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Cold spot microrefugia hold the key to survival for Brazil's Critically Endangered Araucaria tree

Running title: Microrefugia for Brazil's Araucaria tree

Oliver J. Wilson^{a,*} (<https://orcid.org/0000-0002-1834-7542>)

Richard J. Walters^{b,c}

Francis E. Mayle^a (<https://orcid.org/0000-0001-9208-0519>)

Débora V. Lingner^d (<https://orcid.org/0000-0002-6391-9343>)

Alexander C. Vibrans^d (<https://orcid.org/0000-0002-8789-5833>)

^a School of Archaeology, Geography and Environmental Sciences, University of Reading, UK

^b School of Biological Sciences, University of Reading, UK

^c Centre for Environmental and Climate Research, Lund University, Sweden

^d Department of Forest Engineering, Universidade Regional de Blumenau, Santa Catarina, Brazil

* Corresponding author: o.j.wilson@reading.ac.uk, +44 7854 603024

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Abstract

Brazil's Araucaria tree (*Araucaria angustifolia*) is an iconic living fossil and a defining element of the Atlantic Forest global biodiversity hotspot. But despite more than two millennia as a cultural icon in southern Brazil, Araucaria is on the brink of extinction, having lost 97% of its extent to 20th Century logging. Although logging is now illegal, 21st Century climate change constitutes a new – but so far unevaluated – threat to Araucaria's future survival. We use a robust ensemble modelling approach, using recently developed climate data, high-resolution topography and fine-scale vegetation maps, to predict the species' response to climate change and its implications for conservation on meso- and microclimate scales. We show that climate-only models predict the total disappearance of Araucaria's most suitable habitat by 2070, but incorporating topographic effects allows potential highland microrefugia to be identified. The legacy of 20th Century destruction is evident – more than a third of these likely holdouts have already lost their natural vegetation – and 21st Century climate change will leave just 3.5% of remnant forest and 28.4% of highland grasslands suitable for Araucaria. Existing protected areas cover only 2.5% of the surviving microrefugia for this culturally important species, and none occur in any designated indigenous territory. Our results suggest that anthropogenic climate change is likely to commit Araucaria to a second consecutive century of significant losses, but targeted interventions could help ensure its survival in the wild.

Keywords

Araucaria angustifolia; microrefugia; conservation; climate change; species distribution modelling; Brazil

1. Introduction

Araucaria angustifolia (Bertol.) Kuntze (hereafter 'Araucaria') is a member of an ancient genus that dates back to the Jurassic period (Forest et al., 2018). Its iconic candelabra shape defines southern Brazil's Mixed Ombrophilous Forests (MOF) (Oliveira-Filho, Budke, Jarenkow, Eisenlohr, & Neves, 2014), a unique formation of the Atlantic Forest biodiversity hotspot (L. D. S. Duarte, Bergamin, Marcilio-Silva, Seger, & Marques, 2014; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Oliveira-Filho & Fontes, 2000). Araucaria has also been a cultural keystone (Cristancho & Vining, 2004; Garibaldi & Turner, 2004) for millennia: it "could be considered the ritual object par excellence" for the indigenous southern Jê people (Fernandes & Piovezana, 2015), and it is the most frequently-used plant species among Santa Catarina state's rural population (Justen, Müller, &

Toresan, 2012). Presently, *Araucaria*'s chief economic value comes from its seeds (pinhão), which were a critical component in the southern Jê's diets before European arrival (Corteletti, Dickau, DeBlasis, & Iriarte, 2015; Loponte, Carbonera, Corriale, & Acosta, 2016) and remain a popular food source in Brazil today (Adan, Atchison, Reis, & Peroni, 2016; Souza, Uarte de Matos, Forgiarini, & Martinez, 2010; Zechini et al., 2018) – 9,293 tonnes, worth more than US\$5.5 million, were harvested in 2017 (IBGE, 2018). A National Pinhão Festival has been held in Santa Catarina for 30 years, and *Araucaria* is celebrated on Paraná state's coat of arms. But despite its long-standing cultural and economic value, 20th Century deforestation left *Araucaria* Critically Endangered (Thomas, 2013).

Between 1910 and 1970, immigration from Europe, technological advances and Brazil's growing economy sparked a logging boom which destroyed 97% of *Araucaria*'s habitat in just three generations, bringing the species to the brink of extinction (Carvalho & Nodari, 2010; Nodari, 2016; Thomas, 2013). MOF's remaining fragments now cover only 12.6% of the biogeographic region once dominated by the forest (figure 1) (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). This precarious present situation, combined with its long evolutionary history, makes *Araucaria angustifolia* the third most evolutionarily distinct and globally endangered (EDGE) of the planet's 1,090 gymnosperm species (Forest et al., 2018). And despite its legal protections, it is now at risk from 21st Century climate change. MOF occupies the Atlantic Forest's coldest and highest-altitude extremes (Neves et al., 2017), requiring high year-round rainfall, temperate summers and cold minimum temperatures (average annual temperature 12-20°C, with frequent winter frosts) (Alvares, Stape, Sentelhas, De Moraes Gonçalves, & Sparovek, 2013; Hueck, 1953; Oliveira-Filho et al., 2014; Sevegnani, Uhlmann, Gasper, Meyer, & Vibrans, 2016) – conditions likely to become rarer in the near future (Beck et al., 2018; Chou et al., 2014). Brazil is already experiencing anthropogenic warming of up to 1°C per decade, with rainfall regimes in the south disrupted as spring and autumn precipitation increases and winter rainfall declines (de Barros Soares, Lee, Loikith, Barkhordarian, & Mechoso, 2017). Continued warming and further changes to the quantity and seasonality of precipitation are predicted over coming decades (Chou et al., 2014), though their impacts on *Araucaria*'s remaining populations have not yet been tested. Indeed, no species in the genus *Araucaria* and none of the 14 highest ranked EDGE gymnosperm species – many of them with similar climatic requirements and recent population histories to *A. angustifolia* – have had their spatial responses to 21st Century climate change examined.

There is a growing recognition, however, that modelling species' responses to changes at the macroclimatic scale (1-100km) may fail to account for how individual organisms experience local-level climate (Ackerly et al., 2010; Ashcroft, 2010; Dobrowski, 2011; Hannah et al., 2014; Keppel et

al., 2012; Lenoir, Hattab, & Pierre, 2017). Fine-scale (1-100m) topography can modify both the speed and magnitude of environmental changes: shallow aquifers and lithologic contrasts can provide year-round moisture even when rainfall is reduced (McLaughlin et al., 2017); sheltered slopes have reduced rates of evaporation relative to those exposed to wind and direct sunlight (Ashcroft, Chisholm, & French, 2008; Ashcroft & Gollan, 2012); and convergent terrain permits the pooling of cold, moist air (Ashcroft & Gollan, 2012; Daly, Conklin, & Unsworth, 2010). When the “relict climates” (Dobrowski, 2011) in such locations enable a population to persist in a generally less suitable landscape they are referred to as microrefugia (Ashcroft, 2010; Hannah et al., 2014; Rull, 2009). As southern Brazil’s temperatures rise and its rainfall regime continues to change, these relict ‘cold spots’ may become critical for *Araucaria*’s continued survival. Whether these areas will act as potential ‘stepping stones’ to newly available habitats, or merely ‘holdouts’ into which its populations retreat with little hope of recovery, their identification and protection is an urgent conservation priority (Hannah et al., 2014; Keppel et al., 2012; Morelli et al., 2016).

Here we develop species distribution models for *Araucaria angustifolia* for the first time, using two different climatic datasets to project the species’ responses to 21st Century climate change, and incorporate ultra-fine scale topographic variables to investigate the role of cold spot microrefugia in moderating these. We then use high-resolution maps of remotely-sensed natural vegetation cover and the locations of existing protected areas to assess the conservation situation of these most resilient habitat patches.

2. Methods

To assess the role of microrefugia in promoting *Araucaria*’s resilience to 21st Century climate change, we first built ensemble species distribution models using established methodologies with climate data from Worldclim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) and CHELSA (Karger, Conrad, Böhner, Kawohl, Kreft, Soria-Auza, et al., 2017) (~800m resolution). We then generated a further ensemble model (‘CHELSA+’) using CHELSA climate data and three topographic variables (relative elevation, exposure of surfaces to prevailing wind and to direct insolation) inferred from a 30m-resolution elevation model. These models estimated *Araucaria*’s ecological niche at present and in 2070 under two emissions scenarios – RCP4.5 (relatively optimistic) and RCP8.5 (pessimistic, business-as-usual). We considered areas where *Araucaria*’s predicted probability of occurrence (p_{occ}) was $\geq 75\%$ in all three climate scenarios to be potential microrefugia. Using a map of remnant natural vegetation >3ha in area (Fundação SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais - INPE, 2015), we identified potential microrefugia still within natural Campos (high-altitude

grasslands) and forest fragments, as well as the larger vegetation patches these microrefugial populations may support. These locations were then cross-referenced with a database of Brazilian protected areas (UNEP-WCMC & IUCN, 2018) to assess their conservation status.

2.1. Occurrence, climate and topographic data

We modelled *Araucaria*'s potential distribution between 25-30°S and 54-48°W. Presence and true absence records for *Araucaria* were taken from the Santa Catarina forest floristic inventory (IFFSC), a state-wide, systematic survey of natural forests using 4,000 m² sample plots spaced 5-10 km apart (Alexander Christian Vibrans, Sevegnani, Lingner, de Gasper, & Sabbagh, 2010). Overall, 1,670 individual *Araucaria* trees >10cm diameter at breast height were identified in the survey, of which we used one presence record per plot.

Additional occurrences from Misiones province (Argentina), Paraná and Rio Grande do Sul were obtained from the Global Biodiversity Information Facility (GBIF, 10th January 2018, <https://doi.org/10.15468/dl.7b5jat>). After cleaning coordinates from GBIF, this combined dataset yielded 106 presence records (83 from IFFSC plots, 23 from GBIF). *Araucaria* trees were not recorded in 334 IFFSC plots; these localities were treated as true absences, although *Araucaria*'s absence from these plots may be influenced by dispersal limitations, biotic interactions or disturbance history as well as climatic conditions. A random 20% of the locality data was set aside for model evaluation, with the remainder used for building and cross-validating the models. A Mann-Whitney-Wilcoxon test showed no significant differences between these datasets in terms of latitude ($p=0.48$), longitude ($p=0.82$) or altitude ($p=0.17$).

Climate data were downloaded from Worldclim v1.4 (Hijmans et al., 2005) and CHELSA (Karger, Conrad, Böhner, Kawohl, Kreft, Soria-Auza, R.W., Zimmermann, et al., 2017; Karger, Conrad, Böhner, Kawohl, Kreft, Soria-Auza, et al., 2017) at 30 arc-second resolution. We used climate change projections for 2070 (average of 2061-2080, RCP4.5 and 8.5 emissions scenarios) from three General Circulation Models (GCMs): CCSM4, CNRM-CM5, and NorESM1-M were chosen because they have been shown to perform well in Latin America (Hidalgo & Alfaro, 2015; Lovino, Müller, Berbery, & Müller, 2018; Yin, Fu, Shevliakova, & Dickinson, 2013) and were available for both Worldclim and CHELSA at the desired resolution. Best practice in SDM construction advocates restricting inputs to biologically relevant climate factors rather than using the full set of bioclimatic variables (Fourcade, Besnard, & Secondi, 2017). We selected six, based on the subset of all variables which yielded the lowest Bayesian Information Criterion (BIC): isothermality (bio3), minimum temperature of the coldest month (bio6), mean temperature of the

coldest month (bio11), annual precipitation (bio12), precipitation seasonality (bio15) and precipitation of the driest quarter (bio17). Multidimensional scaling showed these variables were not closely correlated (for correlation statistics, see figure S1), and they appear to be biologically relevant as *Araucaria* and MOF are associated with a constantly moist climate with no dry season, and constantly cool conditions with low minimum temperatures (Alvares et al., 2013; Hueck, 1953; Neves et al., 2017; Oliveira-Filho et al., 2014).

Topographic variables (exposure to solar irradiation, exposure to prevailing winds, relative elevation) were derived from the 30m-resolution ASTER global digital elevation model, a product of METI and NASA, downloaded from <https://earthexplorer.usgs.gov>. These variables were chosen as MOF at high elevations has been observed to prefer sheltered valley slopes and river banks (Hueck, 1953; Robinson et al., 2018), and because these areas are likely to represent colder and moister microclimates (Ashcroft et al., 2008; Ashcroft & Gollan, 2012; Dobrowski, 2011; McLaughlin et al., 2017). The two exposure variables were calculated according to the methods in (Ashcroft et al., 2008) using azimuths of 315° (i.e. north-west) for solar irradiation (McCune, 2007; McCune & Keon, 2002) and 30°, 60° and 90°, subsequently averaged, for the region's prevailing winds (Camargo do Amarante, Brower, Zack, & Leite de Sá, 2001). A point's relative elevation has been shown to effectively predict the level of cold air pooling it experiences (Ashcroft & Gollan, 2012); we followed Ashcroft and Gollan (2012) by calculating this as the difference between a pixel's elevation and the minimum elevation within a 500m radius. Although these variables are themselves static (i.e. will not change over the time scales studied here), they interact with changeable climate variables and so were included as explanatory variables in our CHELSA+ model (following Stanton, Pearson, Horning, Ersts, & Reşit Akçakaya, 2012).

2.2. Model construction

Species distribution models (SDMs) were constructed using the biomod2 package (Thuiller, Georges, Engler, & Breiner, 2016) in R v.3.4.2 (R Core Team, 2017). We created ensemble models by averaging high-performing model runs from seven (CHELSA+) or eight (Worldclim, CHELSA) algorithms: generalised linear models (GLMs), generalised additive models (GAMs), artificial neural networks (ANNs), maximum entropy (Maxent (Phillips, Anderson, Dudík, Schapire, & Blair, 2017)), generalised boosting models (GBMs), random forests (RFs), classification tree analysis (CTA), and multiple adaptive regression splines (MARS). For computational reasons, Maxent was not run for CHELSA+. Each algorithm was run ten times, and assessed using the area under the receiver operating curve (AUC) and true skill statistic (TSS) metrics (Allouche, Tsoar, & Kadmon, 2006). TSS

varies from -1 to +1, with 0 signifying a model no different to random; AUC varies from 0 to 1, with a random classifier expected to score 0.5. Projections from model runs with TSS ≥ 0.65 and AUC ≥ 0.9 for both cross-validation and evaluation were averaged to produce 'hibar' ensembles; 'lobar' ensembles averaged model runs with TSS scores ≥ 0.6 and AUC ≥ 0.85 (table 1). These ensemble models were then projected into scenarios for 2070 (relatively optimistic RCP4.5 and pessimistic, business-as-usual RCP8.5) using climate data from each GCM for Worldclim and CHELSA, with an average prediction subsequently taken. Due to the computational demands of CHELSA+, only the CCSM4 scenarios were run – this GCM was chosen as it makes the most accurate predictions of temperature and precipitation in this region (Lovino et al., 2018).

For subsequent analysis we categorised the continuous model output (probability of occurrence, p_{occ}) into four equal classes, with divisions at 25%, 50% and 75%. Because we can be most confident of *Araucaria*'s presence in areas with $p_{occ} \geq 75\%$, we consider locations which fall within it in all three modelled scenarios (present, RCP4.5 and RCP8.5) to be potential microrefugia. We also consider areas which have p_{occ} of $\geq 50\%$ in all three scenarios, but which do not qualify as potential microrefugia, to have moderate climatic resilience.

2.3. Vegetation remnants and conservation areas

To analyse the effects of past habitat loss, we used the 2013-2014 SOS Mata Atlântica atlas of remnant natural vegetation (Fundação SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais - INPE, 2015). This identified areas of natural vegetation larger than three hectares using satellite imagery at 1:50,000 scale (approximately 25m resolution) in the Brazilian states of Paraná, Santa Catarina and Rio Grande do Sul, which constitute >98% of our study area; small parts of São Paulo state and Argentina's Misiones province are excluded. We used this dataset to locate areas of conservation priority, by identifying which microrefugia and moderately resilient areas occur within this remnant vegetation, and which have lost their natural vegetation. We also identified areas of remnant vegetation contiguous with significant microrefugia. We defined these as continuous areas of forest or natural non-forest (almost all of which is Campos in our study region) which either contained ≥ 100 microrefugial cells (0.09 km^2) or had microrefugial cells covering $\geq 5\%$ of their area, i.e. vegetation patches which contain relatively large areas of microrefugia, or which are small but largely resilient.

To assess the present conservation situation of these potential microrefugia, we compared the sites of microrefugia and resilient patches identified above with the locations of all Brazilian protected areas and designated Terras Indígenas within our study area (figure 1), downloaded from the World Database on Protected Areas (UNEP-WCMC & IUCN, 2018).

3. Results

Between 3.9 and 4.5 times as many model runs, from a wider range of algorithms, met our quality thresholds when using CHELSA compared to Worldclim (table 1). Since the 'hibar' Worldclim ensemble model contained only two model runs from a single algorithm, we chose to analyse the 'lobar' Worldclim ensemble; 'hibar' ensembles were used for CHELSA and CHELSA+.

Araucaria's predicted present distribution in all three models (figure 2) is similar to MOF's potential distribution (figure 1) with high-altitude grassland areas also predicted to be suitable, aligning with palaeoecological evidence that the forests have been expanding over Campos through the last 4,000 years (Behling, Pillar, Orlóci, & Bauermann, 2004; Jeske-Pieruschka, Pillar, de Oliveira, & Behling, 2013; Scherer & Lorscheitter, 2014; Silva & Anand, 2011). The future projections based on Worldclim and CHELSA data differ markedly, however (figure 2, table S1). Although both predict a total loss of the most climatically suitable habitat by 2070 (99.9%-100.0% losses of habitat with $p_{occ} \geq 75\%$ under CHELSA, 100.0% under Worldclim), Worldclim also predicts significant losses in all but the least suitable (p_{occ} 0-25%) habitat, which rises to make up 87.2%-91.0% of the study area. The few areas of moderate suitability (p_{occ} 50-75%) are found in the southeast and centre of the highland plateau, with some further marginal areas (p_{occ} 25-50%) in the far northeast of our study area. CHELSA, by contrast, predicts 98.5%-100.0% losses in the least suitable habitat, with marginal and intermediate habitat rising to make up 99.5%-100.0% of the study area. Much of this increase is in presently unsuitable areas in the south-western part of the highlands, the southern edge of the study area where the plateau falls away, and the coastal strip east of the plateau's escarpment; *Araucaria*'s present core areas become less suitable.

CHELSA climate-only models predict 99.9%-100.0% loss of presently highly suitable habitat ($p_{occ} \geq 75\%$) in the future, but the incorporation of fine-scale topographic variables leads CHELSA+ to predict some persistence across the high elevation areas in the central and southeastern areas of the plateau, much of it along river valleys (table S1, figure 2). And although CHELSA+ still projects 85.3%-93.2% losses of this habitat class (table S1), it does identify 4,948 km² of potential microrefugia, as well as 24% more moderately resilient habitat (defined as $p_{occ} \geq 50\%$ in all scenarios)

than predicted by CHELSA alone (table 2). However, the impact of 20th Century land use change can be seen, with 37.4% of potential microrefugia having lost their natural vegetation cover, rising to 82.4% of all moderately resilient habitat (table 2, figure 3). These losses are particularly acute in forest remnants, which make up only 6.7% (333 km²) of all Araucaria's potential microrefugia. This represents a climate-caused reduction of 96.5% from the 9,577 km² of forest where Araucaria is presently $\geq 75\%$ likely to occur.

The majority of the most resilient habitat is predicted to occur in Campos. These naturally non-forested areas make up more than half of all potential microrefugia and 89.3% of those which have retained their natural vegetation, although CHELSA+ predicts that 71.6% of the presently most suitable Campos will be lost in future. The analysis of patches containing significant microrefugial areas shows that 679 patches of Campos, totalling 7,089 km² and covering on average 10.4 km² each, have $\geq 5\%$ of their area covered by potential microrefugia or contain ≥ 100 microrefugial cells. By contrast, the 4,801 km² of forest patches which meet these criteria are found in 1,967 separate forest fragments, averaging only 2.4 km² per patch – a number which falls to 1.4 km² when excluding an outlier patch covering 41% of the total area (despite containing only 6.7 km² of microrefugia).

The great majority of microrefugia, and the habitat patches they reside within, are located outside existing conservation infrastructure (Figure 4). Of all Araucaria's microrefugia which still have natural vegetation cover, only 2.5% are in any protected area, with a higher proportion of microrefugia in remnant forest represented (5.6%, 18.6 km²) than those in Campos (2.2%, 59.5 km²). Two national parks (Aparados da Serra and São Joaquim) contain 83.3% of all the protected Campos microrefugia and the two largest areas of highly resilient forest (6.7 km² and 4.0 km², respectively). Nine other protected areas average 0.9 km² of forest microrefugia each, and four of these hold the remaining 9.9 km² of protected Campos microrefugia. And although natural vegetation patches holding significant microrefugial components are found in fifteen protected areas (with six more, far from microrefugial cells, in the east of the outlier forest fragment discussed above), half (50.8%) of the total protected area is concentrated in São Joaquim National Park, which holds 162.4 km² of forest patches containing microrefugia and 148.3 km² of similar patches in Campos.

4. Discussion

Our results clearly show the disruptive effect that 21st Century climate change will have on Araucaria's already precarious position in southern Brazil, with both Worldclim and CHELSA climate-only models showing that, by 2070 and under both emissions scenarios, there will be nowhere in the region where Araucaria's probability of occurrence is $\geq 75\%$. The differences between the projections of the Worldclim and CHELSA models are primarily due to differences between the datasets' predictions of future climates (figure S3). Worldclim forecasts several degrees of warming at the coldest times of year, making the environment generally less favourable for Araucaria, whereas CHELSA's predictions paint a more complicated picture in which higher isothermality with colder minima than at present favour Araucaria, offset by increasingly seasonal precipitation and drier driest seasons (figure S4). The greater increases in isothermality and dry quarter precipitation in CHELSA's RCP8.5 scenario, and its lower values for coldest temperatures and precipitation seasonality, explain Araucaria's slightly more favourable response under this more pessimistic emissions scenario. Worldclim's projections are based on interpolated weather station records (Hijmans et al., 2005), whereas CHELSA's are based on an orographically-informed statistical downscaling of the ERA-Interim climate reanalysis (Karger, Conrad, Böhner, Kawohl, Kreft, Soria-Auza, et al., 2017). Worldclim is known to perform relatively poorly, particularly when predicting precipitation, in data-sparse and topographically complex environments, where CHELSA's predictions are more accurate (Deblauwe et al., 2016; Hijmans et al., 2005; Karger, Conrad, Böhner, Kawohl, Kreft, Soria-Auza, et al., 2017; Soria-Auza et al., 2010).

Exactly how Araucaria responds to the predicted climatic changes will depend largely on how it is affected by suboptimal conditions, which are predicted to prevail by the models built on the more accurate CHELSA data. The resilience of Araucaria populations will depend on how these conditions affect recruitment (Araucaria trees are most vulnerable as seedlings (Giovani F Paludo, Lauterjung, Dos Reis, & Mantovani, 2016; Giovani Festa Paludo, Mantovani, & Reis, 2011), when their preferred climatic conditions may differ from those around the adults used to build our models) and adult mortality (presently, portions of populations can survive for centuries even when suffering regeneration failure (Giovani F Paludo et al., 2016)). If Araucaria is relatively resilient to these changes its range could theoretically expand, although the intense fragmentation of the seasonally deciduous forests in the west of our study area (figure 1) severely limits dispersal in that direction, and Araucaria may be prevented from moving eastward by competitive exclusion from incumbent taxa in the dense coastal lowland forests (L. S. Duarte, Dillenburg, & Rosa, 2002).

Given the uncertainties around Araucaria's responses to suboptimal conditions, the conservation of

microrefugia – where *Araucaria* has and will retain a high probability of occurring – is essential. That more than a third of potential microrefugial area has already suffered habitat loss highlights the importance of safeguarding remaining natural vegetation from further damage. It also suggests that promoting *Araucaria*'s conservation outside areas of natural vegetation could be a complementary goal. This could take the form of reforestation in resilient areas (though whether other key MOF species would have similar preferred areas in the future is uncertain), or the good stewardship of semi-natural landscapes in these areas. Some such areas, traditionally managed for cattle or non-timber forest products, can conserve *Araucaria*'s genetic diversity as effectively as protected areas while also providing economic incentives to retain the trees (Medina-Macedo et al., 2016; Reis et al., 2018; Zechini et al., 2018), so their inclusion in conservation planning is likely to improve *Araucaria*'s climate resilience. However, the legal restrictions on felling mature *Araucaria* trees (and on land use changes in areas containing them) have led some land owners to actively prevent *Araucaria*'s natural regeneration by removing its seedlings from their properties (Adan et al., 2016; Mello & Peroni, 2015; Alexander C Vibrans et al., 2011); addressing this issue is critical in order for private lands to contribute effectively to the species' long-term conservation.

Our results show that most of *Araucaria*'s microrefugia still found in natural vegetation are in Campos (highland areas classed as 'naturally non-forested' in the SOS Mata Atlântica data). These areas are not only predicted to be more climatically stable than forest areas but are also more intact, with microrefugia spread out over fewer, larger patches. Part of the fragmentation of resilient forest is due to 20th Century habitat loss, but it is also reflective of the natural vegetation mosaic at the high elevations where potential microrefugia are found. Here, where MOF and Campos meet, trees are restricted to small patches and gallery forests embedded within the more extensive grassland matrix; many of the areas classified as natural non-forest in our study also contain additional woodland islands too small to be classified as forest in the SOS Mata Atlântica vegetation map (i.e. <3ha; Fundação SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais - INPE, 2015). The conservation of *Araucaria* in this context raises potential conflicts of priorities. Campos have significant biodiversity and conservation importance in their own right (Iganci, Heiden, Miotto, & Pennington, 2011; Overbeck et al., 2007), so human intervention to accelerate the slow natural expansion of MOF patches over the surrounding grasslands (Müller, Overbeck, Blanco, de Oliveira, & Pillar, 2012; Silva & Anand, 2011), as the southern Jê are hypothesised to have done around 1,000 years ago (Bitencourt & Krauspenhar, 2006; Robinson et al., 2018), may not be desirable. Ecotones between the grassland matrix and embedded MOF areas are maintained by anthropogenic fire and cattle grazing, to which forest species like *Araucaria* are more susceptible (Jeske-Pieruschka, Fidelis, Bergamin, Vélez, & Behling, 2010; Müller et al., 2012; Oliveira & Pillar, 2005), so a delicate

management balance is needed to conserve the Campos habitat itself, the MOF islands and gallery forests within it, and the dynamics between these ecosystems.

However, Campos are among Brazil's most underprotected ecosystems (Overbeck et al., 2007), and an accordingly small proportion (2.5%) of all Araucaria's microrefugia are in any protected area. None occur within existing Terras Indigenas, something that may have significant cultural impacts on the groups to whom Araucaria has long been important (cf. Bond, Anderson, Henare, & Wehi, 2019). In response to this challenge, it is essential that existing protected areas are effectively managed and safeguarded, that Araucaria is promoted and conserved on private land outside protected areas, and that new protections are considered for areas likely to play a major role in securing Araucaria's resilience to 21st Century climate change.

Brazil's Araucaria is far from the only tree species threatened by historic deforestation and future climate change, and applying the multifaceted approach used in this study could improve the realism and effectiveness of distribution models used to guide their conservation. By employing sophisticated CHELSA data alongside Worldclim, we increase our confidence in the predictions of Araucaria's responses – a step which can be applied to other topographically complex regions with sparse climate data where the interpolated climate surfaces of Worldclim may be less appropriate (Deblauwe et al., 2016; Hijmans et al., 2005; Karger, Conrad, Böhner, Kawohl, Kreft, Soria-Auza, et al., 2017; Soria-Auza et al., 2010). Similarly, the inclusion of topographic variables in our species distribution models (cf. Stanton et al., 2012) allows potential microrefugia to be identified at high resolution without prior microclimatic research having taken place (cf. Ashcroft & Gollan, 2012; Slavich, Warton, Ashcroft, Gollan, & Ramp, 2014). Our use of remotely-sensed vegetation maps to analyse the interacting impacts of climate change and habitat loss on Araucaria is a further step which can be applied in the study of other species threatened by these two key drivers of global biodiversity decline.

Fine-scale species distribution models are known to predict patchier distributions and improved persistence compared to those conducted at coarser resolutions (Meineri & Hylander, 2017; Storlie, Phillips, Vanderwal, & Williams, 2013), an effect also found in this study. The concept of microrefugia is one with origins in palaeoecology (Bemmels, Knowles, & Dick, 2019; Dobrowski, 2011; Petit, Hu, & Dick, 2008; Rull, 2009) but which is increasingly recognised as highly relevant for conservation ecology (Ashcroft, 2010; Hannah et al., 2014; McLaughlin & Zavaleta, 2012; Suggitt et al., 2018). Our finding that some areas among the grasslands on southern Brazil's highlands are likely to shelter microrefugia for Araucaria echoes the species' past ecology: previous relatively rapid expansions of forest on the plateau are thought to have been facilitated by the expansion and persistence of

gallery forests through the late Pleistocene and Holocene (Behling et al., 2004; Costa et al., 2017). Whether the patches of microrefugial vegetation we have identified in this study will similarly persist and act as sources of future forest expansion is far from certain, however, as our findings show that significant portions of this resilient habitat have either already been lost or currently lie outside formal protected areas. And, with the next century's climate likely to be highly novel compared to the present and recent past (Fischer et al., 2018; Fitzpatrick et al., 2018), an improved understanding of *Araucaria*'s spatial dynamics throughout the Quaternary may be essential for truly long-term conservation planning.

Araucaria's long evolutionary history, its past and present cultural and economic significance, and its Critically Endangered status combine to make such planning an urgent task. Deforestation between 1870 and 1970 left less than 3% of *Araucaria*'s former forest habitat standing by the late 20th Century (Thomas, 2013). Here we have shown that climate change is likely to repeat these losses within this century: of the 9,577 km² of forest fragments in our study region where *Araucaria* currently has $\geq 75\%$ probability of occurring, only 3.5% will remain similarly suitable by 2070. However, by highlighting the areas whose climatic and topographic conditions give *Araucaria* the best chance of persisting, we hope to encourage the critical conservation measures needed for this iconic tree to see another century on the highlands.

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Author contributions

OJW, RJW and FEM conceived the study; OJW and RJW designed the analysis; DVL and ACV provided IFFSC locality data; OJW built the ensemble models and analysed the results; OJW, RJW and FEM drafted the manuscript, which all authors revised before submission.

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Tables

		Model runs meeting hibar/lobar standard								Total
		GLM	GAM	Maxent	ANN	GBM	RF	CTA	MARS	
WC	hibar						2			2
	lobar	1				2	5			8
CH	hibar	5					3		1	9
	lobar	8	3		2	2	8		8	31
CH+	hibar	5		x		8	7		4	24
	lobar	10	2	x	5	10	10		10	47

Table 1: model runs meeting ‘hibar’ and ‘lobar’ criteria for inclusion in ensembles (see figure S2 for evaluation scores of all model runs).

	Area (km ²)	Worldclim	CHELSA	CHELSA+
Microrefugia ($p_{occ} \geq 75\%$ at present and in both future scenarios)	Total area	0	0	4948.2
	In remnant forest	0	0	332.5
	In naturally non-forested area	0	0	2763.7
Moderately resilient ($p_{occ} \geq 50\%$ at present and in both future scenarios)	Total area	575.7	92212.8	114416.4
	In remnant forest	250.1	13561.9	11438.3
	In naturally non-forested area	166.1	7344.5	8704.1

Table 2: area of microrefugia and moderately resilient habitat predicted by each ensemble model.

Figure captions

Figure 1: Map showing the study region's current potential vegetation (IBGE, 2004) and remnants >3ha within the Atlantic Forest domain of Paraná, Santa Catarina and Rio Grande do Sul states (Fundação SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais - INPE, 2015). Pink outlines show Brazilian protected areas (IUCN category Ia-VI), and blue outlines show designated Terras Indígenas.

Figure 2: Ensemble predictions of habitat suitability for *Araucaria* using Worldclim (top), CHELSA (centre) and CHELSA+ (bottom) at present (left) and in 2070 under the RCP4.5 (centre) and RCP8.5 (right) scenarios.

Figure 3: Map showing the loss of *Araucaria*'s climatically resilient areas (from CHELSA+ ensemble model) to habitat change. Darker/redder areas are more climatically resilient, from light grey/yellow (p_{occ} 50%-75% in all three scenarios) to black/red (potential microrefugia, $p_{occ} \geq 75\%$ in all scenarios). Areas in greyscale have lost their natural vegetation cover; those in yellow, orange and red have retained it.

Figure 4: Map showing microrefugial cells in remnant vegetation (forest in dark green, Campos in orange), patches of remnant vegetation containing ≥ 100 microrefugial cells or which have $\geq 5\%$ of their area covered by microrefugia (forest in pale green, Campos in buff), protected areas and designated Terras Indígenas.







