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ORIGINAL PAPER

Relict populations of *Araucaria angustifolia* will be isolated, poorly protected, and unconnected under climate and land-use change in Brazil

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Abstract

One of Brazil's most threatened tropical biome is the Atlantic Forest. This biome has distinct forest formations, as the Araucaria Mixed Forest, a sub-tropical ecosystem distributed through southern and southeastern Brazil, surrounded by Dense Ombrophilous Forest. The defining tree species of Araucaria Mixed Forest is *Araucaria angustifolia* (known as Araucaria), an endangered, relict, and historically managed conifer. Due to unsustainable exploitation during the twentieth century, the main strategy for Araucaria preservation was the creation of protected areas. However, protected areas' coverage within Atlantic Forest remains scarce and might not prevent connectivity between species' remnant patches. We thus evaluated the potential connectivity of projected Araucaria distribution in the present and future under climate change and current land-use, using a species distribution model with graph theory. Araucaria's current connectivity—through the Mixed and Dense Forests—ranges entirely through the landscape, with 715 connecting arcs (212 within protected areas). However, only 7% of its current distribution is encompassed by protected areas. Under future climate change in 2085, connectivity is expected to decrease by 77% compared with current projections. In the future, Araucaria subpopulations will be concentrated at higher elevations in unprotected suitable areas. We suggest that specific regions in southern and southeastern Brazil might be targeted as priority conservation areas jointly to major existing protected areas. These areas will sustain Araucaria connectivity and protection. As a keystone species, by safeguarding Araucaria we protect the socioecological system in southern and southeast Brazil and potentially promote forest expansion.

Keywords Araucaria forests · Ecological niche modelling · Future climatic changes · Habitat fragmentation · Protected areas effectiveness · Species connectivity

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Introduction

Climate change threatens tropical biodiversity in distinct aspects (Chen et al. 2011). Increased temperatures (Anderson-Teixeira et al. 2013), changing precipitation regimes, and more frequent and severe climate extreme events, such as droughts or wildfires (Garcia et al. 2014) are expected to affect entire biomes (Rodrigues et al. 2006). One of the most threatened biomes in Brazil is the Atlantic Rainforest, which contains more than 1500 plant species vulnerable to extinction (Scarano and Ceotto 2015). Urbanization, deforestation, agricultural expansion, and climate change are some of the anthropic disturbances affecting the Atlantic Rainforest and its biodiversity (Scarano and Ceotto 2015; Rezende et al. 2018).

The Atlantic Rainforest biome has five forest ecosystems: (i) Dense Ombrophilous; (ii) Mixed Ombrophilous; (iii) Semi deciduous Seasonal; (iv) Deciduous Seasonal; and (v) Open Ombrophilous forests (Schneider et al. 2018). The Mixed Ombrophilous Forest, also known as Araucaria Mixed Forest, is characterized by species adapted to lower temperatures (Castro et al. 2019; Wilson et al. 2019). The distribution of Araucaria Mixed Forest originally covered almost entirely southern Brazil besides specific areas in the country's southwestern region (Vibrans et al. 2013), such as Mantiqueira Hills, at the High Rio Preto Microbasin (Castro et al. 2019; Quinteiro et al. 2019), along the borders of São Paulo, Minas Gerais, and Rio de Janeiro states. In these areas, remnant patches of Araucaria Mixed Forest are surrounded by the Dense Ombrophilous Forest (hereafter Dense Forest). The prominent plant species of Araucaria Mixed Forest is the "Critically Endangered"—according to the International Union for Conservation of Nature—*Araucaria angustifolia* (hereafter Araucaria).

Araucaria dominates the upper canopies and accounts for more than 40% of all trees within the Araucaria Mixed Forest (Robinson et al. 2018). It is a pioneer species and acts as a nurse-plant for other native tree seedlings (Duarte et al. 2006; Sühs et al. 2018). Rich plant diversity is found beneath its canopies, including plant species such as *Ilex paraguariensis, Mimosa scabrella,* or *Acca sellowiana*, strengthening ecological interactions (Castro et al. 2019). Not only plant diversity is found underneath Araucaria canopies. By comparing the biodiversity richness of Araucaria preserved patches with managed ones with exotic trees, such as *Pinus* and *Eucalyptus*, Fonseca et al. (2009) showed that preserved patches had richer biodiversity among 13 taxonomic groups, such as fungi, woody plants, spiders, galling insects, lichens, flatworms, opiliones, birds, and amphibians. Considering fungi, the Araucaria seedlings show a high dependency on arbuscular mycorrhizal fungi, indicating a relationship where Araucaria superficial roots develop on dead tree trunks and organic material while maintaining an active internal mycorrhizal community (Moreira et al. 2016). In preserved Araucaria remnants, soil invertebrate macrofauna is also richer than disturbed remnants, containing spider families, springtails, and earthworm species (de Morais et al. 2017). A rich insect community co-exists with Araucaria trees counting at least 100 species, such as coleopterans and hymenopterans developing under the bark, wood, and reproductive organs (Mecke et al. 2001). The attractiveness of Araucaria's highly nutritious nut-like seed, known as "*pinhão*" pulses the species dispersal in the landscape, where parrots (*Amazona pretei, A. vinacea*), parakeet (*Pyrrhura frontalis*), and blue jay species (*Cyanocorax caeruleus* and *C. chrysops*) potentially carry the nut-like seeds from 10 to 500 m in the landscape, contributing to both Araucaria and forest regeneration (Souza 2020). *Pinhão* seeds have been influencing and structuring mammal diversity, from mammal primary consumers (i.e. those feeding on seeds and fruits) to mean and apex-predators (Bogoni et al. 2020a). The nut-like peak production (from April to June) structures fauna diversity spatiotemporally (Bogoni et al. 2020b). Consequently, particularly due to the consumption of nutritious *pinhão* and the consequent structuring of local fauna, Araucaria is defined as an ecological keystone species (Bogoni et al. 2020b).

Moreover, human groups have interacted with Araucaria since Pre-Columbian times, promoting ecosystem expansion, given *pinhão* use and consumption (Reis et al. 2014; Mello and Peroni 2015; Lauterjung et al. 2018; Robinson et al. 2018). Currently, the management and consumption of *pinhão* promote economic and cultural benefits for smallholders in southern and southeastern Brazil (Reis et al. 2014, 2018; Adan et al. 2016; Tagliari and Peroni 2018; Quinteiro et al. 2019). Local smallholder management systems maintain/preserve Araucaria Forest fragments due to *pinhão* use and consumption; a practice known as "conservation-by-use" (Reis et al. 2018). Given Araucaria's ecological, economic, and cultural aspects, the species is a relevant proxy as a whole because of its umbrella-conservation and ecological keystone aspects, influencing the entire ecosystem and its associated sociobiodiversity.

One of the main conservation strategies to curb anthropic threats is the establishment of protected areas (Gray et al. 2016). Protected areas halt biodiversity loss, regulate ecological processes, and provide several ecosystem services (Watson et al. 2014). However, the Atlantic Rainforest biome, which originally covered 17.4% of Brazilian territory (Metzger 2009), accounts for only 4% of Brazil's protected area network (Oliveira et al. 2017). Ongoing problems faced by protected areas include population growth, logging, road expansion, fires, poor management, and lack of effectiveness in preserving biodiversity (Oliveira et al. 2017). A primary goal of these areas is to buffer species from these historical drivers of species decline (Monzón et al. 2011) and long-term impacts, such as climate change (Ferro et al. 2014; Scarano and Ceotto 2015; Caten et al. 2017). Climate change potentially requires species to shift their range to track suitable habitats (Vieilledent et al. 2013; Foden et al. 2019). This potential range shift may occur beyond the existing limits of the protected area network (Parmesan 2006; Vieilledent et al. 2013), influencing the protected area's effectiveness in conserving biodiversity. Chape et al. (2005) defined the extent of biodiversity distribution within protected areas as a metric to evaluate their effectiveness.

The limited effectiveness of the current protected area network to preserve Araucaria reveals that more areas are necessary to guarantee species preservation along the Atlantic Forest (Castro et al. 2019; Marchioro et al. 2020). Given climate change, Araucaria will shift its range and reduce its distribution in the future (Wrege et al. 2016; Castro et al. 2019; Marchioro et al. 2020), reducing the area in which the species is protected as well (Castro et al. 2019; Marchioro et al. 2020). Still, only the identification of potential priority conservation areas overlapped with the existing protected area network (Castro et al. 2019; Wilson et al. 2019) without evaluating the potential connectivity among species' remnant patches may mislead conservation efforts, especially due to land-use change (Joly et al. 2014). Previous studies only shed a light on potentially suitable areas for Araucaria remnant populations under climate change (Castro et al. 2019; Wilson et al. 2019). More recently, Marchioro et al. (2020) showed that climatically suitable areas under climate change for Araucaria would be also affected by land-use, which contributed to reducing potentially suitable areas for the species. We aimed to improve all these efforts for Araucaria conservation using the baseline of these previous studies targeting the Araucaria's vulnerability under both climate change and current land-use and its potential connectivity among remnant patches. First, we followed their steps by projecting Araucaria's current and future distribution under climate change scenarios. Second, we overlapped land-use in the Araucaria projected distribution to define clearly where the species might occur despite habitat change. Third, we calculated the area of Araucaria occurrence already encompassed by the protected area network. Finally, we estimated the connectivity of the species remnant populations inside and outside protected areas to indicate (i) if the species is prone to be more isolated in the future; (ii) to show a light of hope in the Araucaria conservation scenario according to species' connectivity potential through the landscape; (iii) to describe which protected areas are playing a major role by conserving and protecting the species. The effectiveness of the existing protected area network was thus assessed by calculating Araucaria potential occurrence within protected areas in the present and the future, sensu Chape et al. (2005), considering climate change and land-use; and Araucaria's potential connectivity in the present and under projected scenarios in 2085 also considering climate change and current land-use by employing a Species Distribution Modelling approach.

No previous studies have evaluated the Araucaria's conservation potential within its natural occurrence area (i.e. the Mixed and surrounding Dense Forests) nor targeted the species connectivity capacity in the landscape under both climate change and land-use. To assess if Araucaria is effectively protected within its original distribution area, we evaluated the hypothesis on the topic of current and projected scenarios that potential connectivity among occurrence patches would be insufficient to connect Araucaria remnant populations. We expect that because of climate change these Araucaria relict populations will not be encompassed by the existing protected area network nor potentially connected throughout the landscape to major protected areas. Also, relict populations will be isolated in different subpopulations at higher elevations, preventing the connectivity among subpopulations, an unprecedented appraisal over Araucaria's natural extent. We expect that by identifying refuge and climatically suitable areas for Araucaria species in the future, we could strengthen conservation efforts, such as the creation of ecological corridors, the identification of climatic refuge areas, and promote the creation and maintenance of new or existing protected areas to preserve these threatened ecosystems.

Methods

Study area and species occurrences

Our study area covered the natural Araucaria occurrence area—the Mixed Ombrophilous Forest and Dense Ombrophilous Forest (Fig. 1). Occurrence points of Araucaria came from field surveys from March 2018 until January 2019, and from two databases: "Global Biodiversity Information Facility Data Portal" (GBIF, 2021); and "Brazilian Biodiversity Portal" (https://portaldabiodiversidade.icmbio.gov.br/portal/). Our raw dataset initially counted 953 occurrence points. We removed 8 duplicate points (same georeferenced position) in the raw dataset and another 121 occurrence points outside the study area (occurrence points within ecosystems that do not fit ecologically for Araucaria distribution, such as the Cerrado biome). We thus selected only occurrence points within 1 km^2 grid cells with complete climatic data used to perform the SDM. Our final dataset had 324 1 km^2 presence points. Our dataset encompasses properly the climatic variability and current Araucaria distribution because of extensive field-surveys throughout the Mixed and Dense Forests; besides our efforts to understand Araucaria phenology and ecology, which allowed us to correctly project its distribution, level of threat, and potential connectivity in the landscape.

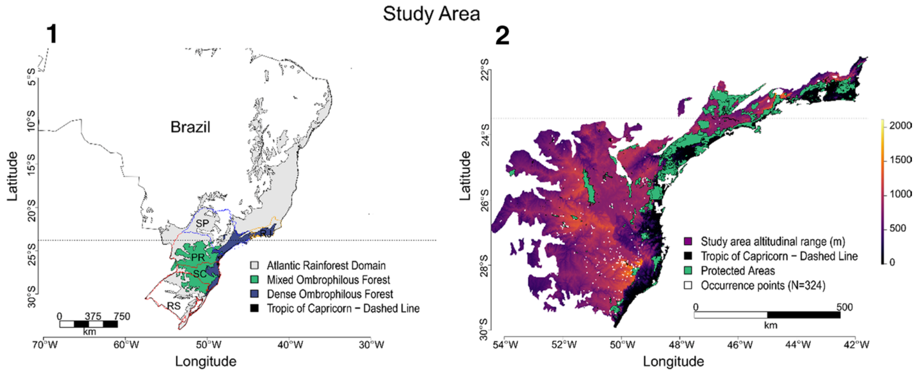

Fig. 1 **1** The Brazilian Atlantic Rainforest biome with the Mixed Ombrophilous Forest (green) and Dense Ombrophilous Forest (blue). The red border represents the three Brazilian southern states where the original Araucaria Forest extent was mainly distributed: Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS). The blue and yellow borders represent respectively the São Paulo (SP) and Rio de Janeiro (RJ) states where relict Araucaria populations remain at higher elevations through the Mantiqueira Hills. **2** The elevational gradient through the Mixed and Dense Ombrophilous Forests. White dots show occurrence points of Araucaria with complete environmental/climatic data in 1 km^2 grid cells. Green polygons indicate the distribution of Brazilian protected areas

Climatic dataset

Current and future climatic data came from the WorldClim Global Climate Database, Version 1.4 (http://worldclim.org/bioclim/), generated from interpolated climatic data from 1950 to 2000 (Hijmans et al. 2005). The 19 WorldClim bioclimatic variables consist of derived variables from (i) maximal, minimal, and average temperatures; and (ii) average precipitation; at 30 arc-seconds resolution (~ 1 km spatial resolution). The altitude variable was downloaded from the 'AmbData' website at 30 arc-seconds resolution—a specialized Brazilian website which supplies environmental and climatic variables for Species Distribution Modelling—(http://www.dpi.inpe.br/Ambdata/). To reduce multicollinearity among our variables and to follow the best practices in SDM construction (Fourcade et al. 2018) we performed (i) Principal Component Analysis (PCA), (ii) correlation comparison among the 20 variables, and (iii) factor analysis. We also assessed Araucaria ecological aspects to select correctly the climatic variables to perform in the SDM, once biological knowledge is important for variables selection (Porfirio et al. 2014). Based on these three criteria and ecological aspects of the target species, we selected 4 variables to use in our models: (i) annual mean temperature; (ii) mean diurnal range (iii) temperature seasonality, and (iv) annual precipitation (Fig. S1).

We selected three Global Circulation Models (GCMs) to simulate future climate for 2085 (average of 2071–2100) according to a hierarchical cluster grouping between nine GCMs correlated with the 19 WorldClim bioclimatic variables (Varela et al. 2015): NASA Goddard Institute for Space Studies E2-R Model—GISS-E2-R; and another hierarchical clustering selecting other two non-related GCM (Knutti et al. 2013): Hadley Global Environmental Model 2—HadGEM-ES; and Norwegian Earth System Model 1—NorESM-M, all available for download at the WorldClim website (https://www.worldclim.org/data/v1.4/cmip5.html). We considered two emissions scenarios (Representative Concentration Pathways) for climate projection in the future—RCPs 4.5 and 8.5. The RCP 4.5 or "mitigation scenario" is considered as a medium stabilization scenario according to its radiative forcing level for 2100 (van Vuuren et al. 2011), whereas the RCP 8.5, a “pessimistic scenario”, is characterized by continuous CO_2 emission and temperature increase from 3.5 to 5 °C (Riahi et al. 2011; Bellard et al. 2014).

Land-use data

We used “Mapbiomas Collection 5” (1985–2019 data; Souza et al. 2020) land-use maps for the Atlantic Forest biome (https://mapbiomas.org/) for the year 2019. These data are classified into five land-use categories (i.e. Forest; Non-Forest Natural Formation; Farming; Non-vegetated areas; and Watercourses). We selected three land-use categories from *Mapbiomas* collection and extracted specific sub-categories: (i) Farming (selection of the ‘Mosaic of Agriculture and Pasture’): a combination of both agriculture and pasture layer; (ii) Forest (selection of ‘Forest Plantation’) because *Pinus* sp. plantations for cellulose fiber production are economically important in southern Brazil; and (iii) Non-Vegetated Areas (selection of ‘Urban Infrastructure’). All spatial data were downloaded in their original resolution (30 m pixels) and were resampled to 30 arc-seconds resolution. We used these land-use sub-categories to further overlap with Araucaria projected distributions (i.e. current and future distribution). We defined a minimum percentage of land conversion to calculate the area change under current land-use for each category before overlapping with Araucaria projected occurrence outputs. Because of Araucaria’s endangered status combined with the historical human-plant interaction which conferred resilience for the species to disturbances (Reis et al. 2018; Tagliari et al. 2021), it is common to find Araucaria trees in transformed ecosystems, such as urban and agricultural landscapes with suitable climatic conditions. Consequently, for ‘Forest Plantation’ and ‘Mosaic of Agriculture and Pasture’ we set a minimum of 30% of land conversion, while for ‘Urban Infrastructure’ we set a minimum of 50% of land change. For the calculation of area change with each “land-use” category overlapped with projected occurrence maps, we used Quantum GIS with the “rasterize” function (QGIS Development-Team version 3.3 2018).

Species distribution models

We selected five different algorithms for the SDM: (i) Artificial Neural Network (ANN); (ii) standard parametric GLM (Generalized Linear Model); (iii) non-parametric GAM (Generalized Additive Model); (iv) Maxent (Maximum entropy; Phillips et al. 2006); and (v) Random Forest (RF), based on classification trees (Breiman 2001). We aimed to quantify output uncertainty and generate a gradient from robust (GLM and GAM) to complex algorithms, such as RF, Maxent, and ANN (Elith and Graham 2009). We combined the outputs of the algorithms following the Ensemble Forecasting (EF) approach (Araújo and New 2007). Ensemble forecasting is a method to reduce uncertainty in SDMs, balancing the accuracy and robustness of SDM models via committee averaging (Araújo and New 2007; Zhang et al. 2015).

We computed current and future projections for Araucaria distribution according to the species presence dataset. We first randomly selected 10,000 pseudo-absences within the study area to generate a presence/pseudo-absence dataset. We thus randomly split our dataset for testing (30% for model validation) and training (70% for model calibration) to evaluate the predictive power of the SDM (Hijmans 2012). We repeated this cross-validation procedure ten times (ten model runs per each selected algorithm) using tested and training data (i) to ensure that the ensemble model encompassed the entire occurrence dataset (Castro et al. 2019), and (ii) because we used regression techniques in our modelling approach, i.e. GAM and GLM (Barbet-Massin et al. 2012). We also made one run using the full dataset (i.e., no test and training data) for each selected algorithm, totalizing 55 model runs. Consequently, we could assess the model performance with both the full and the split datasets and compare the effectiveness of both datasets in predicting the species distribution.

The ensemble modelling performance was evaluated over the full and split datasets using one threshold-independent accuracy index: AUC (Area Under the receiver operating Curve, which calculates the model's probability to rank a randomly chosen species presence site higher than a randomly chosen absence site (Liu et al. 2011); and three threshold-dependent indexes: TSS (*True Skills Statistics* = *Sensitivity* + *Specificity*—1). *Sensitivity* is the ratio of correctly predicted presences to the total number of presences, while S*pecificity* is the ratio of correctly predicted absences to the total number of absences. The AUC varies from 0 to 1, and values > 0.9 indicate highly accurate capacity (Thuiller et al. 2009; Vieilledent et al. 2013; Wilson et al. 2019). TSS varies from − 1 to + 1, with 0 values indicating random previsions. Models with TSS > 0.5 are considered satisfactory to evaluate ensemble models (Zhang et al. 2015; Castro et al. 2019).

Araucaria's current distribution, its bioclimatic niche, projected distribution under both land-use and climate change scenarios

We previously set an evaluation quality threshold (minimum score of 0.6 or 60% according to AUC) to: (i) remove inaccurate models (i.e. predictions < 0.6); (ii) build the ensemble model; (iii) test and evaluate the ensemble model forecasting capacity to correctly predict species presence-absence; and (iv) make binary transformation following the committee averaging method, where the agreement of at least three out of five algorithms predicting the species occurrence indicated the conversion to binary maps (Thuiller et al. 2009). The predictive ability of the ensemble model was based on committee averaging, which sets the agreement among the five selected algorithms used in the SDM. We set "votes" to indicate the prediction of selected algorithms used in the SDM to predict or not Araucaria's current distribution. The "vote" tallies resulted in six outputs: 1 or 100% (where 5 algorithms predicted the species occurrence), $\frac{4}{5}$ or 80%, $\frac{3}{5}$ or 60%… and 0 (no accordance among algorithms). The current Species Distribution Area (SDA_c) was defined as the area where the species was predicted to be present by a majority of algorithms (at least three out of five). We could then calculate the current SDA_c for Araucaria species in km^2. Also, using 1000 random points sampled in the SDA_c, we calculated the frequency, mean values, and 95% quantiles for the selected climatic variables used in the SDM to describe Araucaria bioclimatic niche.

Future ensemble forecasting combines the predictions of SDMs with GCMs, producing multiple distribution maps (Porfirio et al. 2014). We explored the range of projections, creating the same "votes" as for the current distribution (i.e., committee averaging method). We combined climatic data from the three different GCMs (NorESM1-M, GISS-E2-R, and HadGEM2-ES) with the five algorithms previously selected (ANN, GAM, GLM, Maxent, and RF) for the SDM. We thus obtained 16 possible "votes" (i.e., $1,\frac{14}{15},\frac{13}{15},\frac{12}{15}\ldots,\frac{2}{15},\frac{1}{15},0$). The areas where most predictions indicated Araucaria's presence in the future (i.e. > 50% of the combined models) we defined as a suitable area for the species' future occurrence: the SDA_f. These projections were calculated for the year 2085, under both RCPs (4.5 and 8.5), and two novel dispersal hypotheses: Full-Dispersal and Zero-Dispersal (see Vieilledent et al. 2013).

The Full-Dispersal scenario considers the possibility for Araucaria to colonize new climatically favorable sites outside the current species' projected distribution. The Zero-Dispersal hypothesis considers the impossibility for Araucaria to naturally colonize new climatically favorable sites outside the current species' projected distribution. Finally, we converted all suitable projected areas in the present and under future climate change scenarios to binary maps (i.e. 0 for species absence and 1 for species presence). We overlapped these projected binary maps with climatically suitable conditions for Araucaria with the current land-use map (i.e. year 2019) generated by the combination of three land-use sub-categories. We used current land-use data within Araucaria's distribution maps to create a more realistic output of the species distribution in the present and under future climatic scenarios.

Effectiveness of the protected area network and connectivity of Araucaria projected occurrence

To evaluate the protected areas' effectiveness (sensu Chape et al. 2005) and the connectivity of Araucaria remnant areas within the Mixed and Dense Forests, we first overlapped current land-use binary maps within the protected areas polygons. We selected the three main categories of Brazilian protected areas—Sustainable Use ("Uso Sustentável"), Strictly Protected ("Proteção Integral"), and Private Reserves of Natural Heritage ("Reserva Particular do Patrimônio Natural"), from the "SOS Mata Atlântica" and "Protected Planet" websites (http://mapas.sosma.org.br/ and https://www.protectedplanet.net/en, respectively). Second, we calculated the area (in km^2) occupied by Araucaria within and outside protected areas leaning on current land-use data. Third, to calculate the connectivity of Araucaria projected populations we used the graph theory, where we defined a centroid in the center of current and future binary maps distanced ~12 km from each other with arcs connecting different centroids. The centroids were connected if the distance was inferior or equal to 0.15° (we assumed that Araucaria projected remnants are only connected to the neighboring grid cells in the height direction; sensu Vieilledent et al. 2013). Connectivity was defined as the sum of the arcs connecting each nearest node. The sum of the total number of connected arcs between nodes is a direct measure of network connectivity. This measure allows interpreting how Araucaria remnant projected populations could be connected throughout its natural distribution in the present or under climate change scenarios (Matisziw and Murray 2009; Vieilledent et al. 2013), within and outside protected areas, besides considering the land-use change.

All computations involving the SDM were made using "BIOMOD 2" package (Thuiller et al. 2009) and generated using *R* environment (R Core Team 2020). We used R spatial libraries: "sp", "maptools", and "raster" to convert continuous maps to binary maps. To compute Araucaria connectivity we used the package "spatgraph" also under *R* environment. All maps were built with latitude/longitude relative to the coordinate reference system WGS 84 datum.

Results

Model's performance

Araucaria's potential distribution was supported by accurate model predictions and high statistic results evaluating the ensemble modelling and committee averaging predictions (Table S1). From the ensemble modelling before committee averaging, we obtained the mean value of the Area Under the Curve from 55 models (AUC = 0.788). The committee averaging performance was also backed by satisfactory statistics results (TSS > 0.556, Sensitivity > 0.88, and Specificity > 0.67). All performance indices showed that the five algorithms (ANN, GAM, GLM, Maxent, Random Forest) selected for the SDM can be used to predict Araucaria's bioclimatic niche and species distribution. The variables selected to perform the SDM indicated the annual mean temperature and temperature seasonality were the two main variables explaining species distribution (Table S2).

Current species distribution area and its bioclimatic niche

The current occurrence area (SDA_c) calculated for Araucaria was 135,468 km^2 with no current land-use. This climatically suitable area lost another 20% of its extent considering current land-use, resulting in 108,174 km^2 of climatically suitable areas. The SDA_c mainly covers the (i) Santa Catarina's state highlands (southeast Mixed Forest region, in the surroundings of *São Joaquim* National Park) and the state's central region (surroundings of *Araucária* National Park); (ii) the Paraná's state Plateau (Environmental Protection Areas of *Campos Gerais* and *Serra da Esperança* and *Palmas* Wildlife Refuge), and the state's northeast region (surroundings of Curitiba municipality along the *Guaricana* and *Saint-Hilaire* National Parks); and (iii) the "Campos" Highlands at Rio Grande do Sul state, in both natural-forested (within the Araucaria Mixed Forest) and natural non-forested areas, where two major protected areas encompass the predicted occurrence area: *Aparados da Serra* and *Serra Geral* National Parks (Fig. 2). Another Araucaria remnant occurs at the Mantiqueira Hills region and the surrounding areas of *Serra da Bocaina* and *Itatiaia* National Parks, along the border of São Paulo, Minas Gerais, and Rio de Janeiro states. The bioclimatic niche (Table S3) of Araucaria indicates that the species is adapted to areas where the seasonality of the temperature varies from 25.69 to 32.58 °C; the mean annual temperature ranges from 14.1 to 17.8 °C; and mean diurnal temperature averages 10.9 °C. The species occurs at a mean altitude of 645 m above sea level, ranging from 5 to 1653 m. The annual precipitation average was 1701 mm $year^{-1}$.

Araucaria vulnerability to climate change and protected areas network effectiveness

All future climatic scenarios (RCP 4.5 and 8.5, Full and Zero-Dispersal hypothesis in 2085) were pessimistic for the species. Projections indicated a range contraction of climatically suitable areas for Araucaria from 65 to 88% when compared to the current occurrence area with land-use (i.e. 108,174 km^2). Furthermore, future climatic suitable areas shifted to more elevated areas (i.e. from 1056 to 1142 m). Under the Zero-Dispersal hypothesis and RCP 8.5, the future suitable area is expected to be reduced by 88% (i.e. only 15,766 km^2 of climatically suitable areas). Assuming current land-use and future climate change scenarios, it is expected that climatically suitable areas will reach no more than 12,000 km^2, primarily at more elevated regions (from a mean of 645 m in the present to a mean of 1142.5 m in 2085, under RCP 8.5 and Zero-Dispersal hypothesis; see Table S4 for a complete description of the upward elevational shift for the species).

Also, protected areas do not effectively encompass Araucaria distribution (Fig. 3). Current projections showed that only 7500 km^2 (or 7%) are covered by the protected area network, despite the 108,174 km^2 of climatically suitable areas for Araucaria occurrence in the present (see Table 1 for a complete comparison of Araucaria projections encompassed or not by protected areas). Finally, projections for 2085 under RCP

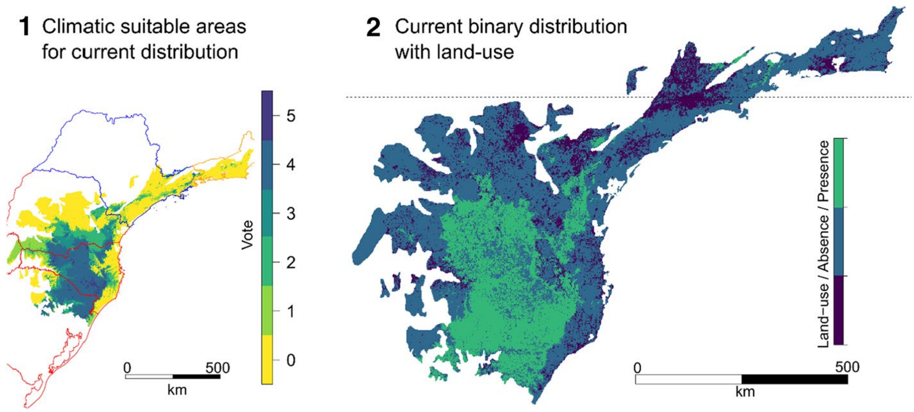

Fig. 2 The *Araucaria angustifolia* (Araucaria) current predicted distribution. **1** From three votes (light blue) up to five votes (dark blue) suggests, according to the committee averaging method, the species presence. Other color shaded areas (votes 2 and 1) represent incertitude among algorithms; 0 vote (yellow) shows that no algorithm predicted species' potential occurrence. The species distribution area was calculated over the agreement of at least 3 votes, totalizing 135,468 km^2. **2** The current binary (presence and absence) occurrence under current land-use for Araucaria. Land-use reduced suitable occurrence areas up to 20% (i.e. 108,174 km^2)

8.5 showed that only 11,993 km^2 will be climatically suitable areas for Araucaria. However, only 11% of this projected occurrence area will be covered by the existing protected area network (i.e. 1352 km^2).

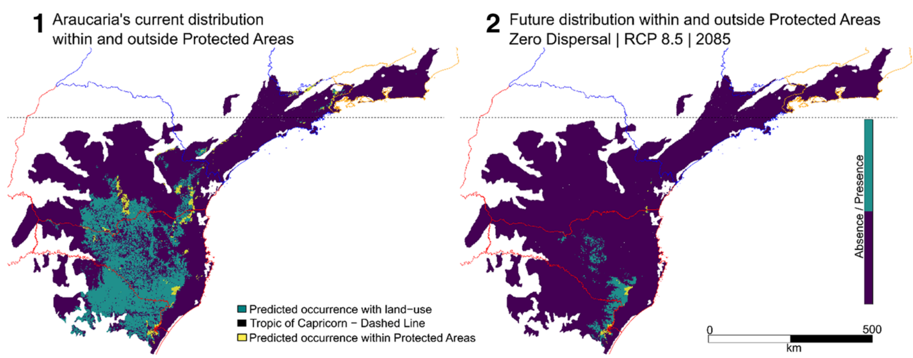

Fig. 3 Predictive scenarios for Araucaria distribution encompassed or not by existing protected area network (i.e. current distribution and under climate change: Zero-Dispersal hypothesis in 2085 and RCP 8.5) with current land-use. **1** From 108,174 km^2 climatically suitable for araucaria occurrence (species presence in blue), only 7500 km^2 are encompassed by protected areas (yellow-green). **2** The future predictive scenario in 2085 (Zero-Dispersal hypothesis and RCP 8.5) indicates that few existing protected areas throughout the Mixed and Dense Forests will encompass species occurrence. These remnant areas covered by existing protected areas are mostly distributed at Santa Catarina highlands (*São Joaquim* National Park) and the "Campos" ecosystem region, at Rio Grande do Sul state. In this worst-case scenario, only 1353 km^2 (i.e. 11%) of 11,993 km^2 will be encompassed by the protected area network

The connectivity projected for Araucaria distribution and potential refuge areas

Along the 108,174 km^2 predicted to be climatically suitable for araucaria in the present assuming current land-use, we identified 715 arcs connecting 744 adjacent nodes (Fig. 4). Also, 202 arcs are connected within protected areas, whilst another 513 are distributed mainly at the three Brazilian southern states and through elevated areas at Mantiqueira and Bocaina hills, in the border region of Minas Gerais, São Paulo, and Rio de Janeiro states. Consequently, projected occurrence in the present indicates the connection between protected and unprotected Araucaria remnants populations. Future scenarios in 2085 indicated connectivity loss from 58% (298 connecting arcs—RCP 4.5) to 79% (144 connecting arcs—RCP 8.5) compared to current connectivity (Table 2). The most pessimistic climate change scenario (Zero-Dispersal hypothesis and RCP 8.5) indicated only 36 connected arcs within the current protected area network (Fig. 4); and another 108 arcs outside areas protected by Brazilian legislation. Additionally, this scenario revealed that Araucaria's projected occurrence will be mainly connected through Santa Catarina and Rio Grande do Sul states. Protected areas such as *São Joaquim* (SC); *Aparados da Serra* (RS) and *Serra Geral* National Parks (RS) will be key regions to connect potential refuge areas for Araucaria in the future. The central region of Santa Catarina state could also be prioritized as a key-spot for Araucaria future protection, where *Araucaria* National Park (SC) and *Palmas* Wildlife Refuge (PR) protected areas might connect future projected remnants. Future optimistic scenarios (Full-Dispersal hypothesis and RCP 4.5) showed that *Itatiaia* and *Serra da Bocaina* National Parks, at Mantiqueira hills region, could be also relevant refuge areas for Araucaria in the future.

Discussion

Araucaria will be threatened by climate change in the long-term future. The species will not be effectively covered by the existing protected area network and remnant subpopulations will be poorly connected. Two different regions could embrace a *hopespot* (Rezende et al. 2018) for Araucaria's future conservation as climatic refuge areas. In southern Brazil, key-areas could connect remnant populations with major protected areas: (i) in Santa Catarina central and southeastern regions (surroundings of *São Joaquim* National Park and *Serra da Francisca* Environmental Protection Area); (ii) Paraná central region along with the Environmental Protection Areas of *Campos Gerais* and *Serra da Esperança*, besides the *Palmas* Wildlife Refuge; (iii) Rio Grande do Sul northern region could also connect unprotected remnant patches in the surroundings of *Aparados da Serra* and *Serra Geral* National Parks. The second refuge occurs through the Mantiqueira Hills (alongside the states' border of Rio de Janeiro, São Paulo, and Minas Gerais), near *Itatiaia* and *Serra da Bocaina* National Parks.

Our predictive models indicated Araucaria range contraction upwards as the species climatic suitable niche is favorable under milder temperatures. This is particularly important because the species is associated with constant moist and cool conditions with no dry season (Neves et al. 2017). Consequently, we also recommend the creation of new protected areas in these climatically refuge areas (i.e. 1000 m above sea level). Araucaria's current distribution along the Mixed and surrounding Dense Ombrophilous Forests allows the connectivity between potential remnant populations and existing

Table 1 The effectiveness of protected area network for *Araucaria angustifolia* (Araucaria) under current and future (2085) climate change and land-use: RCP 4.5 and 8.5; Full and Zero-Dispersal hypotheses

Species	Year	RCP	Dispersal scenario	Suitable area presuming current land-use (km^2)	Area within protected area network (km^2)	Percentage of projected occurrence area within protected areas according to area calculated with land-use (%)
Araucaria angustifolia	Present	NA	NA	108,174	7500	7
	2085	4.5	Full	36,365	2443	7
		4.5	Zero	36,240	2361	7
		8.5	Full	11,993	1352	11
		8.5	Zero	11,993	1352	11

We calculated the area (km^2) within the protected area network according to the SDM. The results indicated that protected areas poorly encompass projected outputs. For current distribution, more than 100,000 km^2 are climatically suitable (despite land-use) for Araucaria occurrence, however, only 7500 km^2 lies within protected areas. As climate change will reduce the species range until 2085 (between 11,993 to 36,365 km^2), only 7 to 11% of these predicted occurrence areas will be encompassed by the protected area network

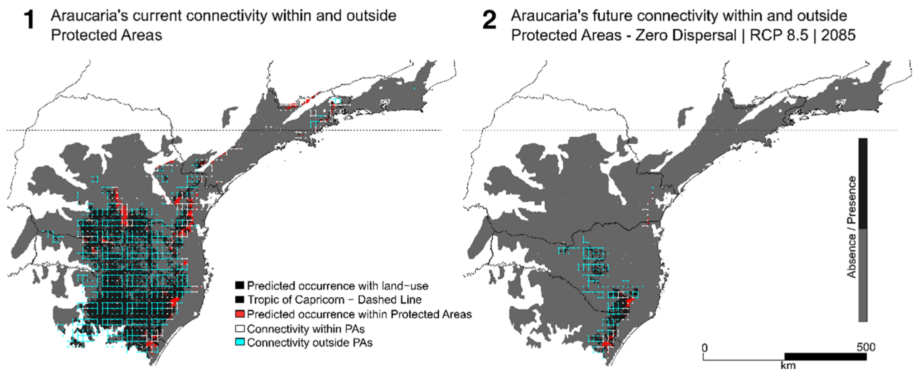

Fig. 4 The Araucaria projected connectivity at the present and under climate change (RCP 8.5, Zero-Dispersal hypothesis). We overlapped predicted connectivity over the Araucaria occurrence area (presence/absence binary maps). We set a node where models indicated Araucaria presence and arcs connecting adjacent nodes (turquoise, and white segments). The sum of the arcs is the result of computed connectivity (C). **1** The Araucaria current connectivity outside protected areas was C = 513, while C = 202 within the protected area network (C = 715 throughout the entire extent). Current connectivity through the Mixed and Dense Forests indicates an optimistic scenario despite current land-use (i.e. habitat change). **2** Connectivity scenario for 2085—RCP 8.5—Zero-Dispersal was predicted to decrease by 79% (C = 144, where C = 36 within protected areas). Future connectivity reduced from 58.32% (RCP 4.5/Full-Dispersal) until 79% (RCP 8.5/Zero-Dispersal) compared to current computation

protected area network (Fig. 4), an optimistic appraisal that has not been foreseen in this study.

Protected areas within the Mixed and Dense Ombrophilous Forests are concentrated especially in eastern regions of the states of Paraná, Santa Catarina, Rio Grande do Sul, and São Paulo states (Fig. 1). These protected areas interconnect both the Mixed Forest and the Dense Ombrophilous Forest as part of conservation efforts focused on the coastal Atlantic Forest domain. However, less than 15% of the current Araucaria distribution area is encompassed by protected areas, especially in the southern inland of the Atlantic Forest, i.e. the Mixed Forest (Fig. 3). As the current patches of projected remnant populations in the present still allow species connectivity in the landscape (Fig. 4), we could affirm that the existing protected area network might connect remnant populations through the landscape, despite not being effectively covered by protected areas (sensu Chape et al. 2005).

Climatically suitable regions in the future, nevertheless, will not be effectively covered by the existing protected area network. Therefore, it is paramount that conservation strategies should be prioritized by reinforcing the creation and maintenance of the protected area network. Interestingly, the proportional increase of protected patches under climate change scenarios may be explained because Araucaria future projections showed range contraction to more elevate areas within already existing protected area network (Fig. 3; Table 2). Castro et al. (2019) and Marchioro et al. (2019) showed that projected distribution under climate change of Araucaria was also inefficiently covered by protected areas, especially "*Integral Protection*" category of protected areas. We added another step to araucaria conservation indicating where and which protected areas could connect future species' projected distribution (Fig. 3; Table 2). We also identified that the upward elevational pattern will occur especially at Santa Catarina's highlands, Rio Grande do Sul's grasslands, and the central plateau of Paraná state. These regions should also be prioritized for conservation efforts as refuge areas, potential ecological corridors, or climatic key-areas to

Table 2 Araucaria connectivity under current baseline and climate change scenarios assuming current land-use

Species	RCP (2085)	Dispersal Scenario (2085)	Total connectivity|outside PA|within PA	Connectivity loss compared to current baseline (%)	Remnant projected populations remain connected?
Araucaria angustifolia	Current scenario	Current scenario	715/513/212	NA	Possible. Through the entire southern states and more elevated areas at eastern regions of Mantiqueira and Bocaina Hills
	4.5	Full	298/221/77	− 58.32	Partially. Through southern states; specific regions at Mantiqueira Hills, *Serra da Bocaina* and *Itatiaia National* Parks
	4.5	Zero	295/221/74	− 58.74	
	8.5	Full	144/108/36	− 79.86	Poorly. Isolated remnant populations at Santa Catarina (*São Joaquim* National Park) and Rio Grande do Sul states (*Serra Geral*, *Aparados da Serra* National Parks)
	8.5	Zero	144/108/36	− 79.86	

Connectivity will decrease from 58.32% (RCP 4.5/Full-Dispersal) to almost 80% (RCP 8.5/Zero-Dispersal) in 2085. These future scenarios show that Araucaria remnant populations might remain isolated at higher elevations, uncovered by current protected area (PA) network, and unconnected with other subpopulations throughout the Mixed and Dense Forests create new protected areas. Also, specific protected areas, such as *São Joaquim* (SC); *Campos Gerais* (PR); *Aparados da Serra* (RS); *Serra Geral* (RS/SC); *Itatiaia* (RJ), *Serra da Bocaina* (RJ/SP) National Parks ("Integral Protection" category) are essential to integrate conservation strategies aiming to reduce anthropic threats to the species, such as deforestation, logging, habitat loss, and climate change. These actions would also benefit the maintenance of genetic diversity among subpopulations (Carnaval et al. 2009). For species with low dispersal potential—such as Araucaria, with dispersal ranges from 35 to 291 m, and averaging 92 m (Bittencourt and Sebbenn 2007)—preserving adjacent areas climatically or environmentally stable over time could be a relevant strategy (Oliveira et al. 2015), especially when climate change may shift the species' range outside existing protected areas (Hannah et al. 2007).

Uncertainty in SDMs and strategies to improve the modelling approach

Any modelling exercise involves uncertainty (Araújo et al. 2019). Despite the arbitrary choice of algorithms to perform the SDM, there is no "silver bullet" in correlative SDM algorithms, which means that there is no uniquely better algorithm to specifically perform an SDM (Qiao et al. 2015). The SDM generated in this study disregarded biological aspects of Araucaria; such as gene flow (Stefenon et al. 2007), phenotypic plasticity (Reis et al. 2018), or ecological interactions with local fauna (Iob and Vieira 2008; Bogoni et al. 2020b), and human-groups (Reis et al. 2014; Tagliari and Peroni 2018; Sühs et al. 2018). These are adaptive mechanisms that confer resilience to species under climate change (Caten et al. 2017). Adaptive mechanisms, however, are challenging to add to predictive models (Foden et al. 2019). The "Zero-Dispersal" and "Full-Dispersal" hypotheses were a strategy to improve our correlative SDM (Dormann et al. 2012), as we could infer about species capacity to occupy or not newly climatic suitable areas. Connectivity computation was also an approach to enhance ecological implications using an SDM (Vieilledent et al. 2013). We also added current land-use as a proxy to infer about habitat change aiming to improve the reliability of our models, once we add to our predictive occurrence maps the influence of urban structures, forest plantations and agriculture, besides pasture mosaics (Marchioro et al. 2020). Our study considered three classes of protected areas: *Integral Protection, Sustainable Use*, and *Private Reserves of Natural Heritage*. We did not include Indigenous Lands and private conservation areas according to Brazilian environmental legislation: *Permanent Preservation Areas* and *Legal Reserves*, which may contribute to enhancing species' connectivity (Rylands and Brandon 2005) and protection. Legal Reserves in Brazil encompass one-third of Brazilian protected areas (Metzger et al. 2019). We also suggest that further studies could target the importance of Legal Reserves as a strategy to enhance protected areas' effectiveness for Araucaria.

Conservation strategies and study implications

Our results were consistent when compared to previous studies in specific aspects: (i) analogous priority conservation areas identified in 2085 within the Mixed and Dense Forests; (ii) similarity in the identification of climatically suitable areas in the future for Araucaria, especially at Santa Catarina and Rio Grande do Sul highlands, Paraná central region, besides Mantiqueira and Bocaina hills (Castro et al. 2019; Wilson et al. 2019; Marchioro et al. 2020); (iii) ineffectiveness of protected area network in preserving Araucaria in the present and under future climate change scenarios (Castro et al.

2019; Marchioro et al. 2020) The novelty showed in our study indicates that Araucaria future populations will be isolated, poorly protected, and unconnected within what once was a majestic occurrence area through the Mixed and Dense Forests. Major protected areas that encompass Araucaria potential distribution (Table 2) are not connected along the landscape, an unprecedented appraisal over Araucaria conservation assessment. Our results indicate the necessity of new protected areas and the identification of climatic refuge areas for the species. The combination of refuge area identification with the species connectivity potential could generate prolific improvements in species conservation. From a more holistic perspective of conservation assessment for the relict Araucaria, we recommend the joint application of the recent studies about the species vulnerability to climate change (Castro et al. 2019; Wilson et al. 2019; Marchioro et al. 2020) with our main result about the importance of connectivity between remnant occurrence patches and protected area network. This might boost Araucaria conservation in the short and long-term. As an ecological keystone and umbrella species, by safeguarding Araucaria we protect the socioecological system and its vast associated biodiversity both in southern and southeast Brazil (Bogoni et al. 2020b), potentially promoting forest expansion (Robinson et al. 2018) and resilience to anthropic disturbances (Tagliari et al. 2021).

We recommend integrated conservation measures, such as the creation, expansion, and identification of ecological corridors and refuge areas, as well as the maintenance and expansion of protected area networks, along with collaborative management initiatives with local human groups, stakeholders, researchers, and decision-makers. This integrative scenario could enable Araucaria's connectivity, resilience, maintenance, and conservation in a fragmented, disturbed, and vulnerable ecosystem.

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Data availability The R script to reproduce entirely the results of the study is available on the GitHub digital repository (see git github.com/masemuta/araucaria_sdm).

Declarations

Conflict of interest The authors declare no conflict of interest.

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