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ORIGINAL PAPER

Will the emblematic southern conifer *Araucaria angustifolia* survive to climate change in Brazil?

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Abstract

Conifer forests dominated by Araucaria pines (*Araucaria angustifolia*) are emblematic of the humid forests in the southeast of Brazil, South America. However, these forests are highly fragmented and threatened by climate change. Despite the ecological and cultural importance of the dominant species (*A. angustifolia*), our knowledge of its climatic niche is incomplete. We aimed to understand the environmental drivers of the distribution and the climatic vulnerability of *A. angustifolia* in Brazil by modelling the extent of suitable climatic niches available for the species under the current climate and future climate scenarios. The potential distribution predicted by our model for the present was consistent with the real distribution of this species. However, our projections for future distributions show a decline in suitable climatic niches for the species, and a tendency for the species to be confined to high altitude mountain ranges and plateaus of south and southeast Brazil. Critically, most of the current protected areas will cease to harbor suitable climatic niches for the species. We conclude that prioritizing and expanding protected areas in important mountain ranges will be essential for protecting of the species in situ and to safeguard it from further habitat loss. Further research on population-level physiological responses of the species to climatic change and the role of biotic interactions will help optimize future modelling work.

Keywords Brazilian pine · Global warming · Extinction risk · Potential species distribution modelling · Climatic envelope

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Introduction

Climate change is predicted to instigate large-scale changes in species distributions and complete turnover of future ecosystems across the globe (Parmesan and Yohe 2003; Williams et al. 2007). In particular, tropical regions are of great concern (Laurance et al. 2011), as these environments harbor the bulk of earth's biodiversity. Among these, Brazil encompasses the largest extent of tropical forest in the world, thus qualifying among the main strongholds of megadiversity on the planet (Gentry 1992; Myers et al. 2000).

In the southeastern part of Brazil, the phytogeographical region known as the Atlantic Forest Domain harbors some of the highest biodiversity values (1–8% of the world species) and is an important centre of plant, insect, mammal and bird endemism (Silva and Casteleti 2003). Deservedly, this region has been assigned as a globally significant biodiversity hotspot (Mittermeier et al. 1998; Myers et al. 2000). Historically, these forests have contracted and expanded in extent throughout the last 120,000 years due to climatic changes (Carnaval et al. 2014; Carnaval 2018; Costa et al. 2018). However, more recently during the last five centuries since colonization, these forests have suffered unprecedented habitat loss, with an estimated of 28%, or 32 million hectares (Mha) of the original extent of these forests remaining (Rezende et al. 2018). Critically, deforestation of these forests continue at an alarming rate of 29,000 ha year^{-1} (SOS Mata Atlântica 2017).

Among the most emblematic and visually-striking subcategories of Atlantic Forest is mixed needle-broadleaved forest (Oliveira-Filho 2009), characterized by the occurrence of the conifer *Araucaria angustifolia* (Araucariaceae) as emergent above a forest canopy of broad-leaved angiosperm trees (Fig. 1). The species and other related members in the genus *Araucaria* are also relicts of a much more extensive Araucaria conifer forest that dominated the southern hemisphere in the Cretaceous (Ledru and Stevenson 2012). Currently however, mixed needle-broadleaved forests are restricted to highland plateaus in southern Brazil at altitudes above 500 m a.s.l. (Souza et al. 2009), covering 177,600 km^2 in Brazil (Leite and Klein 1990; Fig. 1) and a small extent (2100 km^2) in northeast Argentina (Giraudo et al. 2003).

In stark contrast to the seemingly endless resource of *Araucaria* timber in pre-colonial times, the area of extent of *A. angustifolia* is now diminishing rapidly due to wood exploitation (Wrege et al. 2009). In addition, many *A. angustifolia* populations are located in densely populated areas, and are therefore under considerable pressure from human disturbance. Even though *A. angustifolia* has been conferred legal protection, and is considered "Endangered" or "Vulnerable to extinction" in the official list of IBAMA (Brasil 2008), and also "Critically Endangered" by the International Union for Conservation of Nature (IUCN; Thomas 2013), only a tiny fraction of the former distribution of *A. angustifolia* is currently protected in reserves and national parks (Indrusiak and Monteiro 2009). The combination of considerable habitat loss, and the recent and predicted future climate changes represent a challenge for the survival of remnant populations of the species (Wrege et al. 2017).

Understanding the environmental drivers of *A. angustifolia* distribution is not solely of local relevance. Members of the genus *Araucaria* play prominent ecological and biogeographical roles in Southern Hemisphere forest ecosystems (Kershaw and Wagstaff 2001; Leslie et al. 2012), and are also of ethnoecological importance where they occur (Tibbett 2004; Aslam et al. 2013; Mello and Peroni 2015). Not surprisingly for a taxon with high conservation priority, various aspects of the biology and ecology of *A. angustifolia* have been extensively researched (Souza 2007, 2017; Silva et al. 2009). Yet, an understanding

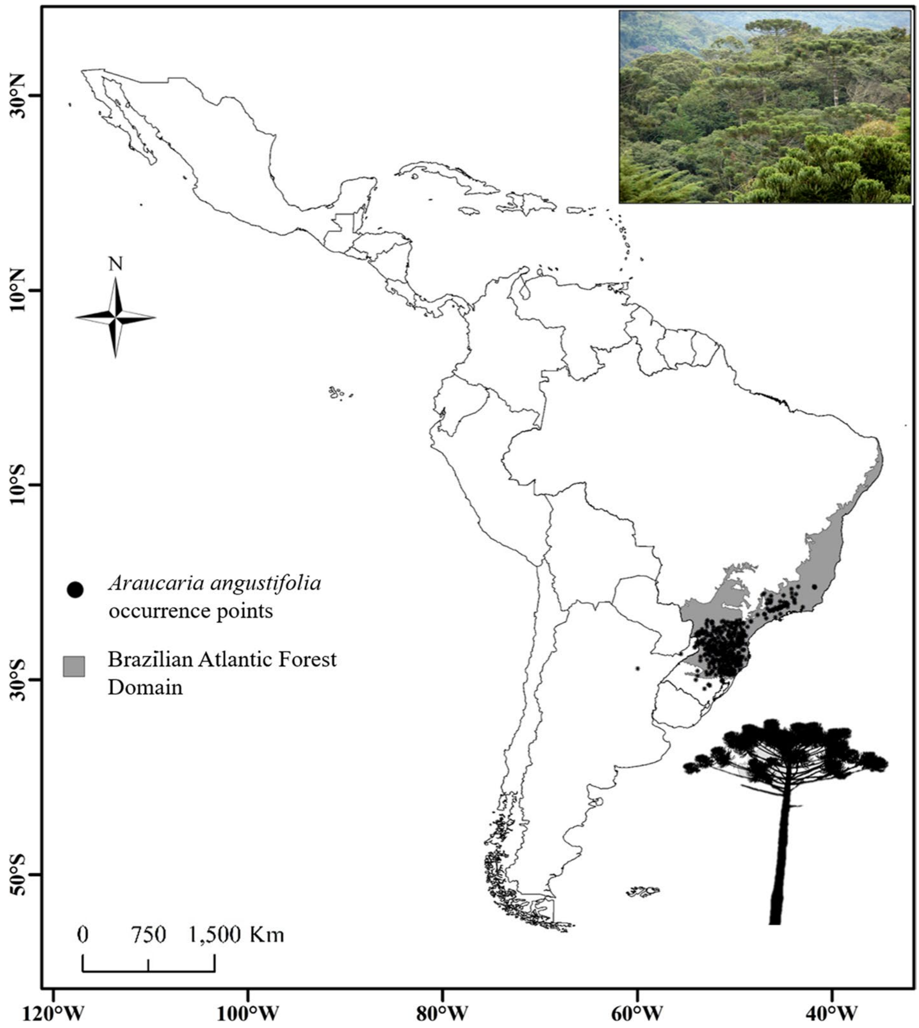

Fig. 1 Distribution of the conifer *A. angustifolia* within the South American Neotropics. Black dots denote the occurrence points used for species distribution modelling. The grey shading denotes the spatial extent of the Brazilian Atlantic Forest Domain, which is the stronghold of the species. The silhouette of a mature *A. angustifolia* tree (*c.* 30 m height) beside the map demonstrates the distinctive architecture of the species. The inset picture features a mixed needle broadleaved forest, characterized by *A. angustifolia* emergents over a broad-leaved angiosperm canopy, Itamonte, Serra da Mantiqueira range, Brazil

of the climatic niche suitability and potential distribution of *A. angustifolia* under future climate scenarios is still incomplete, and will be paramount for guiding its effective conservation and restoration (Nóbrega and de Marco 2011), especially given the critically diminished extent of the species' natural habitat. Because *A. angustifolia* is considered a key species for the ecosystem functioning of Araucaria forest (Jarenkow and Budke 2009; Käffer and Marcelli 2009; Wilberger et al. 2009), an understanding of the climatic niche of the species can also be expected to provide insights into the potential suitable area for mixed needle-broadleaved forest at large.

One way to evaluate the consequences of climate change on the potential occurrence area of a species is predictive species distribution models, or bioclimatic models (Hijmans and Graham 2006; Elith and Leathwick 2009; Franklin 2010). These methods are now widely used to predict the changing distributions of plants and animals under future climate change scenarios (Williams et al. 2009; Oliveira and Cassemiro 2013). The future potential distribution of *A. angustifolia* has yet to be modelled across its entire range—previous attempts at modelling the species' potential distribution have been limited to the southern range of the species in Brazil (Wrege et al. 2009, 2017). Additionally, these studies were based primarily on a single or two modelling algorithms, (Rezende et al. 2015; Wrege et al. 2017), thus limiting the robustness of conclusions that may be made about the species' future distribution. Critically, still little is known of the extent to which current protected areas will continue to harbor suitable climatic niches for the species. With an awareness of these gaps in our knowledge, we set out to answer the following research questions: (1) How will the suitable climatic niche of *A. angustifolia* be impacted under climate change?; (2) Will the current configuration of protected areas be sufficient for the in situ conservation of *A. angustifolia*? We hypothesized that climatic factors related to temperature and rainfall are the main drivers of *A. angustifolia* distribution. Therefore, we expected that climate change will significantly reduce the distributional extent of the species, and also critically, the extent of inclusion of the species within currently known protected areas in Brazil. To test these predictions, we use nine potential species distribution modelling algorithms to assess the change in the geographical extent of the climate niche of the species within the near future (2070) under forecasted climate scenarios.

Methods

Geographical region studied and sampling of *A. angustifolia* occurrences

The present study was focused on the Brazilian Atlantic Forest Domain (Fig. 1) which originally spanned from 1° to 30°S in latitude and 29° to 56°W in longitude, encompassing a total area of 1,117,850.79 km^2 (*Instituto Brasileiro de Geografia e Estatística*, IBGE 2014). Spread along the Brazilian coast and also inland in the southern portion of the country, the domain is extremely heterogeneous in terms of climate, geomorphology, soil and altitude (Câmara 2003; Veloso 2012). Therefore, the Atlantic Forest consists of several forest types varying widely in species composition (Oliveira-Filho and Fontes 2000; Oliveira-Filho 2009; Eisenlohr and Oliveira-Filho 2015). Among these forests types, mixed needle-broadleaved forest, dominated by our target species *A. angustifolia*, extend mainly along the Brazilian coast but also reaches Argentina (Giraudo et al. 2003) and Paraguay (Huang et al. 2007).

Mixed needle-broadleaved forest is found primarily in the south of Brazil, where it is bound by the Central Depression of Rio Grande do Sul. The original extent of these forests is estimated to be approximately 254,000 km^2, but only 1.26% (c.32,000 km^2) of this original cover remains (Ribeiro et al. 2009). At its northern limit, mixed needle-broadleaved forest experiences a tropical climate, and persists only under certain thermal conditions at high altitudes. Likewise in the coastal mountain ranges along the Brazilian southeastern coast, mixed needle-broadleaved forest are restricted entirely to the western slope of the mountain range (Backes 2009). To sample the species occurrence of *A. angustifolia* throughout its entire known distribution, we retrieved a total of 684 natural occurrence points of the species from the *SpeciesLink* database (http://www.splink.org.br/), Global Biodiversity Information Facility (GBIF, 2016), Reflora (*Virtual Herbarium*) (2018) and from vegetation plots coordinates contained in the NeoTropTree website (Oliveira-Filho 2017). The points retrieved from the databases were screened manually in Google Earth to ensure the accuracy of the location data. We also excluded points in urban areas. For our analysis, we kept only occurrence records with a distance of more than 10 km from each other (spatially unique records), so as to match the resolution of the GIS environmental layers from which we would obtain environmental data for each point (see later). Therefore, we used 434 of the 684 occurrence points in the final analysis (Fig. 1).

Environmental variables and modelling of suitable climatic niche for *A. angustifolia*

Our definition of "suitable climate" follows Costion et al. (2015) in referring to an area or areas providing a climatic niche that is currently occupied by the species studied (henceforth "suitable climatic niche"). To investigate the suitable climatic niche of *A. angustifolia*, we considered 19 bioclimatic variables as candidate predictors, which were extracted from the CHELSA network (climatologies at high resolution for the earth's land surface areas; Karger et al. 2017), using a spatial resolution of 5 arc-min (~ 10 km). We used data from CHELSA because it incorporates recent (1979–2013) climate data and also because of the robustness of the data for mountainous areas (Karger et al. 2017). The 19 bioclimatic variables are derived from monthly temperature and precipitation averages and the detail information of each one is presented in the website http://chelsa-climate.org/bioclim/.

We modelled the suitable climate for *A. angustifolia* under current and future climatic scenarios using nine algorithms from 'biomod2' package (Thuiller et al. 2014) of R including: generalized boosting model (GBM), Classification tree analysis (CTA), Random forest (RF), Generalized linear model (GLM), Generalized additive model (GAM), Artificial neural network (ANN), Flexible discriminant analysis (FDA), Multiple adaptive regression splines (MARS) and Maximum Entropy (MAXENT), sensu Phillips et al. 2018). All algorithms were used with the default settings from 'biomod2' package. For each algorithm, we applied ten runs. We chose ten runs to ensure that our ensemble model encompassed the entire presence set of the species. Our strategy for extracting pseudo-absence data was through the selection of random points, which is more realistic in representing what is expected for *A. angustifolia*, since it creates pseudo-absences where we do not expect to find the species. We obtained random points along the Neotropic to represent the entire projection area of the models. Identifying suitable areas throughout the Neotropic using presence-background and presence-absence algorithms such as Maxent and GLM, respectively, requires sampling of pseudo-absences beyond the known region of the species (i.e. the Atlantic Forest). In addition, using only the Atlantic Forest region to select these pseudo-absences could inflate our omission errors by mistakenly treating a locality as "absence", since the total area would be too narrow. In our analysis, we opted to give equal weights to pseudo-absence with presence data (a prevalence ratio of 0.5), since the real prevalence ratio of *A. angustifolia* is unknown. We followed Barbet-Massin et al. (2012) and chose the same number of pseudo-absences as available presences for classification techniques (GBM, CTA and RF), and a larger number (10,000 pseudo-absences) for the remaining methods. We created 10 sets of pseudo-absences, thus totalling 100 models (10 sets of pseudo-absences × 10 runs) per algorithm.

Taking into consideration that the inclusion of a large number of parameters in a model may lead to a misrepresentation of species potential distribution (Kriticos and

Randall 2001; Chilcott et al. 2003; Williams et al. 2003), we applied a principal component analysis (PCA) and retained the first six axes, which represent ~ 95% of total inertia. We generated the PCA axes for the present and created projections of these axes on future variables using the PCAProjection function in 'ENMGedgets' package (https://github.com/narayanibarve/ENMGadgets; see also Zwiener et al. 2017). Here, the proportion of variation and the importance of each variable in the axes of the present and the future are kept equal.

We applied a cross-validation procedure, randomly splitting the data into 70% of training data and 30% of testing data in each run, a common procedure in predictive modelling that follows the guidelines of Huberty (1994) (see also Pearson 2007). The final model was based on the mean of the runs and evaluated using two metrics: (i) the area under the receiver operating characteristic curve (AUC) and (ii) the true skill statistic (TSS) (Thuiller et al. 2009). We considered successful models as those presenting $TSS > 0.4$ (e.g. Zhang et al. 2015). The successful models were then used to produce an ensemble model for each climatic scenario. To generate binary maps, we applied the vertical distance from lift curve (VD*l*) threshold, which is the most indicated choice when using presence-only data or absence data represented by selected random points in the study area (i.e. pseudo-absences data) (Liu et al. 2013a, b). As our main interest was to demonstrate potential changes in suitable area for *A. angustifolia*, we reported the current and future areas with suitable climatic niches (km^2) for the species based on our ensemble model.

To evaluate the impact of the predicted climate change, we modelled the potential distribution of suitable climatic niches for the species in 2070, using the projected variables mentioned above. We focused on the most realistic scenario of the Representative Concentration Pathway (RCP) CO_2 emissions for our projections (RCP 8.5). This emission scenario is considered realistic and corresponds to an atmospheric CO_2 level of c. 6180 $GtCO_2$ emission (2012 to 2100) and a temperature increase mean of 2.0 °C by mid-twenty first century and 3.7 °C by late-twenty first century (IPCC 2013). To allow comparisons among different future scenarios, we also obtained models that were projected based on the RCP 4.5, which is a more optimistic scenario corresponding to an atmospheric CO_2 level of c. 2860 $GtCO_2$ emission (2012 to 2100) and a temperature increase mean of 1.4 °C by mid-twenty first century and 1.8 °C by late-twenty first century (IPCC 2013). These CO_2 emissions scenarios were simulated with three global circulation models (GCMs)—CanESM2, CSIRO-Mk3-6-0, IPSL-CM5A-LR-prepared for the IPCC Fifth Assessment Report (IPCC 2013). These GCMs are the least intercorrelated, thus avoiding the use of redundant information (Pires-Oliveira et al. in preparation).

Finally, to assess the extent of *A. angustifolia* populations currently protected within protected areas in Brazil, and how these protected areas will be effective in protecting the species in the future, we overlapped areas with suitable climatic niches for all modelled scenarios on shapefiles of the boundaries of existing protected areas in Brazil under the two categories used in Brazil, viz. Protected Areas with Full Protection and Protected Areas with Sustainable Use under Law No. 9985/2000 (Brazilian System of Conservation Sites-SNUC). We calculated the area of suitable climatic niches for *A. angustifolia* within these protected areas under the current and future scenarios (RCP 4.5 and RCP 8.5) in the year 2070 and whenever both categories overlapped, the Full Protection category prevailed, avoiding overestimation in total amounts. The shapefiles for the boundaries of the protected areas were retrieved from the Brazilian Ministry of the Environmental website (MMA 2018). All maps were built using the Universal Transverse Mercator (UTM) coordinate system and the WGS 84 datum.

Results

Current distribution and environmental drivers

Based on our ensemble model, we identified a current extent of suitable distributional area of 502,769 km^2 for *A. angustifolia* within the Neotropics, with Brazil corresponding to approximately 90% (454,102 km^2) of the total predicted area (Fig. 2a), consistent with the actual distribution of the species (Fig. 1). Other countries with significant occurrences are Paraguay and Argentina (Fig. 2a). The main areas highlighted as having the optimum environmental suitability for the species were within Brazil, specifically in the two main mountain ranges of the southeast (Serra do Mar and Serra da Mantiqueira) and in the Serra Geral mountain range of the south Brazilian region. These areas are predominantly mesothermal (mean temperature of 14 °C), with rainfall regularly distributed throughout the year and altitude ranging between 400 and >1200 m. Our predictive models presented high average performance, where the minimum values were approximately TSS >0.73; AUC >0.90 (Table 1).

Models of *A. angustifolia* suitable climatic niche under future scenarios

Our projections of *A. angustifolia* suitable climatic niche under the carbon emission scenario (RCP 4.5) for 2070 show a reduction of suitable area for the species from 502,769

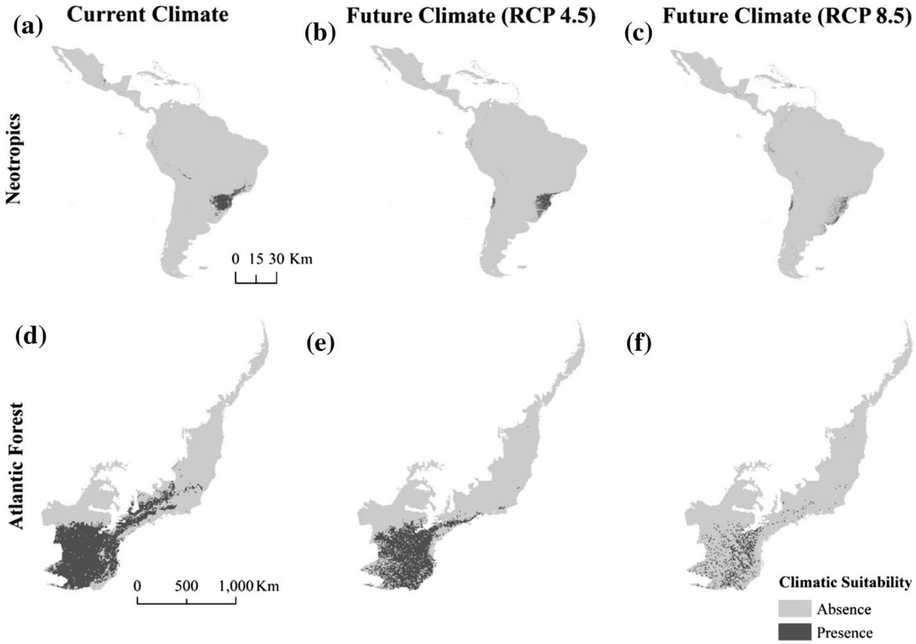

Fig. 2 Projected current (**a**) and future (**b**, **c**) areas with suitable climatic niches for the conifer *A. angustifolia* in South America. Modelling of future climatic niches is based on the Representative Concentration Pathway (RCP) 4.5 and 8.5 CO$_2$ emissions scenarios by the year 2070 in Brazil. Projections of current (**d**) and future (**e**, **f**) suitable climatic niches for the species within the Brazilian Atlantic forest domain are enlarged for clarity

Table 1 Evaluation of models produced by nine algorithms applied to obtain the potential distribution areas for the icon conifer *A. angustifolia* in South America

Algorithm	TSS mean (± SD)	AUC mean (± SD)
ANN	0.936 (± 0.016)	0.983 (± 0.006)
CTA	0.844 (± 0.031)	0.941 (± 0.018)
FDA	0.757 (± 0.032)	0.938 (± 0.010)
GAM	0.858 (± 0.032)	0.959 (± 0.008)
GBM	0.910 (± 0.023)	0.982 (± 0.006)
GLM	0.756 (± 0.027)	0.932 (± 0.012)
MARS	0.809 (± 0.027)	0.949 (± 0.009)
MAXENT	0.726 (± 0.048)	0.895 (± 0.028)
RF	0.929 (± 0.019)	0.985 (± 0.005)

The metrics used for model evaluation are the true skill statistic (TSS) and the area under the receiver operating characteristic curve (AUC)

to 363,688 km^2 in the Neotropics of South America, representing a decline of 27.7% of the current suitable climatic niche area of the species, with Brazil corresponding to 82% (299,450 km^2) of the total future predicted area under this scenario. The projection under the scenario RCP 8.5 shows a reduction of suitable area from 502,769 to 201,138 km^2 in the Neotropics, representing a decline of 60% of the current suitable climatic niche area, with Brazil corresponding to 55% (109,671 km^2) of the total future predicted area under this scenario. This reduction area in Brazil compared to the Neotropics as a whole is due the fact that the increase in suitable niches in Chile, Patagonia, under our future RCP 8.5 projections. However, it is unlikely that *A. angustifolia* will be able to migrate across natural barriers to these regions (Fig. 3c). In particular, there was a notable retraction of suitable climatic niches in the South and Southeast region of Brazil. Additionally, we found a higher isolation of the species to hilly areas in three orographic systems: Serra da Mantiqueira, Serra do Mar and the eastern parts of the Serra Geral mountain range (Figs. 2, 3).

Current and future representation of *A. angustifolia* in Brazilian protected areas

Areas with suitable climatic niches for *A. angustifolia* are currently present in 279 protected areas, representing a total of 35,202 km^2 under some kind of protection, or only 7.7% of its current climatically suitable area in Brazil. From this total, 131 are Protected Areas with Full Protection, representing 9206 km^2 or 2.0% of current climatically suitable area, and 148 are Protected Areas with Sustainable Use, representing 25,996 km^2 or 5.7% of the current climatically suitable area. Our projections for both RCP 4.5 and 8.5 scenarios in 2070 show a decline in number and total area of protected areas relative to its current projected suitable area (Fig. 3). In 2070, under the RCP 4.5 scenario, suitable climatic niches for *A. angustifolia* will only be present in 226 total protected areas, representing a total area of 18,060 km^2 or only 6.0% of its current climatically suitable area (Fig. 3). Of this total, 97 represent Protected Areas with Full Protection (6415 km^2 or 2.1% of projected climatically suitable area) and 129 are Protected Areas with Sustainable Use (11,645 km^2 or 3.9% of the projected climatically suitable area). Under the RCP 8.5 scenario, *A. angustifolia* will only be present in 101 total protected areas, representing a total area of 5603 km^2 or only 5.1% of its projected climatically suitable area under this scenario (Fig. 3). From this total, 43 represent Protected Areas with Full Protection (1341 km^2 or 1.2% of projected climatically suitable area) and 58 represent

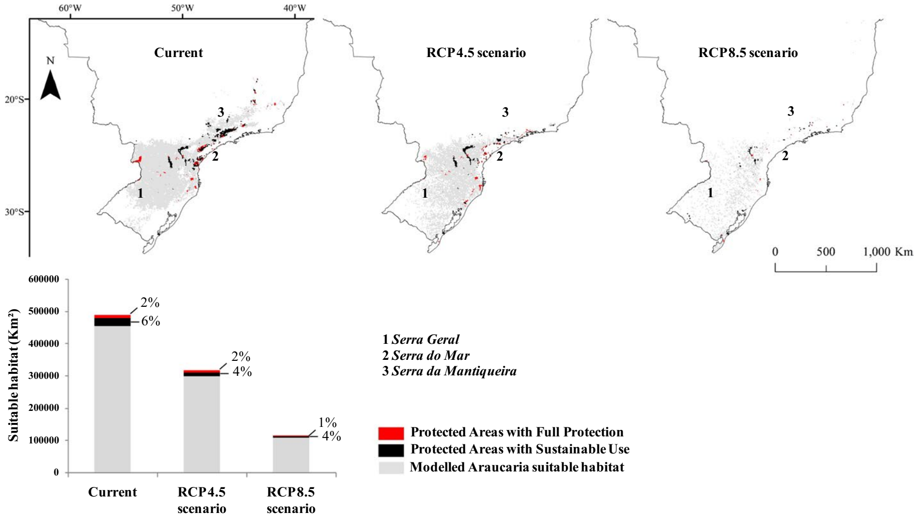

Fig. 3 The extent of protected areas separating the two conservation categories within the Brazilian Conservation System overlain onto projected areas with suitable climatic niche (light grey areas) for the conifer *A. angustifolia* in Brazil under current and future climate scenarios in 2070. Where, the red areas are Protected Areas with Full Protection and the black areas are the Protected Areas with Sustainable Use. Bar chart shows the total amount (%) of suitable habitat under protection status. The numbers represent the main mountain ranges

Protected Areas with Sustainable Use (4262 km^2 or 3.9% of the projected climatically suitable area).

Discussion

The emblematic southern conifer *A. angustifolia* is a critically endangered, but ecologically important species facing an uncertain future. To obtain a more concrete picture of the suitable climatic niches that *A. angustifolia* may be able to inhabit under climatic change, we used a robust modelling approach involving nine modelling algorithms to project the potential extent of the species in the present and under a number of climate change scenarios. Our findings paint a pessimistic picture of the future for the species, with a 27.7% reduction areas with climatic suitable for the species considering a modest scenario (RCP 4.5) and 60% reduction considering the most realistic scenario (RCP 8.5), and also a declining in relative percentage of remaining areas with climatic suitability in Brazil being protected by the year 2070 under both scenarios. Our results show that a very low percentage relative of suitable climatic niches for the species will be protected under the Full Protection category—the most effective protection in Brazil. The remaining protected areas fall under the Sustainable Use category, which allows human occupation and for which biodiversity conservation is of a lower priority (Rylands and Brandon 2005).

Accuracy of the predictions

Our predictions of current potential climatic suitability show similarities with the maps presented by Wrege et al. (2017), although this author did not present actual quantitative data. Additionally, our models corroborate with the known preference of the species for subtropical climates with mild temperatures and more pronounced seasonality (i.e. Koppen classification Cfb; Alvares et al. 2013).

Projections of future climatic scenarios are projections of probable changes that may happen due to the increase in greenhouse gases, and there remains a level of uncertainty in terms of what will eventuate (Valverde and Marengo 2010). Nonetheless, our results are fairly consistent with the literature. For instance, previous work by Wrege et al. (2009) and Rezende et al. (2015) showed similarly trends for *A. angustifolia*, although their models encompassed only the southern region of Brazil (states of Paraná, Santa Catarina and Rio Grande do Sul). One of the predicted consequences of climatic change is the displacement of species to higher altitudes and lower latitudes. There is growing evidence that higher-altitude environments undergo faster temperature changes than lower-altitude environments, with great implications for the ecosystems and species that reside at these altitude zones (Mountain Research Initiative EDW Working Group 2015; Costion et al. 2015). Because of a thermal barrier of warmer temperatures (mean maximum summer temperatures > 32 °C) resulting from the Central Depression of Rio Grande do Sul (Backes 2009), *A. angustifolia* is not displaced to lower latitudes under the RCP 8.5 emission scenario for the year 2070. Therefore, the only option for this species is uphill displacement, and therein lies the importance of mountain regions, especially coastal ones, such as the Serra Geral mountain range. These conclusions are also supported by palynological studies, which show that *A. angustifolia* would be restricted to living in increasingly less favorable and more elevated environments due to climatic change (Behling 2002; Bauermann and Behling. 2009). In the Serra da Mantiqueira mountain range, *A. angustifolia* has already been recorded at altitudes of 2000 m.

Intrinsic and other biotic factors

While we forecast an alarming scenario that may develop for *A. angustifolia* in Brazil, care must be taken in interpreting our results because they assume that the current climate or conditions occupied by the species is essential for its survival. For instance, although the species has little specificity to soil and topographic conditions, it is not clear whether their occurrence on specific soils with better water holding capacities or higher fertilities may enable them to deal with changing climatic conditions. Soil depth may be another factor worth considering. Studies show that when soil depth is reduced, there is a decrease in the mean length of the main root that is compensated by the proportional increase of its diameter and by the dense proliferation of fine roots at the superficial layer of the soil (Fonseca et al. 2009). Such shallow root architecture may compromise on adult plant support, and increase the susceptibility of plants to drought. Higher areas with shallow soils and rocky substrates may therefore continue to be unsuitable for *A. angustifolia* establishment even if these areas become climatically suitable for this species in the future. These factors remain to be examined experimentally and in the field.

Another intrinsic factor of the species that requires consideration in future modelling is the degree to which certain populations may be more resistant to changing climatic conditions. Recent studies have demonstrated a high genetic diversity across relict *A. angustifolia* populations (Stefenon et al. 2007; Souza et al. 2009), but whether some of these different populations will be physiologically more resistance to climatic change is unknown. According to Fonseca et al. (2009), the species shows several anatomical and physiological characteristics of drought tolerance that are typical of conifers. Another recent study demonstrates that *A. angustifolia* has the capacity to obtain water from clouds (Cassana and Dillenburg 2012), which suggests that the species may be able to persist in mountain regions with seasonal climates regions by intercepting cloud condensation, thus minimizing the effects of droughts, which may last up to 5 months. The inter-population variation in these characteristics deserve to be examined in greater detail.

Various authors have acknowledged problems associated with the lack of consideration of biotic interactions in potential species distribution modelling (e.g. Guisan and Thuiller 2005). Likewise, we acknowledge that biotic interactions are important aspects of *A. angustifolia* distribution (see Jarenkow and Budke 2009; Putzke 2009; Vieira and Lobo 2009) that will require addressing in future modelling. One conspicuous biotic factor relates to the co-occurrence of *A. angustifolia* with broad-leaved angiosperms (Souza 2017). According to Wrege et al. (2009), the distribution of *A. angustifolia* is associated with the occurrence of frosts, which suggests that frosts may prevent broad-leaved angiosperms from totally dominating a site, and that *A. angustifolia* may have low competitiveness in warmer climates than tropical broad-leaved species (Rambo 1951; Fonseca et al. 2009). Another level of complexity is added if underground microbial relations (Moreira-Souza et al. 2003; Moreira et al. 2016) are taken into account, considering the immense amount of interactions that must exist. Until more data of biotic interactions at the population level become available, the inclusion of these variables in potential species distribution modelling will likely remain limited.

Conclusions and future directions

Mixed needle-broadleaved forests with their conspicuous *A. angustifolia* emergents are focal points in discussions on the conservation of Brazil's endangered Atlantic Forest and also for related South American forest ecosystems. Although *A. angustifolia* is an endangered species protected by law, its broader habitat continue to be threatened by illegal wood extraction, expansion of agricultural borders, and forest fragmentation.

Our projections of the future suitability for *A. angustifolia* are cause for concern, with a reduction of c. 60% of the areas with suitable climatic niches considering the most realistic scenario and $<1.2\%$ of these suitable climatic niches within full protection reserves by the year 2070. Under the modelled scenario, only the higher parts some mountain ranges will remain favorable for *A. angustifolia* by 2070, and these areas are therefore of critical importance for the conservation of the species. Likely, these mountain ranges will require the maximum protection possible to ensure the perpetuation of suitable areas for *A. angustifolia*. Studies on other groups of imperiled biota have also demonstrated that more protected areas or establishing protected areas in mountain ranges will be important to alleviate the effects of climate change (Marsden et al. 2005; Pinto and Grelle 2009; Lemes et al. 2014). We advocate that the strategic demarcation of more legally protected areas within the original area of *A. angustifolia* occurrence will be the most effective course of action for effective conservation of mixed needle-broadleaved forest. In tropical regions, parks have been efficient in protecting ecosystems and species within their limits, mainly by preventing deforestation (Bruner et al. 2001) and also by providing a buffer against increased pressure for agricultural crop production land-use (Pinto et al. 2002). Remnant mixed needle-broad-leaved forest show great potential for long-term forest increase (Engels 2009), and having protected areas in place may facilitate the recovery of these forest remnants.

While we acknowledge limitations of modelling of potential species distribution solely on climatic bases, such models can be useful when they are applied to large scales where climatic influence prevails over biotic interactions (Pearson and Dawson 2003; Garcia et al. 2014), and also serve as a framework for future work. Studies on population-level variation in growth physiology and biotic interactions are research priorities that need addressing, and future potential species distribution modelling work on the species should incorporate these biotic variables.

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