521   downscaled for fitting our spatial scale (see Lima-Ribeiro et al. 2015). Therefore, we

522   assume that our climatic projections capture only part of the climate variability changes

523   associated with the habitat suitability models. However, downscaling climate

524   projections is a widely used technique for exploring the regional and local-scale

525   responses to global climate change for simulating low-resolution climate models

526   (Hewitson and Crane 2006; Cabral et al. 2016). Given the on-going challenges to the

527   future development of climate downscaling, data scarcity and scale issues need to

528   diminish the overestimation of suitable habitats for future species distributions by

529   better-capturing landscape heterogeneity (Tabor and Williams 2010).

530

531   **Challenges and opportunities for the Central Corridor of the Brazilian Atlantic**

532   **Forest**

533

534   Our findings show that the proportion of forest fragments with good connectivity is very

535   low along the Central Corridor of the Brazilian Atlantic Forest, which consequently

536   may reduce the flow of species among the fragments and significantly restricts the

537   functional role of this ecological corridor. Using expert knowledge to distinguish

538   species records can be a practical way of improving conservation-relevant decisions

539   even with a paucity of biodiversity data (Akçakaya et al. 2018). We focus on an

540   approach for allowing decision-makers to make the best use of the available data at a

541   local scale, considering the extent to which such decisions might affect conservation

542   outcomes at broad scales. The complementary use of species range maps with

543   occurrence data is a promising route for advancing efforts to local-scale conservation

544   decisions, supporting our species distribution data (Maréchaux et al. 2017). Such

545   approaches for improving decision-making effectiveness are even more urgent in

546   species-rich regions, where conservation strategies should ensure the lack of

547   biodiversity data (Maréchaux et al. 2017; Lourenço-de-Moraes et al. 2019). In this

548   context, we suggest that the forest fragments located in the coastal parts of the southern

549   Bahia region and the Espírito Santo state deserve special attention in conservation plans

550   because they hold the highest proportion of ecological connectivity along the Central

551   Corridor of the Brazilian Atlantic Forest.

552   Our proposal of special attention to southern Bahia is reinforced due to their

553   resistance surface values within a landscape matrix composed by shaded cocoa

554   plantations (i.e., "cabrucas"), as indicated by Pardini et al. (2009). This agroforestry

555   system has allowed the conservation of large numbers of native plant species, besides

556   hosting typical mature forest fauna species (Pardini et al. 2009). Many amphibian

557   species use the bromeliads that are in the "cabrucas" system during their entire life cycle

558   and others only as diurnal shelter (Ferreira et al. 2016). Given their forest-like structure,

559   shaded cocoa plantations of the Forest remnants from southern Bahia perform a

560   fundamental role in maintaining connectivity between forest fragments (Sperber et al.

561   2004; Delabie et al. 2007; Faria and Baumgarten 2007). Our results, integrating graph-

562   based connectivity metrics into forecast models, indicate that this region has a high

563   probability of forest occurrence in a climate change scenario, which suggests

564   climatically suitable habitats and potential ecological corridors.

565   Forest remnants management is critical to ensure the persistence of species, but

566   dynamic threats such as land use change and climate change can directly reduce the

567   effectiveness of PAs planned under a static approach (Faleiro et al. 2013). Due to

568   developing technologies in remote sensing, there are several approaches to improve how

569   we assess and monitor forest remnants through a variety of spatial and temporal scales

570   (Tehrany et al. 2017). In this context, there is an urgent need to incorporate species

571   range shifts in spatial conservation plans to ensure their effectiveness in the future

572   (Hannah 2010). We recommend that the design of new conservation plans in the Central

573   Corridor of the Brazilian Atlantic Forest must attempt to re-establish ecological

574   connectivity between the remaining fragments and the higher altitude areas. This

575   recommendation may represent an alternative mechanism to mitigate potential impacts

576   related to climate change and land use change in the Atlantic Forest Hotspot.

577   Corroborating our findings, other amphibian studies in the Atlantic Forest have also

578   warned about the need to invest in PAs near high altitude areas (Lemes and Loyola

579   2013; Loyola et al. 2014; Lourenço-de-Moraes et al. 2019), mainly in the southern

580   Bahia region (Carnaval et al. 2009), which retain high humidity provided by well-

581   preserved forest cover. Climate threats to amphibian biodiversity have often been

582   related to their high humidity dependence (Hopkins 2007), where moisture conditions

583   are associated with microhabitats, rainfall regimes and terrestrial water balance, limiting

584   the species' dispersal abilities (Early and Sax 2011). Dispersal limitation is a critical

585   determinant of amphibian geographical ranges, assuming a general metapopulation

586   structure related to habitat patch isolation (Smith and Green 2005). Our predictions on

587   the environmental variables for amphibian species richness in the Atlantic Forest are

588   dependent on their limited dispersal patterns. Therefore, dispersal capability might

589   severely limit the ability of species to track suitable climatic conditions geographically

590   (Massot et al. 2008; Early and Sax 2011). The use of various environmental variables

591   has been demonstrated as an efficient strategy to reach outcomes closer to reality, being

592   one of the keys to understanding how communities can respond to climatic factors

593   (Araújo and New 2007; Marmion et al. 2009).

594

595   **Implications for conservation planning under climate change**

596

597   Our findings show that potential impacts of climatic changes should occur in almost the

598   entire Central Corridor of the Brazilian Atlantic Forest, which could affect the

599   ecological connectivity of the whole biome. We suggest that the PAs with the better-

600   expected connectivity under climate change need critical attention in future

601   conservation plans (e.g., RPPN Renascer, RPPN Refúgio do Guigó I and II, and RPPN

602   Boa União, in the Bahia state, and RPPN Mata da Serra, APA Serra da Vargem Alegre,

603   and Parque Estadual do Forno Grande, in the Espírito Santo state). In this context, these

604   mitigations can be useful to avoid potential extinction process expected for the

605   amphibians from the Central Corridor of the Brazilian Atlantic Forest PAs.

606   Amphibian species from Atlantic Forest PAs are more threatened with

607   extinction than in other Brazilian protected networks (Campos et al. 2016). This

608   phenomenon happens mainly because the Southeast Region of Brazil is the economic

609   core of the country, with highly fragmented forest remnants (Ribeiro et al. 2009), with a

610   high human population density, and the presence of mining and logging activities

611   (Lemes et al. 2014). Atlantic Forest reserves close to urban ecosystems are also failing

612   to protect amphibian species (Lourenço-de-Moraes et al. 2018). Our approach does not

613   specifically estimate a quantitative species extinction risk but shows evidence of a

614   potential regional extinction within limited dispersal models. We highlight that many

615   PAs will become less effective in future scenarios, which can dramatically affect the

616   diversity and distribution of the amphibian species that occur in the forest remnants

617   assessed.

618   Conserving biodiversity under climate change comes out as a challenge for

619   conservation scientists. For being a dynamic system, controlling all the climatic

620   variables and synergies related to environmental conditions and its consequences is a

621   huge task. If the rates of climate change overtake the response potential of biological

622   systems to ecological connectivity and its impacts on ecosystem functioning, effects on

623   community structure and species distributions can be irreversible. Therefore, enhanced

624 conservation efforts of forest management will play a critical role for mitigating effects

625 of environmental change. In some human-modified landscapes characterized by

626 secondary forest, environmental heterogeneity can be maintained and even increased,

627 thus contributing to the community structure (Tscharntke et al. 2012). A recent meta-

628 analysis showed that ecological restoration success can be higher for natural

629 regeneration than for active restoration in tropical forests (Crouzeilles et al. 2017). In

630 this context, our research highlights the importance of maintaining the mosaic of forest

631 remnants and the landscape heterogeneity in the Central Corridor of the Brazilian

632 Atlantic Forest, providing dynamic tools to prioritize conservation investment for

633 ecological connectivity assessments.

634   Practical strategies should be sensible for species adaptation, impact mitigation,

635 and must prioritize the protection and connectivity of heterogeneous landscapes to

636 improve conservation management (Richardson and Whittaker 2010). In the particular

637 case of the Atlantic Forest, the response of amphibians to anticipated declines depends

638 on local climatic conditions (Lourenço-de-Moraes et al. 2019). Regarding adaptation to

639 climate change, we show that species tend to use potential corridors in high altitude

640 areas with better-preserved forest cover. Our research highlights that integrating the

641 amphibian-climate refuges in the well-connected areas is essential for spatial decision-

642 making in the Atlantic Forest hotspot, which can reduce extinction risk and avoid

643 species loss. This work has advanced knowledge of the analytical methods that can be

644 used to incorporate landscape paths with low resistance into potentially connected areas

645 for amphibian conservation in the Central Corridor of the Brazilian Atlantic Forest. The

646 methodological approach proposed here is not only amphibian-specific but can also be

647 used in conservation plans for other taxonomic groups. This innovative approach has

648   sought to move forward the knowledge on ecological connectivity of endangered forest

649   remnants and supports conservation actions in the face of climate change.

650

659

660   **Appendix A. Supplementary files**

661

662   Supplementary files associated with this article can be found in the online version

663   (Tables S1 to S2).

664

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1148 **Tables**

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1150 **Table 1.** Results from the PERMANOVA on the species richness and PA categories by

1151 the variables altitude, temperature, precipitation and forest cover in the Central Corridor

1152 of the Brazilian Atlantic Forest.

Environmental Variables	df	F model	R^2	P value
Altitude	1	21.27	0.06	0.98
Temperature	1	43.70	0.14	0.00*
Precipitation	1	130.71	0.42	0.00*
Forest cover	1	27.88	0.09	0.02*
Residuals	105	–	0.29	–
Total	109	–	1.00	–

1153 *Significant values

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1171 **Table 2.** Statistical significance for Mantel test between dPC values (Present and Future)

1172 and resistance distances (IBD, IB3D and IBR) for calculating the landscape connectivity

1173 between forest remnants in the in the Central Corridor of the Brazilian Atlantic Forest.

1174 IBD: null model through isolation by Euclidean distance; IB3D: null model through

1175 isolation by Euclidean 3D distance with elevation data; IBR: resistance model through

1176 isolation-by-resistance between patches based on landscape heterogeneity.

Matrix	Mantel r	P-value
dPC Present-IBD	0.01091	0.00000
dPC Present-IB3D	0.01055	0.00000
dPC Present-IBR	0.00962	0.00000
dPC Future-IBD	0.00316	0.03253
dPC Future-IB3D	0.00295	0.04637
dPC Future-IBR	0.00310	0.03871

1177 All tested pairs for dPC-Present and dPC-Future are significant ($p > 0.05$).

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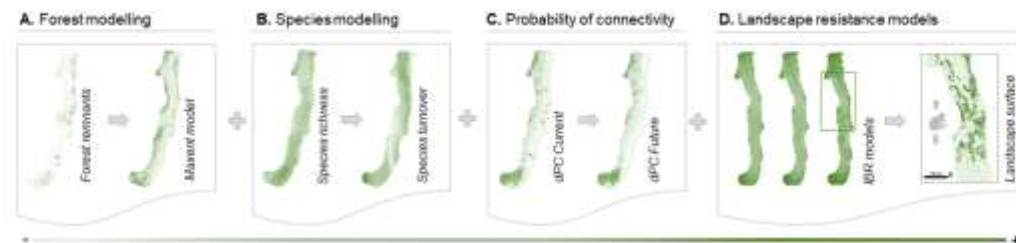
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1195 **Figures**

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1197 **Fig. 1.** Schematic representation of the methodological steps used in the landscape

1198 modelling approach for amphibian conservation in the Central Corridor of the Brazilian

1199 Atlantic Forest, Brazil. Forest modelling (A), Species modelling (B), Probability of

1200 connectivity (C) and Landscape resistance models (D).
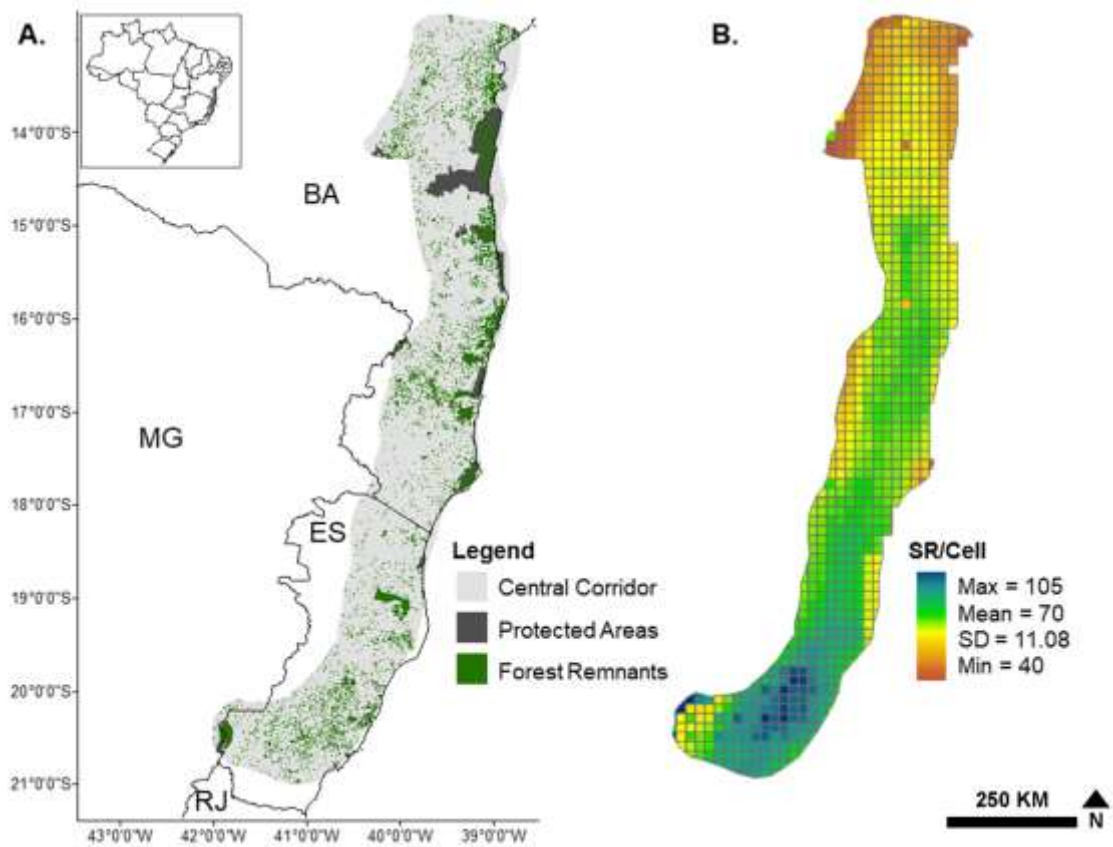
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1203 **Fig. 2.** Location of the Central Corridor of the Brazilian Atlantic Forest, in eastern
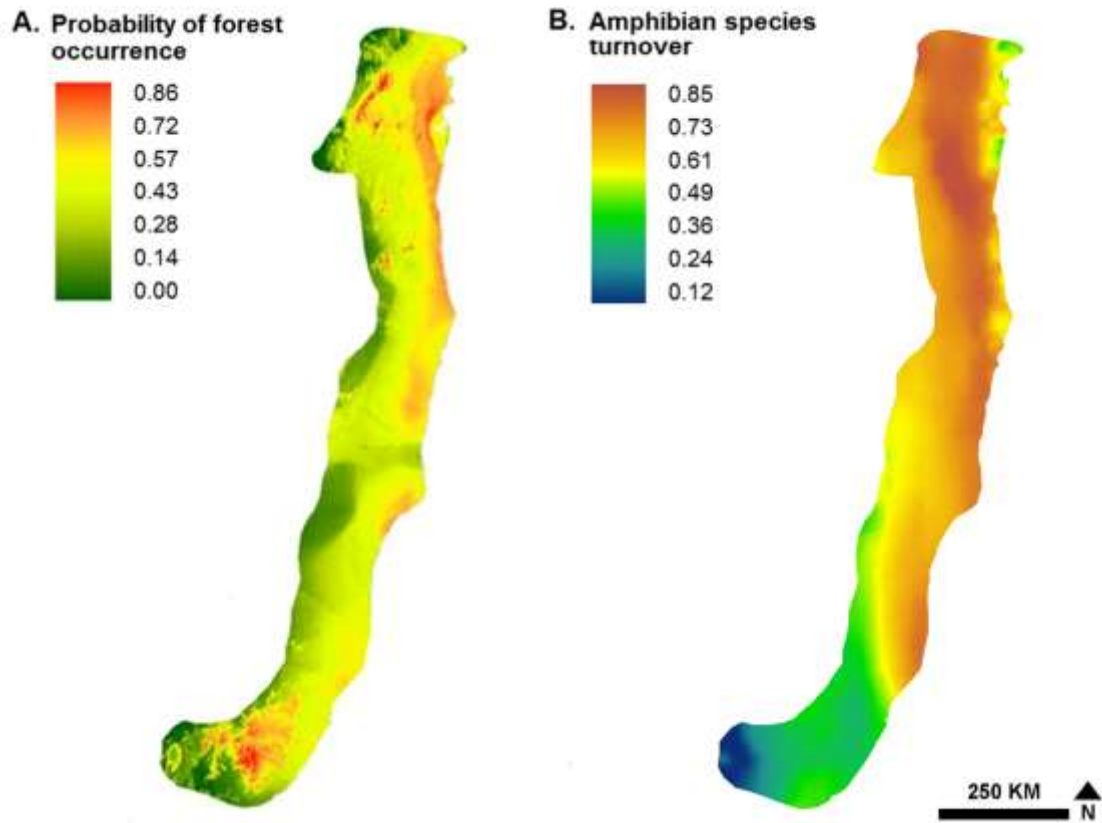
1204 Brazil, representing their Protected Areas and Forest Remnants. BA: Bahia state; MG:

1205 Minas Gerais state; ES: Espírito Santo state; RJ: Rio de Janeiro state (A). Species

1206 Richness per grid cell with summary statistic values such as Maximum, Mean, Standard

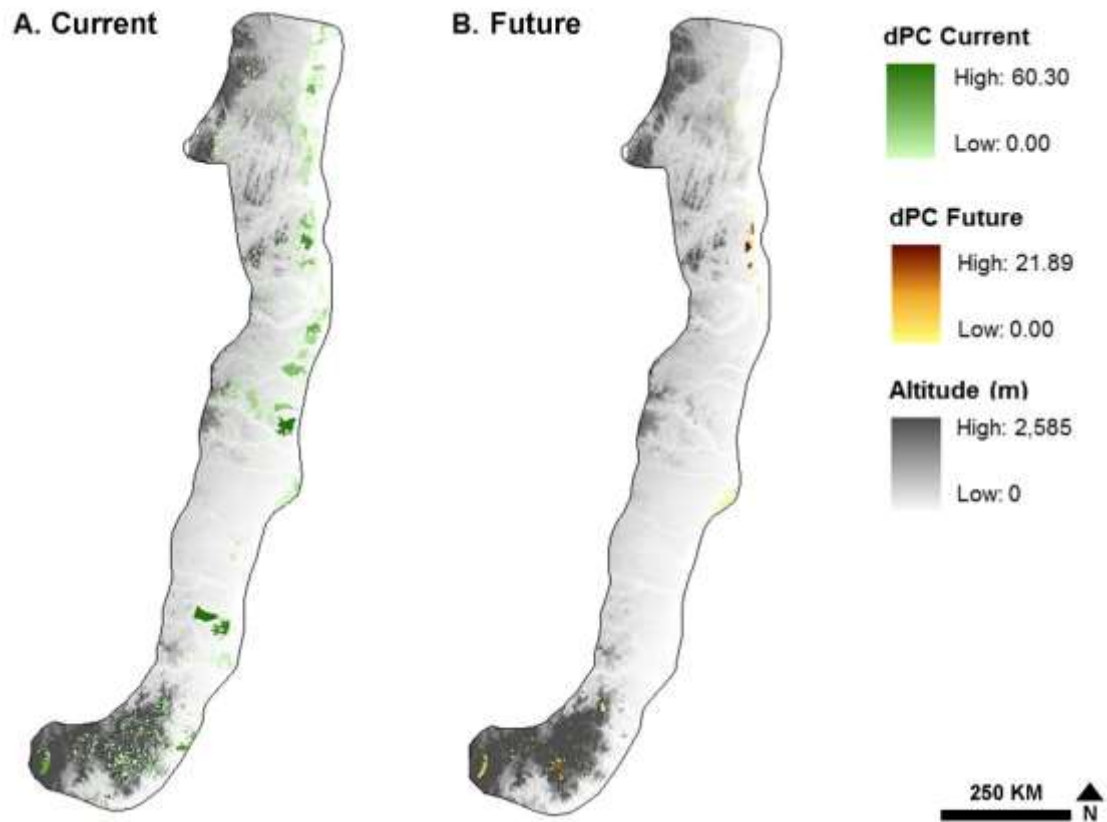1207 Deviation and Minimum (B).

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1210 **Fig. 3.** Probability of forest cover according to the MaxEnt model (A), and amphibian

1211 species turnover rate (B), under climate change in the Central Corridor of the Brazilian
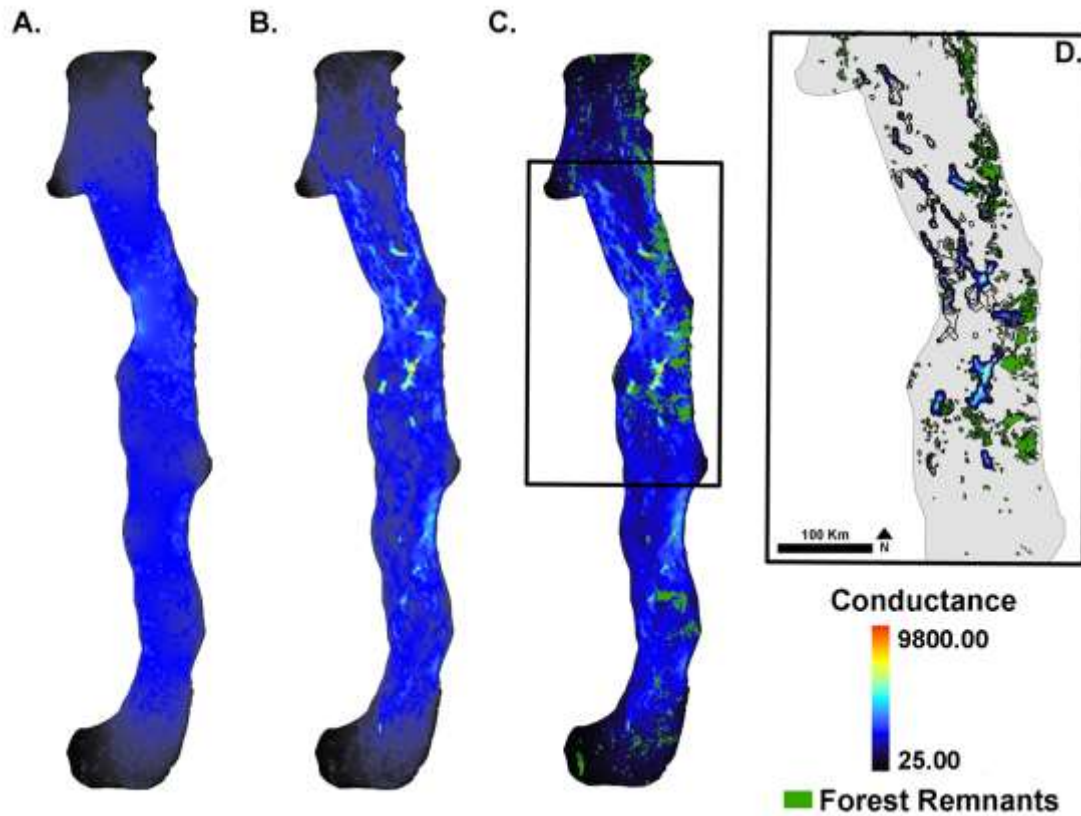
1212 Atlantic Forest.

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1215 **Fig. 4.** Potential amphibian ecological connectivity under dPC models for current (A),

1216 and future (B) scenarios, across the forest remnants in the Central Corridor of the

1217 Brazilian Atlantic Forest with altitudinal representation.

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1220   **Fig. 5.** Maps of landscape resistance models for amphibian ecological connectivity

1221   between forest remnants in the Central Corridor of the Brazilian Atlantic Forest. Null

1222   model for isolation-by-distance – IBD/IB3D (A), landscape model for isolation-by-

1223   resistance – IBR (B); landscape model for IBR showing the distribution of forest

1224   remnants with a frame in the highest conductance areas (C); zoom in the frame with

1225   high-conductance areas showing the potential landscape connectivity between patches

1226   with low resistance surface (D).

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