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Abstract

Ecological connectivity depends on key elements within the landscape, which can support ecological fluxes, species richness and long-term viability of a biological community. Landscape planning requires clear aims and quantitative approaches to identify which key elements can reinforce the spatial coherence of protected areas design. We aim to explore the probability of the ecological connectivity of forest remnants and amphibian species distributions for current and future climate scenarios across the Central Corridor of the Brazilian Atlantic Forest. Integrating amphibian conservation, climate change and ecological corridors, we design a landscape ranking based on graph and circuit theories. To identify the sensitivity of connected areas to climate-dependent changes, we use the Model for Interdisciplinary Research on Climate by means of simulations for 2080-2100, representing a moderated emission scenario within an optimistic context. Our findings indicate that more than 70% of forest connectivity loss by climate change may drastically reduce amphibian dispersal in this region. We show that high amphibian turnover rates tend to be greater in the north-eastern edges of the corridor across ensembles of forecasts. Our spatial analysis reveals a general pattern of low-conductance areas in landscape surface, yet with some well-connected patches suggesting potential ecological corridors. Atlantic Forest reserves are expected to be less effective in a near future. For improved conservation outcomes, we recommend some landscape paths with low resistance values across space and time. We highlight the importance of maintaining forest remnants in the southern Bahia region by drafting a blueprint for functional biodiversity corridors.

Keywords

Anura, Atlantic Forest, functional corridor, climate models, dispersal ability

Introduction

The implementation of Protected Areas (PAs) is among the most effective methods for long-term biodiversity conservation plans (Rodrigues et al. 2004), working as a key strategic tool in the development of environmental policies and efforts to sustain natural ecosystem processes (Le Saout et al. 2013; Laurance et al. 2014). The selection of PAs is often aimed to preserve either species of different taxonomic groups, conservation target species (e.g., threatened and/or endemics), or combinations of different abiotic conditions favourable to local ecosystems that will likely protect a wide range of biodiversity (Lawler and White 2008). Given that habitat loss is the most important threat to species survival (Haddad et al. 2015), the protected sites chosen by decision-makers can determine which species will be able to survive in the area (Jenkins et al. 2015). The effectiveness of these selected sites in reaching conservation goals depends on how many of the target species are represented in a given area (Dietz et al. 2015). Although generally unseen, amphibians are the most abundant land vertebrates in humid tropical forests (Stebbins and Cohen 1995). Globally, they include over 7,000 species of frogs (Anura), 700 species of salamanders (Caudata) and 200 species of caecilians (Gymnophiona) (Frost, 2019). However, amphibian conservation actions have overlooked the biodiversity patterns in an effective conservation policy (Campos et al. 2017).

Among all vertebrates, amphibians are the group with the most species (24%) whose geographical ranges are unprotected and not included in PAs (Nori et al. 2015). More than 2,000 amphibian species are listed as threatened by extinction, which makes them the most threatened vertebrate group worldwide (Stuart et al. 2004; IUCN 2018). Many reductions and extinctions of amphibians have occurred due to the habitat loss (Stuart et al. 2004; Becker et al. 2007; Ferreira et al. 2016), mainly in the Neotropical region, which harbours a significant amount of the global amphibian diversity (Young et al. 2004; Silvano and Segalla 2005; Becker et al. 2007). Amphibian conservation in fragmented landscapes is directly related to the establishment of protected areas and requires special management tools such as habitat restoration and management of forest patches, ensuring habitat quality and, hopefully, the permanence of the species (Ochoa-Ochoa et al. 2009; Lourenço-de-Moraes et al. 2018). Therefore, compiling data about species distribution ranges is key to planning conservation actions (Verdade et al. 2012; Morais et al. 2013; Campos et al. 2017).

Conservation strategies aimed at protecting threatened amphibians were proposed by previous studies that highlighted parts of the Brazilian Atlantic Forest as high priority areas (e.g., Loyola et al. 2008; Campos et al. 2013; Lemes and Loyola 2013; Dias et al. 2014). In addition, some taxonomic groups of amphibians from small areas within the Atlantic Forest were identified as potential surrogates of biodiversity in Brazil (Campos et al. 2014). Species with access to mountainous regions may migrate to higher altitude areas with lower temperatures (Colwell et al. 2008), which in the case of the Atlantic Forest, should retain greater humidity due to better-preserved forest cover (Ribeiro et al. 2009). However, the survival of threatened amphibians in fragmented tropical landscapes is dependent on the integrity and persistence of their PAs(Urbina-Cardona 2008; Ochoa-Ochoa et al. 2009; Lourenço-de-Moraes et al. 2019).

The economic growth policy in Brazil is widely based on the expansion of agricultural frontiers (Ribeiro et al. 2009), directly affecting the availability and the distribution of forest remnants in scattered private lands, which are gradually becoming crop and pasture production areas (Tabarelli et al. 2004). Forest isolation can affect many species' distributions by habitat loss, leading to long-term changes in the structure of the remaining fragments (Metzger 2009; Lourenço-de-Moraes et al. 2018). This factor means that the use of ecological connectivity metrics can be good indicators for measuring the isolation of PAs and their ecosystem functions (Gurrutxaga et al. 2011). Assessing ecological connectivity among PAs is becoming a relevant subject of growing international effort in relation to nature conservation policies (Bennett and Mulongoy 2006; Worboys et al. 2006). By using connectivity in planning, managers attempt to avoid functional isolation of PAs (Carroll et al. 2004; Liang et al. 2018) and mitigate the effects of climate change on the population structure of endemic species by allowing for range shifts (Bennett and Mulongoy 2006; Triviño et al. 2018). Thus, an understanding of future climate conditions is essential for predicting the effects of habitat isolation and species range shifts. In an attempt to understand these effects, modelling species responses to different climatic scenarios of environmental conditions has proven to be an effective tool (Carnaval and Moritz 2008; Diniz-Filho et al. 2009; Austin and Van Niel 2011; Araújo and Peterson 2012). Researchers are combining environmental spatial data with ecological and evolutionary processes to predict how species will shift their ranges in the future (Elith et al. 2010; Kearney et al. 2010;

Martensen et al. 2017; Triviño et al. 2018; Lourenço-de-Moraes et al. 2019). Ecological niche models (ENMs), also referred to as species distribution models (SDMs) (Peterson et al. 2011; Rangel and Loyola 2012), have been increasingly used to estimate the spatial ranges of species for future scenarios of climate change (Peterson et al. 2011). These predictions may provide useful contributions to decision-making regarding biodiversity conservation (Loyola et al. 2014).

Ecological implications of species tolerances to climate change are increasing and contributing to a better understanding of how spatiotemporal connectivity information can be incorporated into dispersal patterns (Bled et al. 2013). Climatic change may alter species distributions (Pearson and Dawson 2003; Raxworthy et al. 2008), as well as significant species turnovers (Peterson et al. 2012). In this context, ecological connectivity of forest landscapes is of paramount importance to ensure the flow of species among potential climate refuges (Pearson and Dawson 2005). Considering that climate change can aggravate environmental stresses from habitat loss and fragmentation, there is high interest in maintaining ecological connectivity in changing climates (Hamilton et al. 2016). However, only a few studies considered the potential impact of climate change on the fragmentation of populations (Duan et al. 2016).

Ecological connectivity strategies depend not only on the existence of structural connections between habitat patches but also on habitat suitability, stepping stones, matrix permeability and the target organisms’ responses to these elements (Tischendorf and Fahrig 2000; Baum et al. 2004). Complex agroforestry systems are often used as suitable habitats for different species across fragmented landscapes, also improving dispersal pathways and connecting local species assemblages (Faria et al. 2007). Advances in conservation biogeography have addressed many interactions between habitat suitability and species response, varying in complexity, realism and data requirements (Franklin 2010). Graph and circuit theories are complementary methods that have been used to provide efficient approaches for identifying biodiversity corridors (McRae et al. 2008; Spear et al. 2010). While circuit theory models outline high-conductance areas between patches (McRae et al. 2008), graph-based models determine the optimal least-cost routes pairwise landscape distances (Urban and Keitt 2001). However, efficient ecological corridors must facilitate dispersal movements and consider species life-history requirements (Rosenberg et al. 1997). In this context, amphibians have been cited as highly appropriate species for examining landscape effects on community structure, due to their relatively limited mobility, sensitivity to dispersal barriers and strong microhabitat associations (Austin et al. 2002; Spear et al. 2005; Lee-Yaw et al. 2009).

To answer where the amphibian species could disperse in the face of climate change, we assess how changing climate might affect the protected network effectiveness for amphibian distributions. Here, we explore the probability of the ecological connectivity of forest remnants and amphibian species for current and future climate scenarios. Specifically, we aim at modelling the ecological connectivity to represent forest remnants that most contribute to upholding amphibian connectivity in the Central Corridor of the Brazilian Atlantic Forest, estimating the species turnover between current and future amphibian species distributions. We evaluate if the PAs network of this corridor safeguards amphibian species that occur in this region, testing if this network can work as an effective biodiversity corridor for amphibians. Then, we show the relationship between environmental variables and amphibian species distributions across the protected network. We highlight the importance of maintaining forest remnants in the main Atlantic Forest biodiversity corridor (i.e., the Central

Corridor), suggesting implications for amphibian conservation planning and providing new approaches on ecological connectivity in different climatic conditions. These results may be useful as a tool for designing conservation strategies that incorporate the effects of climate change and habitat fragmentation in a landscape planning approach.

Materials and Methods

Study area

The Atlantic Forest represents one of the five most important biodiversity hotspots on Earth (Mittermeier et al. 2011). Originally, it covered around 1,500,000 km^2, of which only about 12% (i.e., 194 524 km^2) still remains in Brazil, Paraguay and Argentina (Ribeiro et al. 2009), corresponding to about 100,000 km^2 of Brazilian forest remnants (Tabarelli et al. 2005). Despite having high rates of habitat loss (Teixeira et al. 2009), which is one of the main factors driving amphibians to extinction (Stuart et al. 2004; Becker et al. 2007), the Atlantic Forest is the leader biome in amphibian diversity in Brazil (Haddad et al. 2013), accounting more than 50% of all Brazilian amphibian species (Haddad et al. 2013).

We focused our study on the Central Corridor of the Brazilian Atlantic Forest, which comprises about 8% of the total biome area (i.e., 7,913.42 km^2), covering 14% of forest remnants (SOS Mata Atlântica and INPE 2015). Here, we used the term Brazilian Atlantic Forest to refer to the forest remnants map provided by SOS Mata Atlântica and INPE (2015).

Protected networks

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 only occur in the forest remnants within the limits of distribution of the Central Corridor of the Brazilian Atlantic Forest, excluding all urban and non-forested areas (SOS Mata Atlântica and INPE 2015). Hence, we combined vector files based on expert knowledge of the species' ranges and forest remnant polygons into an overall coverage for species distribution modelling, through both sources of species presences (Fourcade 2016).

We used ArcGIS 10 software (ESRI 2011) to build presence/absence matrices from the species distribution data by overlapping a grid system with cells of 0.1 latitude/longitude degrees, creating a matrix with 838 grid cells. A total of 146 amphibian species were spatially represented in this grid system after using the “Spatial Join” tool available in ArcGIS. We only considered spatial occurrences by those species in which the distribution data intersected at least one grid cell (i.e., ~ 10 km^2). We used forest remnant data to meet the habitat patch requirements based on visual interpretation at a scale of 1:50,000, delimiting more than 260,000 forest remnants with a minimum mapping area of 0.3 km^2. Therefore, we considered a species present in a cell if its spatial range intersected more than 0.3 km^2. To improve coarse species distribution data, the “Count Overlapping Polygons” ArcGIS toolbox was used to obtain the species richness at the spatial resolution assessed, removing all duplicate records from the analyses (i.e., repeated records of a species at the same location).

Climate models and environmental data

Given that species occurrence patterns are determined at large-scales by responses of organisms to different climatic conditions (reflecting the ecological niche; see Soberón 2007; Booth et al. 2014), we used ecological niche models (ENMs) to predict the distribution area of amphibian species. We used the species occurrence matrix and the layers of climatic variables, resulting in a suitability matrix, which we used to model and map the potential distribution of each species evaluated (Loyola et al. 2014).

We used current and future climate data according to the Coupled Model Intercomparison Project Phase 5 – CMIP5 (http://cmip-pcmdi.llnl.gov), from coupled Atmosphere-Ocean Global Climate Models (AOGCMs) to develop the spatial range models. These simulations show a high sensibility to detect potential impacts of land use changes on climate in human-induced landscapes (Dirmeyer et al. 2010). We implemented the Model for Interdisciplinary Research on Climate (MIROC5) by 2080 (mean of simulations for 2080-2100), which represents a moderated emission scenario within an optimistic context (Representative Concentration Pathway – RCP 4.5; Taylor et al. 2012). This moderate scenario (RCP4.5) incorporates historical emissions pathways and land cover information to meet potential climate policies (Thomson et al. 2011). We based the model projections on seven independent climatic variables tested by stepwise multiple regression analyses, using a confidence interval of 95%: 1) annual mean temperature, 2) temperature seasonality, 3) mean temperature of the warmest and 4) coldest quarters, 5) annual precipitation, and 6) precipitation of the driest and 7) wettest quarters. We obtained these climatic data through the EcoClimate database (Lima-Ribeiro et al. 2015) and downscaled them from 0.5 to 0.1 latitude/longitude degrees for fitting our spatial scale. We also used altitude as an environmental filter to predict the species richness from the dataset available at WorldClim Global Climate Data (Hijmans et al. 2005). Given that temperature and humidity are the main climate components that directly affect the biology of amphibians (Carey and Alexander 2003), we compared these variables along altitudinal gradients to evaluate which environmental features are the best predictors of amphibian richness.

We employed the maximum entropy method implemented in the MaxEnt software (Phillips et al. 2006) to develop the potential distribution map for the forest remnants associated with all the climatic variables adopted in the future predictions by 2080 (i.e., mean of simulations for 2080-2100). We randomly partitioned presence and pseudo-absence data for each species into 75% of calibration (i.e., training) and 25% of evaluation (i.e., tests), repeating this process ten times by cross-validation to avoid over-fitting biases in the least-suitable environmental conditions. We converted the continuous predictions of suitability into a binary vector of 1/0, finding the threshold that maximizes sensitivity and specificity values in the receiver-operating characteristic curves (Phillips et al. 2017) to build each ecological niche model. These curves are generated by plotting values of the relative frequency of true positive records predicted by a given model against the values of the relative frequency of pseudo-absence records, generating the Area Under the Curve (AUC). For this purpose, one-third of the occurrence records are set aside from modelling as test points (Phillips et al. 2006). Values of AUC range from 0.5 (i.e., random) for models with no predictive ability to 1.0 for models giving perfect predictions. According to the Swets (1988) classification, AUC values above 0.9 describe “very good”, 0.8 “good”, and 0.7 “useful” discrimination abilities.

The main reason behind our choice of the MaxEnt modelling approach was to look for a straightforward combination of environmental predictors that best explains the presence-only species distribution across forest remnants. Using presence-only data, MaxEnt is considered one of the most efficient methods for habitat suitability modelling in terms of predictive performance (Elith and Graham 2009; Phillips et al. 2017; Duflot et al. 2018). This predictive modelling approach has a high analytical power to combine continuous and categorical environmental variables (Phillips et al. 2006), accounting for potential interactions among them (Phillips and Dudik 2008). MaxEnt also has been considered as less sensitive to sample sizes and layer resolutions when compared with other habitat suitability models (Merow and Silander 2014; Wisz et al. 2008). In addition, this multi-attribute approach works in free, user-friendly software that provides input and output files totally compatible with geographic information system tools (Phillips et al. 2006).

We assessed the potential current and future distributions of the forest cover according to the current vegetation remnants map of the Brazilian Atlantic Forest (SOS Mata Atlântica and INPE 2015), of which we excluded all the areas where there are currently agriculture, urban zones or settlements, only representing forest remnants without overlaps on the land use/cover changes.

Species turnover

We also applied the maximum entropy method implemented in the MaxEnt software (Phillips et al. 2006), to determine the species geographic distributions patterns, following the same climatic variables adopted in the modelling process for the forest remnants assessed. However, in this case, we employed the modelling strategy at the community level of “predict first, assemble later” (Overton et al. 2002), where the ranges of individual species are modelled one at a time as a function of environmental predictors and then overlapped for obtaining the species richness. We calculated the species turnover between current and future amphibian species distributions according to the equation proposed by Thuiller et al. (2005) (1):

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

where “*G”* refers to the number of species gained, “*L”* the number of species lost and “*S”* the contemporary species richness found in the forest remnants assessed. We obtained the final maps of species richness for the current and future times, as well as the species turnover rates through the average of values projected by the MaxEnt model for each grid cell assessed (i.e., 0.1 latitude/longitude degrees of spatial resolution).

Probability of connectivity

We assessed the forest remnants through the probability of connectivity (PC) index (Saura and Rubio 2010), calculated for the patches of the Central Corridor of the Brazilian Atlantic Forest under two environmental scenarios (i.e., current and future), using Conefor 2.6 software (Saura and Torné 2009). The PC is a graph-based habitat availability metric that quantifies functional connectivity (Saura and Rubio 2010). It is defined as the probability that two points randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected) given a set of “n” habitat patches and the links (direct connections) among them (Saura and Pascual-Hortal 2007) (2).

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

where *ai* and *aj* are the attributes of patches *i* and *j* (i.e., ID and area). AL is the maximum landscape attribute, which corresponds to the total landscape area (i.e., area of the study region, comprising both habitat and non-habitat patches). The product probability of a path is the product of all the values of the probability of direct dispersal

(*Pij*) for all the links in that path. Thus, *Pij* is the maximum product probability of all of the possible paths between patches *i* and *j*, including direct dispersal between the two patches.

We performed a prioritization ranking of the landscape elements (i.e., patches) by their contribution to overall habitat availability and connectivity from the percentage of the variation in PC (dPC_k), achieved by the removal of each patch from the overall landscape (see Saura and Pascual-Hortal 2007; Saura and Rubio 2010). The dPC_k is a relative measure of the increase in the PC value that resulted from the improvement in the strength of that link after the implementation of the defragmentation measures (Saura and Rubio 2010) (3).

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

where $PC_{remove.k}$ is the index value after removal of the landscape element (i.e., after a certain habitat patch loss). This measure corresponds to the “link change” analysis mode implemented in the Conefor 2.6 software (Saura and Torné 2009). For all the connectivity analyses, we used a mean dispersal distance for amphibians according to the review conducted by Smith and Green (2005), where an estimative average distance of 400 m for amphibians, in general, was proposed. Whereas some amphibians can disperse over distances greater than 400 m (Smith and Green 2005), we also assessed scenarios with a greater potential for dispersal, using distances of 600 and 800 m. To assess the ecological connectivity results for the future scenario, we considered only the areas with an assessed likelihood greater than 50%, considering the potential distribution areas with a minimum favourable condition for the forest persistence under the climate change predictions used.

Landscape resistance models

We performed a landscape resistance approach to calculate the functional connectivity between the forest remnants expressed as least-cost paths. To compare the sensitivity of dPC models within the landscape, we used a resistance surface based on the landscape heterogeneity with isolation-by-resistance (IBR), following the model proposed by McRae (2006). We also assessed null models through isolation by Euclidean distance (IBD), and isolation by Euclidean 3D distance with elevation data (IB3D), both of which did not consider the influence of landscape heterogeneity. IBD and IB3D represent landscape-free models and consider a maximum conductance for different land use types, while IBR is strongly based on landscape heterogeneity. We estimated the resistance values on the potential amphibian dispersal across the land use types within the landscape matrix, according to a systematic mapping of land use at a 1:250,000 scale, provided by the Brazilian Institute of Geography and Statistics (IBGE 2014).

We considered a conceptual framework for scoring the matrix permeability (cost surface) associated with landscape features based on empirical data and expert opinion (e.g., Ray et al. 2002; Joly et al. 2003; Semlitsch et al. 2008; Janin et al. 2009; Popescu and Hunter 2011) to determine the resistance values assigned to each land use type. Thus, we followed a rank-based criterion to reflect the relative order of landscape conductance for amphibian ecological connectivity (e.g., Gibbs et al. 2005; Grant 2005; Patrick 2006; Semlitsch et al. 2008; Popescu and Hunter 2011; Decout et al. 2012). We used 27 detailed land use classes to generate our land cover input file, assuming different resistance values to each land use type (Table S1). We estimated null conductance values to each land use type for evaluating the extent to which the results were influenced by the magnitude of these values, where a low conductance value indicates a high resistance to dispersal. Considering the current landscape heterogeneity, we examined the relationship between landscape resistance distances (IBD, IB3D and IBR) and ecological connectivity under present and future climate conditions (dPC present and dPC future). For this, we used Mantel tests to account for statistical significance in pairwise comparisons. We performed the Mantel tests through 200,000 permutations in the PASSaGE 2 software (Rosenberg and Anderson 2011). We used Circuitscape 2.2 software (McRae 2006) to generate the pairwise matrices of landscape resistance and to produce the cumulative land conductance maps based on circuit theory.

Spatial prioritization framework

Finally, we selected the most suitable habitats defining different representation targets based on four methodological steps (i.e. forest modelling, species modelling, probability of connectivity and landscape resistance models) (Fig. 1). Combining these targets into a landscape modelling approach, we designed a spatial representation to select priority areas for conservation, which might work as a suitability surface for ecological connectivity in the Central Corridor of the Brazilian Atlantic Forest. Therefore, this approach favoured the selection of habitats less disturbed by human-induced actions for improved conservation outcomes.

Results

We showed that 110 PAs are covered by the Central Corridor of the Brazilian Atlantic Forest (i.e. 70% of sustainable use and 30% of strict protection), which comprise to 6,607.98 km^2 and correspond to only 8% of the total corridor area (Fig. 2a). Considering the 146 amphibian species distributed in the forest remnants assessed (Fig. 2b), only 20% are distributed within the current PAs network. According to the PERMANOVA, when we compared species richness and PA categories with all the environmental variables together, we found direct relations with precipitation, temperature, evapotranspiration and forest cover (Table 1), where precipitation was the variable most associated with the amphibian species richness in the Central Corridor of the Brazilian Atlantic Forest. According to the stepwise multiple regression analyses, there was no correlation among any of the climate variables ($R^2 = 0.26$; $F = 92.57$; $P = 0.078$). The potential distribution of the forest remnants for the future scenario showed an average AUC value of 0.86, which indicated a good predictive ability by the dataset provided (Fig. 3a). The climate change models predicted a reduction of 75% in the probability of occurrence of the Atlantic Forest remnants in the central region of the Central Corridor. The northern and southern edges of the Central Corridor, as well as high altitude areas, showed the higher probability of forest occurrence. On the species distribution models under climate change, we predicted a high amphibian turnover rate, given that more than 50% of the grid cells had species turnover ratios greater than 0.7 (Fig. 3b). However, these expected changes in species composition tend to be greater on the northern edge than the southern edge of the Central Corridor.

Considering a dispersal distance of 400 m, our analyses of connectivity showed that the Central Corridor of the Brazilian Atlantic Forest does not guarantee good connectivity among the fragments, with an average dPC value of 8.43. When we assessed the dispersal distances of 600 and 800 m, the average dPC was the same than that observed with a 400 m distance. However, our results showed higher connectivity areas in the northeastern region of the Central Corridor of the Brazilian Atlantic Forest, mainly in the southern Bahia region (Fig. 4). We found that 95% of the values pointed out by the connectivity index were directed to the sustainable use areas, only of which 5% are classified as integral protection areas (Table S2)

For the current scenario, we only found 10 PAs with high connectivity (dPC > 60.0), although 71 had very low values (dPC < 1.0). This situation can be aggravated considering the climate model results for the future (2080-2100), which showed a high probability of forest remnants retraction in the evaluated region. This represents 74% of connectivity loss in a total of 4,889.90 km^2 of Atlantic Forest areas (Fig. 4). According to these future predictions, we estimated that 83 PAs would be without any ecological connectivity by the years 2080-2100 (dPC < 0.0), while only six PAs will remain with dPC higher than 1.0, which correspond to a plausible conservation attribute in terms of interpatch connectivity and habitat suitability. RPPN Renascer, RPPN Refúgio do Guigó I and II, and RPPN Boa União, in the Bahia state, and RPPN Mata da Serra, APA Serra da Vargem Alegre, and Parque Estadual do Forno Grande, in the Espírito Santo state represented the PAs with a better expected connectivity under climate change.

Circuit theory current flow maps predicted a high likelihood of connectivity in the central portion of our study area (i.e., in southern Bahia) for the current scenario (Fig. 5). The landscape surface was represented by a general pattern of low-conductance areas (i.e., low potential for amphibian dispersal), yet with some well-connected areas showing low resistance for species moving between patches. These well-connected areas (i.e., with high-conductance) can be potential amphibian biodiversity corridors, which would connect the Monte Pascoal, Pau Brasil and Serra das Lontras PAs, located in the southern Bahia region. Landscape resistance models that incorporated absolute dispersal barriers resulted in significant correlations when compared with those based on landscape-free models (i.e., null resistances). The Mantel tests showed significantly different relationships between dPC values (present and future) and resistance distances (IBD, IB3D and IBR) (Table 2), indicating the sensitivity of the functional connectivity models within the landscape.

Discussion

Habitat suitability assessment

Considering the effectiveness of habitat suitability models of our landscape planning, we highlight the southern Bahia region and the Espírito Santo state with the best ecological distances between forest remnants (i.e., high-conductance areas with low resistance values). The use of resistance surfaces in landscape ecology incorporate multiple pathways that rely on the habitat quality for identifying important landscape elements connecting suitable environments for conservation (McRae et al. 2008; Zeller et al. 2012). Interactions between habitat suitability and species dispersal movements can be crucial for functional connectivity strategies in landscape change (Hodgson et al. 2009; Doerr et al. 2011). Therefore, given the landscape resistance surface and the connectivity metrics used as an aid for our amphibian conservation approach, we suggest some potential ecological corridors under current and future conditions.

Based on shifts in geographic ranges and climatically suitable habitats, our results reveal that the areas with high turnover rates are not the same areas with high occurrence probability of forest remnants under climate change. The selection of critical habitats for amphibian conservation under climate change is important for making effective management decisions (Guisan et al. 2013). Forecasting approaches in spatial planning suggest that regions with high species turnover rates are expected to have more restricted-range species than regions with low species turnover rates (Diniz-Filho et al. 2009). Areas with high turnover rates can be associated to areas with low species richness under the current climate (Duan et al. 2016), which in the case of the Atlantic Forest may be represented by higher altitude areas. Moreover, low turnover rates in high altitude areas can strengthen mountainous regions as potential climatic refuges (Carnaval et al. 2009; Randin et al. 2009; Araújo et al. 2011; Lourenço-de-Moraes et al. 2019).

The use of MaxEnt as a single modelling algorithm for ecological approaches also has some concerns regarding data acquisition and analysis, which should include the full environmental range of the species (Elith et al. 2011). One of the main limitations of this presence-only modelling seems to be a biased approach for species–habitat relationships, given the unknown sampling effort intensity (Elith et al. 2011). Addressing possible sampling limitations by combining local field records with environmental layers is a promising strategy to improve the relevancy of habitat suitability models for effective landscape planning (Maréchaux et al. 2017). Possible solutions to avoid this sample selection bias can be corrected by adding a mask as an explanatory variable or by discarding some of the presence points in oversampled areas (Phillips et al. 2009; Radosavljevic and Anderson 2014; Stevenson-Holt et al. 2014). Another limitation of our habitat suitability models is that climate datasets needed for this modelling approach are not always available, and some of them need to be downscaled for fitting our spatial scale (see Lima-Ribeiro et al. 2015). Therefore, we assume that our climatic projections capture only part of the climate variability changes associated with the habitat suitability models. However, downscaling climate projections is a widely used technique for exploring the regional and local-scale responses to global climate change for simulating low-resolution climate models (Hewitson and Crane 2006; Cabral et al. 2016). Given the on-going challenges to the future development of climate downscaling, data scarcity and scale issues need to diminish the overestimation of suitable habitats for future species distributions by better-capturing landscape heterogeneity (Tabor and Williams 2010).

Challenges and opportunities for the Central Corridor of the Brazilian Atlantic Forest

Our findings show that the proportion of forest fragments with good connectivity is very low along the Central Corridor of the Brazilian Atlantic Forest, which consequently may reduce the flow of species among the fragments and significantly restricts the functional role of this ecological corridor. Using expert knowledge to distinguish species records can be a practical way of improving conservation-relevant decisions even with a paucity of biodiversity data (Akçakaya et al. 2018). We focus on an approach for allowing decision-makers to make the best use of the available data at a local scale, considering the extent to which such decisions might affect conservation outcomes at broad scales. The complementary use of species range maps with occurrence data is a promising route for advancing efforts to local-scale conservation decisions, supporting our species distribution data (Maréchaux et al. 2017). Such approaches for improving decision-making effectiveness are even more urgent in species-rich regions, where conservation strategies should ensure the lack of biodiversity data (Maréchaux et al. 2017; Lourenço-de-Moraes et al. 2019). In this context, we suggest that the forest fragments located in the coastal parts of the southern

Bahia region and the Espírito Santo state deserve special attention in conservation plans because they hold the highest proportion of ecological connectivity along the Central Corridor of the Brazilian Atlantic Forest.

Our proposal of special attention to southern Bahia is reinforced due to their resistance surface values within a landscape matrix composed by shaded cocoa plantations (i.e., “cabrucas”), as indicated by Pardini et al. (2009). This agroforestry system has allowed the conservation of large numbers of native plant species, besides hosting typical mature forest fauna species (Pardini et al. 2009). Many amphibian species use the bromeliads that are in the “cabrucas” system during their entire life cycle and others only as diurnal shelter (Ferreira et al. 2016). Given their forest-like structure, shaded cocoa plantations of the Forest remnants from southern Bahia perform a fundamental role in maintaining connectivity between forest fragments (Sperber et al. 2004; Delabie et al. 2007; Faria and Baumgarten 2007). Our results, integrating graph-based connectivity metrics into forecast models, indicate that this region has a high probability of forest occurrence in a climate change scenario, which suggests climatically suitable habitats and potential ecological corridors.

Forest remnants management is critical to ensure the persistence of species, but dynamic threats such as land use change and climate change can directly reduce the effectiveness of PAs planned under a static approach (Faleiro et al. 2013). Due to developing technologies in remote sensing, there are several approaches to improve how we assess and monitor forest remnants through a variety of spatial and temporal scales (Tehrany et al. 2017). In this context, there is an urgent need to incorporate species range shifts in spatial conservation plans to ensure their effectiveness in the future (Hannah 2010). We recommend that the design of new conservation plans in the Central Corridor of the Brazilian Atlantic Forest must attempt to re-establish ecological connectivity between the remaining fragments and the higher altitude areas. This recommendation may represent an alternative mechanism to mitigate potential impacts related to climate change and land use change in the Atlantic Forest Hotspot. Corroborating our findings, other amphibian studies in the Atlantic Forest have also warned about the need to invest in PAs near high altitude areas (Lemes and Loyola 2013; Loyola et al. 2014; Lourenço-de-Moraes et al. 2019), mainly in the southern Bahia region (Carnaval et al. 2009), which retain high humidity provided by well-preserved forest cover. Climate threats to amphibian biodiversity have often been related to their high humidity dependence (Hopkins 2007), where moisture conditions are associated with microhabitats, rainfall regimes and terrestrial water balance, limiting the species' dispersal abilities (Early and Sax 2011). Dispersal limitation is a critical determinant of amphibian geographical ranges, assuming a general metapopulation structure related to habitat patch isolation (Smith and Green 2005). Our predictions on the environmental variables for amphibian species richness in the Atlantic Forest are dependent on their limited dispersal patterns. Therefore, dispersal capability might severely limit the ability of species to track suitable climatic conditions geographically (Massot et al. 2008; Early and Sax 2011). The use of various environmental variables has been demonstrated as an efficient strategy to reach outcomes closer to reality, being one of the keys to understanding how communities can respond to climatic factors (Araújo and New 2007; Marmion et al. 2009).

Implications for conservation planning under climate change

Our findings show that potential impacts of climatic changes should occur in almost the entire Central Corridor of the Brazilian Atlantic Forest, which could affect the ecological connectivity of the whole biome. We suggest that the PAs with the better-expected connectivity under climate change need critical attention in future conservation plans (e.g., RPPN Renascer, RPPN Refúgio do Guigó I and II, and RPPN Boa União, in the Bahia state, and RPPN Mata da Serra, APA Serra da Vargem Alegre, and Parque Estadual do Forno Grande, in the Espírito Santo state). In this context, these mitigations can be useful to avoid potential extinction process expected for the amphibians from the Central Corridor of the Brazilian Atlantic Forest PAs.

Amphibian species from Atlantic Forest PAs are more threatened with extinction than in other Brazilian protected networks (Campos et al. 2016). This phenomenon happens mainly because the Southeast Region of Brazil is the economic core of the country, with highly fragmented forest remnants (Ribeiro et al. 2009), with a high human population density, and the presence of mining and logging activities (Lemes et al. 2014). Atlantic Forest reserves close to urban ecosystems are also failing to protect amphibian species (Lourenço-de-Moraes et al. 2018). Our approach does not specifically estimate a quantitative species extinction risk but shows evidence of a potential regional extinction within limited dispersal models. We highlight that many PAs will become less effective in future scenarios, which can dramatically affect the diversity and distribution of the amphibian species that occur in the forest remnants assessed.

Conserving biodiversity under climate change comes out as a challenge for conservation scientists. For being a dynamic system, controlling all the climatic variables and synergies related to environmental conditions and its consequences is a huge task. If the rates of climate change overtake the response potential of biological systems to ecological connectivity and its impacts on ecosystem functioning, effects on community structure and species distributions can be irreversible. Therefore, enhanced conservation efforts of forest management will play a critical role for mitigating effects of environmental change. In some human-modified landscapes characterized by secondary forest, environmental heterogeneity can be maintained and even increased, thus contributing to the community structure (Tscharntke et al. 2012). A recent meta-analysis showed that ecological restoration success can be higher for natural regeneration than for active restoration in tropical forests (Crouzeilles et al. 2017). In this context, our research highlights the importance of maintaining the mosaic of forest remnants and the landscape heterogeneity in the Central Corridor of the Brazilian Atlantic Forest, providing dynamic tools to prioritize conservation investment for ecological connectivity assessments.

Practical strategies should be sensible for species adaptation, impact mitigation, and must prioritize the protection and connectivity of heterogeneous landscapes to improve conservation management (Richardson and Whittaker 2010). In the particular case of the Atlantic Forest, the response of amphibians to anticipated declines depends on local climatic conditions (Lourenço-de-Moraes et al. 2019). Regarding adaptation to climate change, we show that species tend to use potential corridors in high altitude areas with better-preserved forest cover. Our research highlights that integrating the amphibian-climate refuges in the well-connected areas is essential for spatial decision-making in the Atlantic Forest hotspot, which can reduce extinction risk and avoid species loss. This work has advanced knowledge of the analytical methods that can be used to incorporate landscape paths with low resistance into potentially connected areas for amphibian conservation in the Central Corridor of the Brazilian Atlantic Forest. The methodological approach proposed here is not only amphibian-specific but can also be used in conservation plans for other taxonomic groups. This innovative approach has sought to move forward the knowledge on ecological connectivity of endangered forest remnants and supports conservation actions in the face of climate change.

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Appendix A. Supplementary files

Supplementary files associated with this article can be found in the online version (Tables S1 to S2).

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Tables

Table 1. Results from the PERMANOVA on the species richness and PA categories by the variables altitude, temperature, precipitation and forest cover in the Central Corridor 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	–

*Significant values

Table 2. Statistical significance for Mantel test between dPC values (Present and Future) and resistance distances (IBD, IB3D and IBR) for calculating the landscape connectivity between forest remnants in the in the Central Corridor of the Brazilian Atlantic Forest. IBD: null model through isolation by Euclidean distance; IB3D: null model through isolation by Euclidean 3D distance with elevation data; IBR: resistance model through 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

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

Figures

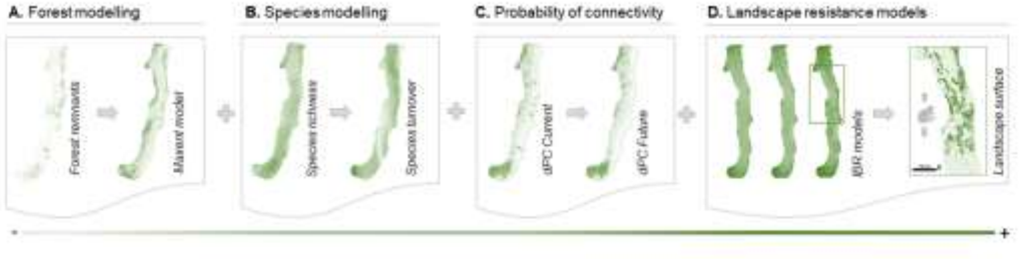

Fig. 1. Schematic representation of the methodological steps used in the landscape modelling approach for amphibian conservation in the Central Corridor of the Brazilian Atlantic Forest, Brazil. Forest modelling (A), Species modelling (B), Probability of connectivity (C) and Landscape resistance models (D).

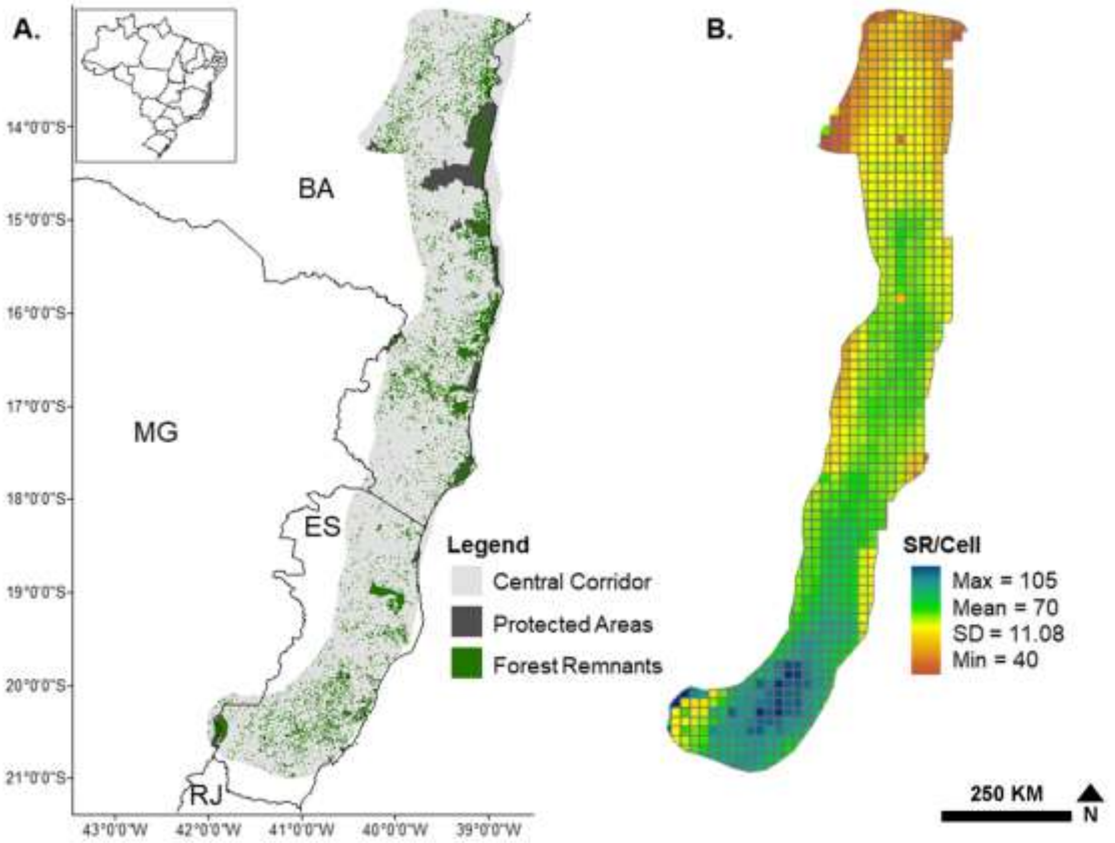

Fig. 2. Location of the Central Corridor of the Brazilian Atlantic Forest, in eastern Brazil, representing their Protected Areas and Forest Remnants. BA: Bahia state; MG: Minas Gerais state; ES: Espírito Santo state; RJ: Rio de Janeiro state (A). Species Richness per grid cell with summary statistic values such as Maximum, Mean, Standard Deviation and Minimum (B).

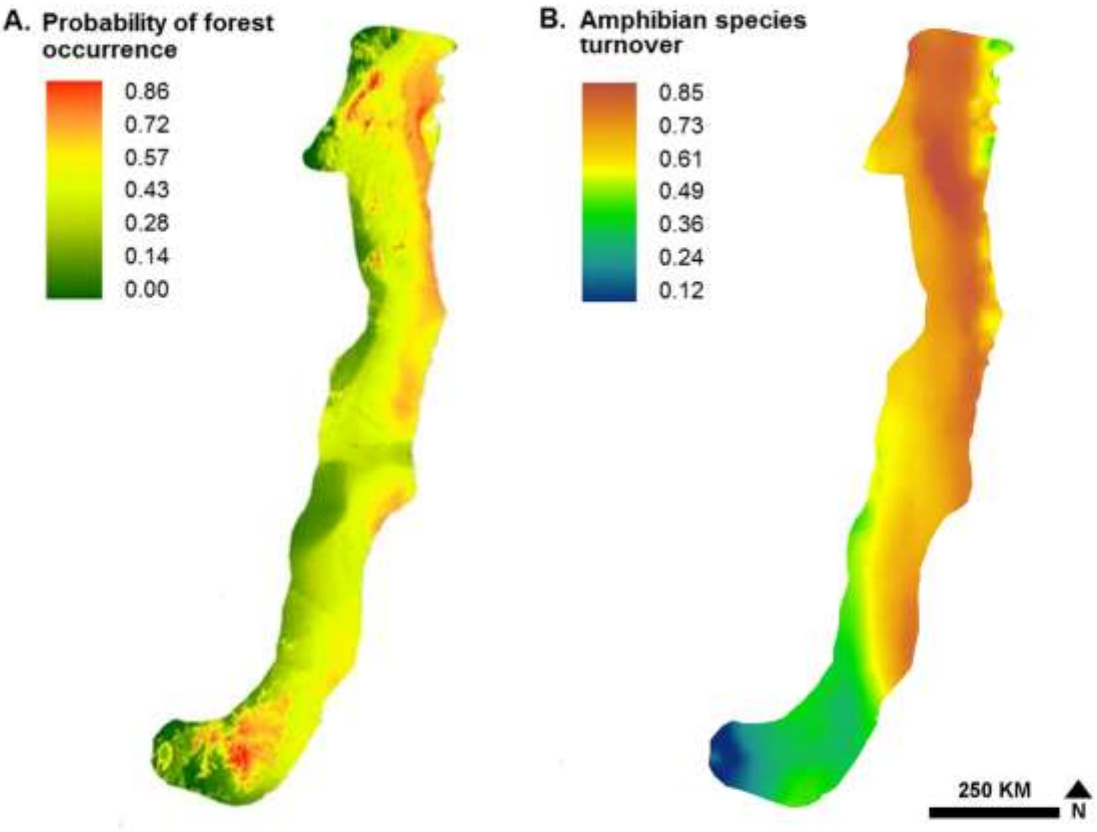

Fig. 3. Probability of forest cover according to the MaxEnt model (A), and amphibian species turnover rate (B), under climate change in the Central Corridor of the Brazilian Atlantic Forest.

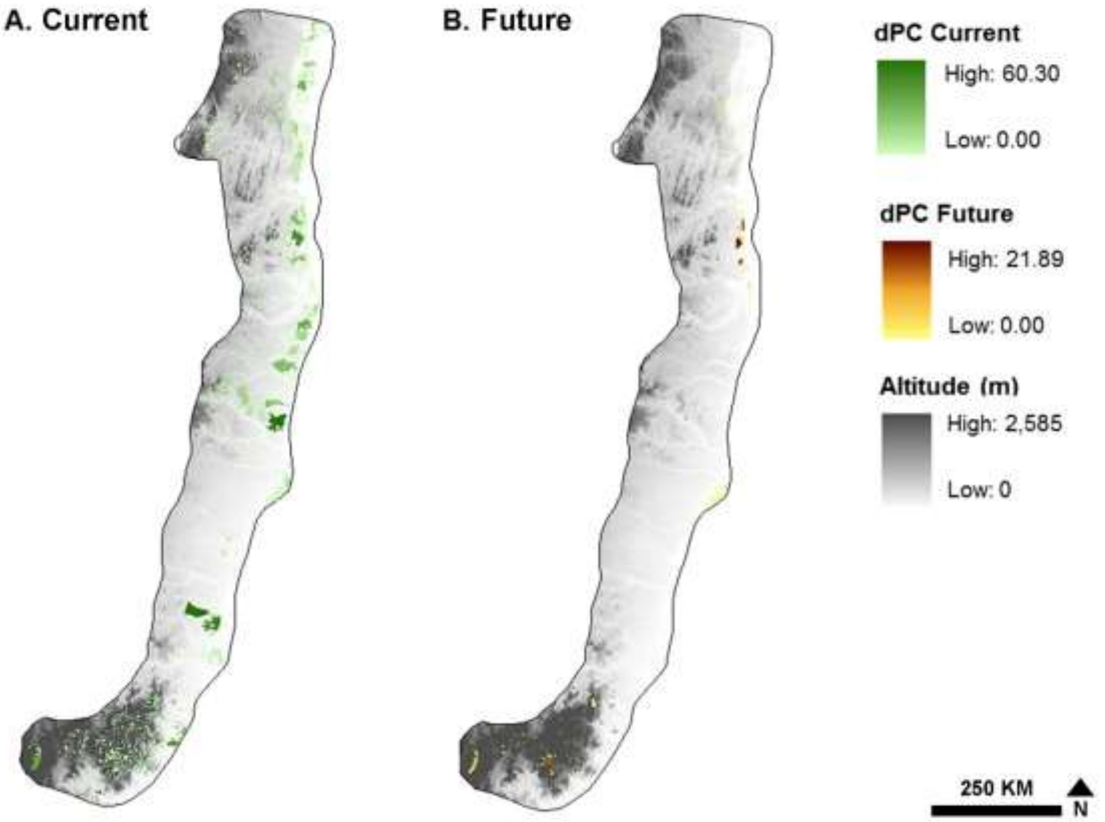

Fig. 4. Potential amphibian ecological connectivity under dPC models for current (A), and future (B) scenarios, across the forest remnants in the Central Corridor of the Brazilian Atlantic Forest with altitudinal representation.

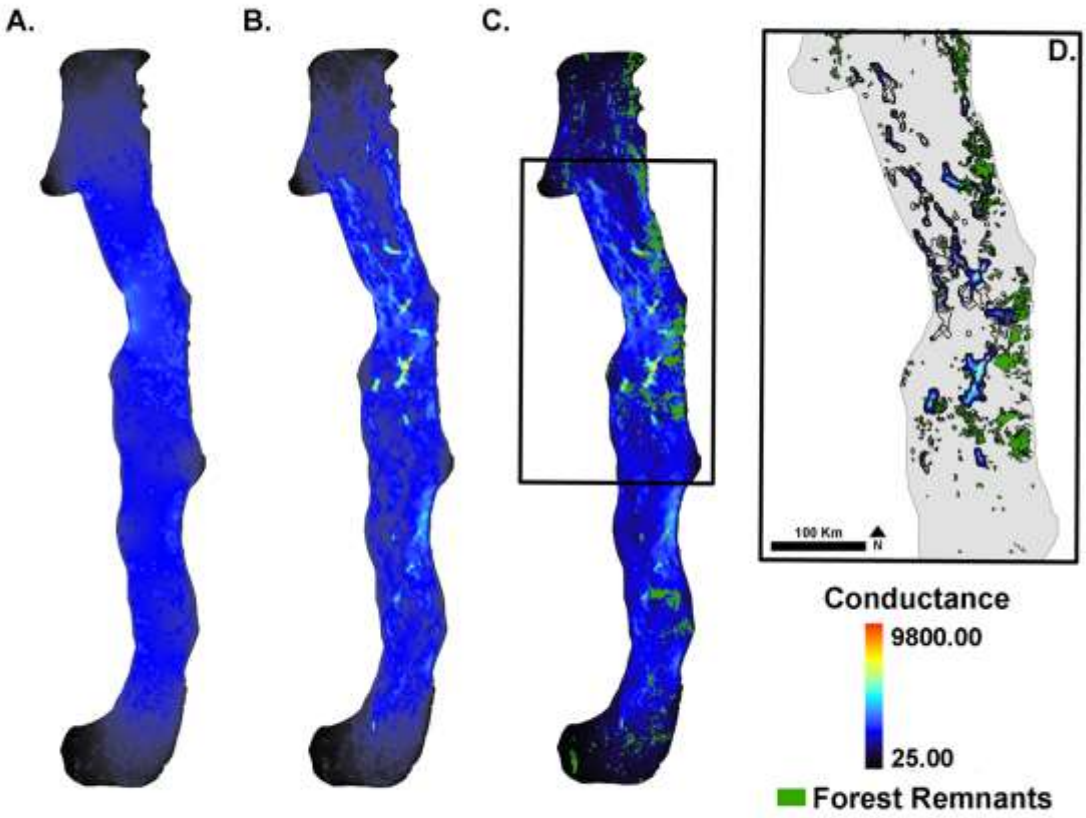

Fig. 5. Maps of landscape resistance models for amphibian ecological connectivity between forest remnants in the Central Corridor of the Brazilian Atlantic Forest. Null model for isolation-by-distance – IBD/IB3D (A), landscape model for isolation-by-resistance – IBR (B); landscape model for IBR showing the distribution of forest remnants with a frame in the highest conductance areas (C); zoom in the frame with high-conductance areas showing the potential landscape connectivity between patches with low resistance surface (D).