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Floristic change in Brazil's southern Atlantic Forest Biodiversity Hotspot: from the Last Glacial Maximum to the late 21st Century

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Highlights

- Combining models and proxy data yields novel insights into past floristic changes
- 21,000 years of climate-driven species turnover drove frequent community change
- Early-Holocene no-analogue assemblages found in plateau areas away from proxy sites
- Non-climatic factors were most likely drivers of LGM forest-grassland structure
- By the 2070s, S. Brazil could see more floristic change than any time since the LGM

Abstract

Brazil's Atlantic Forest biome is one of the world's biodiversity hotspots, whose heterogeneous ecosystems are threatened by habitat loss and climate change. Palaeoecological research can provide essential context for the impacts of anthropogenic climate change in the 21st Century and beyond, but existing studies have notable limitations in the insights they can provide: vegetation proxy data are spatially and temporally skewed with inconsistent taxonomic resolution; existing modelling studies typically overlook individualistic species-level responses, are limited in temporal coverage, and lack close integration with empirical palaeoecological data. Here, we investigate the impact of major climate changes upon the species-level floristic composition of southern Brazil's Atlantic Forest, from the Last Glacial Maximum (LGM) to the late 21st century, by modelling the distributions of 30 key species at seven time slices since the LGM and comparing the assemblages they form with an unprecedented dataset of palaeoecological proxy data. We find notable compositional changes through time across our study area, especially during the early Holocene, which was characterised by extensive no-analogue plant communities. Aspects of these modelled floristic changes are captured in proxy records but many occur in data-sparse regions, highlighting geographic foci for future palaeoecological investigation to test these model predictions. Our findings highlight the individualistic responses of Atlantic Forest plant species to climate change and help resolve long-standing palaeoecological questions – explaining the dominance of highland grasslands at the Last Glacial Maximum (likely due to low atmospheric CO_2 concentrations), clarifying the LGM extent of coastal tropical forest (probably in a grassland matrix on exposed continental shelf), and explaining the origins of *Araucaria angustifolia's* western populations (from climatic (micro-)refugia rather than human-mediated dispersal). Our results also set the 21st Century's impending climate and vegetation changes in a 21,000-year temporal context, revealing that, under a high emissions scenario, more than 100,000 km^2 of the southern Atlantic Forest will experience more climate-driven floristic change in the coming decades than it has in the last 21 millennia.

Key words

Late Quaternary; Present; Anthropocene; Palaeoecology; Conservation; South America; Vegetation dynamics; Atlantic Forest; Biodiversity Hotspot; Climate change.

Abbreviations

SDM: species distribution model

ARF: Atlantic rainforest

AMF: Araucaria mixed forest

SDF: seasonally deciduous forest

LGM: Last Glacial Maximum

1. Introduction

Brazil's Atlantic Forest biome is a global biodiversity hotspot: around one in every fifty species of vascular plants and non-fish vertebrates on Earth is endemic to this heterogeneous mix of ecosystems, which stretches over 3,000 km along the country's coast and inland as far as Argentina and Paraguay (Myers et al., 2000; Neves et al., 2017; Oliveira-Filho and Fontes, 2000; Ribeiro et al., 2009). This biome is gravely threatened by intense historical and ongoing habitat loss, which has already removed 84-89% of its natural vegetation (Ferrer-Paris et al., 2019; Ribeiro et al., 2009), impending anthropogenic climate change (Bergamin et al., 2019; Colombo and Joly, 2010), and the intersection of the two, which may cause a quarter of the Atlantic Forest's endemic species to be lost (Bellard et al., 2014; Brown et al., 2020; Wilson et al., 2019).

These threats are particularly acute around the Atlantic Forest's subtropical southern limits – arguably the most heterogeneous part of the biome (Oliveira-Filho et al., 2014), comprising Atlantic Rainforest *sensu stricto* (ARF, also known as Dense Ombrophilous Forest) along the coast, Araucaria Mixed Forest (AMF, also known as Mixed Ombrophilous Forest) and Campos grasslands on the highland plateau, Cloud Forest at the very highest elevations, and Seasonally Deciduous Forest (SDF) in the west (Fig.1, section 2.2) (IBGE, 2012; Oliveira-Filho and Fontes, 2000). Each of these distinct and diverse ecosystems is already under threat from habitat conversion: ARF and AMF are Endangered and SDF is Critically Endangered, with their risk of collapse within 50 years estimated at ≥20% and ≥50% respectively (Ferrer-Paris et al., 2019); 25% of Campos was lost between 1970 and 1996 to timber plantations, agricultural expansion and inappropriate management (Overbeck et al., 2007). Furthermore, these tropical and subtropical forests and natural grasslands hold significant populations of more cold-adapted taxa, which are already range-constrained under the present interglacial climate and so at elevated risk from anthropogenic climate change (Bellard et al., 2014; Carnaval et al., 2014; Ribeiro et al., 2009). Understanding how these ecosystems and their component species will respond to changing conditions over the coming decades is therefore a key research priority.

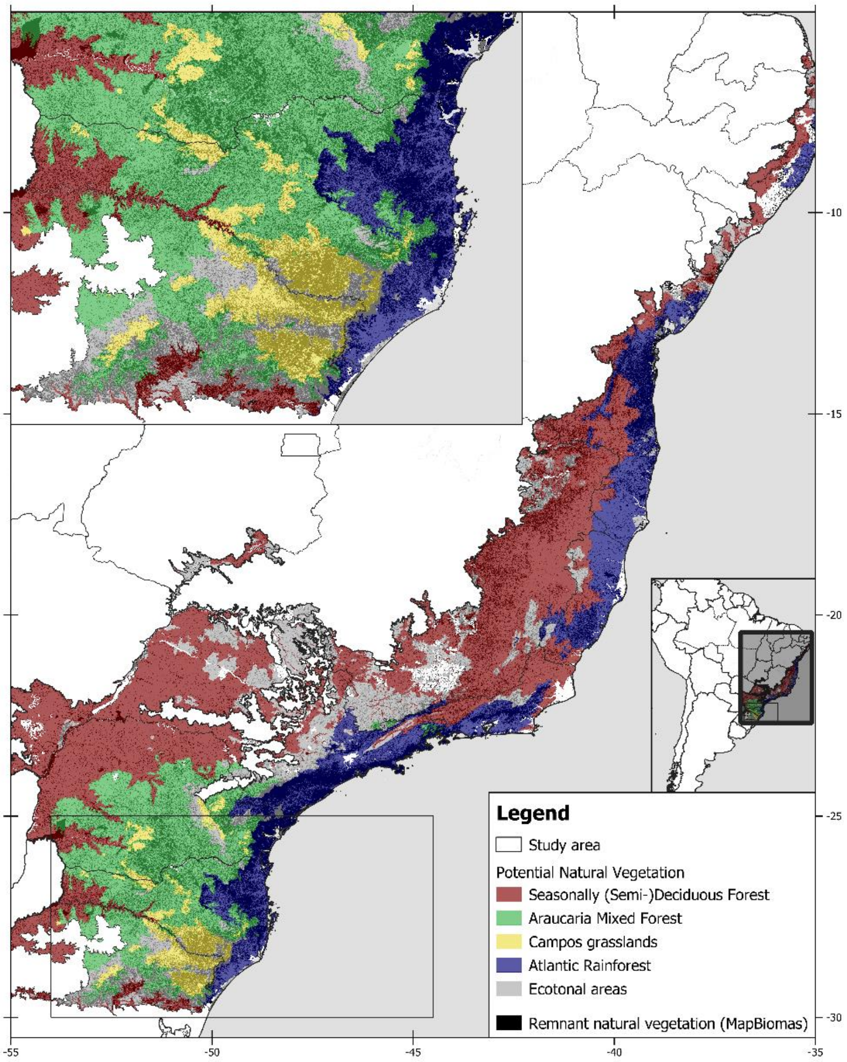


Fig. 1: Brazil's Atlantic Forest vegetation (IBGE, 2012) and its natural remnants in 2018 (shaded; Souza et al., 2020)*; ecosystems not prominent in our study area are not shown in colour.*

One key approach for predicting the impacts of climate change is to use species distribution models (SDMs, also known as ecological niche models). However, significant uncertainties about the planet's longer-term climate trajectory under anthropogenic forcing, as well as the spectre of increasing climate novelty, mean that no SDM study can make precise forecasts beyond the current century (Fitzpatrick et al., 2018; Williams and Jackson, 2007). Palaeoecology is valuable in this context, illuminating vegetation responses to wide ranges of past climates which may present useful analogues for future scenarios (Barnosky et al., 2017; Dietl et al., 2015; Jackson and Blois, 2015;

McElwain, 2018). These insights can come from palaeoecological proxies (e.g. fossil pollen, soil carbon isotopes, phytoliths) and/or distribution modelling. These approaches are complementary: proxy studies provide rich, empirical records on individual sites' vegetation histories; SDMs can provide high spatial- and taxonomic-resolution predictions for times, taxa and places poorly covered by proxy data; integrating the two therefore yields highly detailed, generalisable, ground-truthed insights into palaeoecological dynamics (Svenning et al., 2011).

Southern Brazil's late-Quaternary vegetation history has been better studied than much of the Neotropics, especially with fossil pollen and, to a lesser extent, soil carbon isotopes and phytoliths (synthesised in Smith and Mayle, 2017). There are limits, however, to the insights available from these proxies. The overwhelming majority of studied sites have small catchments recording local-scale vegetation changes (Smith and Mayle, 2017), and their uneven spatial distribution (skewed towards the plateau's (south-)eastern edges and the southern part of the coastal lowlands) mean that large parts of the region are unstudied (Fig. 3). Temporal coverage is similarly uneven, with few sites providing continuous records from the Last Glacial Maximum (LGM, ca. 21,000 years ago). Finally, each proxy has significant limits on the taxonomic resolution it can provide for vegetation reconstructions. Soil carbon isotopes ($\delta^{13}C$) distinguish C4-dominated (sub-tropical/tropical grassland) and C3-dominated (generally, but not always, woody) vegetation (Dümig et al., 2008; Silva and Anand, 2011); phytoliths can effectively differentiate herbaceous or monocotyledonous taxa, and fossil pollen discriminates between woody dicots (Daniau et al., 2019; Plumpton et al., 2019) – yet despite its higher taxonomic resolution, fossil pollen records under-represent or omit significant parts of southern Brazil's flora (Behling and Negrelle, 2006; Cárdenas et al., 2019), leaving their dynamics unrecorded.

Although projecting SDMs to past time slices is a potentially powerful way to complement these data, studies which have attempted this for the southern Atlantic Forest generally share limitations around their links to proxy records and their taxonomic and temporal coverage. A relatively restricted subset of the available proxy data tends to be used, with no study using a denser dataset than Ledo & Colli's (2017) 56 sites across all Amazonia and the Atlantic Forest; Smith & Mayle (2017) identified 50 proxy sites in south-eastern Brazil alone. Many studies also examine only the LGM (21,000 BP) and mid-Holocene (6,000 BP), the time slices for which spatialised climate data are most widely available at ecologically meaningful resolutions (Arruda et al., 2017; Bergamin et al., 2019; Carnaval and Moritz, 2008; Ledo and Colli, 2017; Porto et al., 2013; Vitorino et al., 2016). Important as these periods are, southern Brazil's ecosystems responded to a wide array of other conditions in the intervening millennia which may better illuminate present and potential future distributions or patterns of diversity (Cruz et al., 2007, 2005; Maksic et al., 2019).

Most critically, many palaeo-modelling studies in the Atlantic Forest have examined the distributions of whole ecosystems or significant parts of the entire biome, treating them as single units with uniform responses (Arruda et al., 2017; Carnaval et al., 2014; Carnaval and Moritz, 2008; Costa et al., 2017; Ledo and Colli, 2017). However, palaeoecological data shows that species respond individualistically to climate changes depending on their niche requirements, which can lead to the formation of novel floristic assemblages without modern analogues (Davis, 1983; Davis and Shaw, 2001; Mayle et al., 2004; Williams and Jackson, 2007). Although much evidence for this comes from temperate regions (e.g. Williams et al., 2004), past novel or no-analogue assemblages have been documented from Amazonia to south-eastern Brazil, generally characterised by the co-occurrence of cold- and warm-adapted pollen taxa during (late) glacial times (Behling, 1998; Bush et al., 2004; Colinvaux et al., 2000, 1997; De Oliveira, 1992; De Oliveira et al., 2020; Francisquini et al., 2020; Haberle and Maslin, 1999; Hermanowski et al., 2012; Horák-Terra et al., 2020; Lima et al., 2018; Raczka et al., 2013; Whitney et al., 2011). Southern Brazil's forests are characterised by floristic gradients – each contains significant compositional diversity, and differences between forest types are generally marked most by gradual species turnover (Bergamin et al., 2017; Brown et al., 2020; Duarte et al., 2014; Esser et al., 2019; Oliveira-Filho et al., 2014; Oliveira-Filho and Fontes, 2000). These characteristics mean there is a significant chance that any past or future reassembly of these communities would be poorly captured by modern-day ecosystem classifications. It is especially important, therefore, that the effects of past and future climate change on the southern Atlantic Forest are considered at species level, as these potential 'ecological surprises' (Williams and Jackson, 2007) cannot be examined in ecosystem- or biome-level modelling studies.

The present study addresses these limitations in existing proxy and SDM research in the southern Atlantic Forest, by providing a species- and community-level view of vegetation change throughout the last 21,000 years and into the coming decades through close integration of high resolution SDMs and extensive palaeo-data synthesis. Building SDMs for 30 key species from the region's principal ecosystems and projecting them in high spatial resolution across nine time slices covering the coming century and the past 21,000 years, we analyse the changing distributions of 22 floristic assemblages and closely compare our predictions against 67 published vegetation and climate proxy records. The unprecedented scope and granularity of this combined approach allows us to comprehensively investigate past compositional change in the southern Atlantic Forest, advancing our understanding of when, where and how the region's species and communities responded to past climatic changes and providing 21,000 years of context, spanning the full amplitude of glacial-Holocene climate change, in which to assess the impending impacts of 21st-Century anthropogenic climate change.

2. Methods

2.1. Overview

We built SDMs for 30 key species from the southern Atlantic Forest's main ecosystems; projected these at ca. 800m-resolution to nine time slices: the present day, seven time slices at 3,000-year intervals since the LGM, and a climate change scenario for the 2070s; analysed species' co-occurrences (i.e. potential floristic assemblages) and their distributions through time; and closely compared our modelling results with a dense dataset of palaeo-proxy sites (fig. 2). Our study area is located between 25-30ºS, covering the southern extent of the Atlantic Forest biome.

In this study, we use a 'predict-then-assemble' distribution modelling approach (sensu Nieto-Lugilde et al., 2018), modelling the distributions of each species independently before combining them into potential floristic assemblages (see sections 2.4 and 2.5). Because it allows for more realistic compositional changes through time – including the development of assemblages without modern analogue – this method is preferable to the 'assemble-then-predict' approach commonly used in previous modelling studies focusing on the Atlantic Forest (see section 1; Nieto-Lugilde et al., 2018). An alternative approach would be to use community-level 'assemble-and-predict-together' models (Nieto-Lugilde et al., 2018). Like our stacked SDM method, these models reproduce important compositional changes across time and space, but they require co-occurrence or presence/true absence data for all species at all localities – data which are scarce in the tropics. Additionally, while they do present some modest computational advantages, the approach used here produces comparably accurate predictions to community-level models (tested by Maguire et al., 2016; reviewed by Nieto-Lugilde et al., 2018).

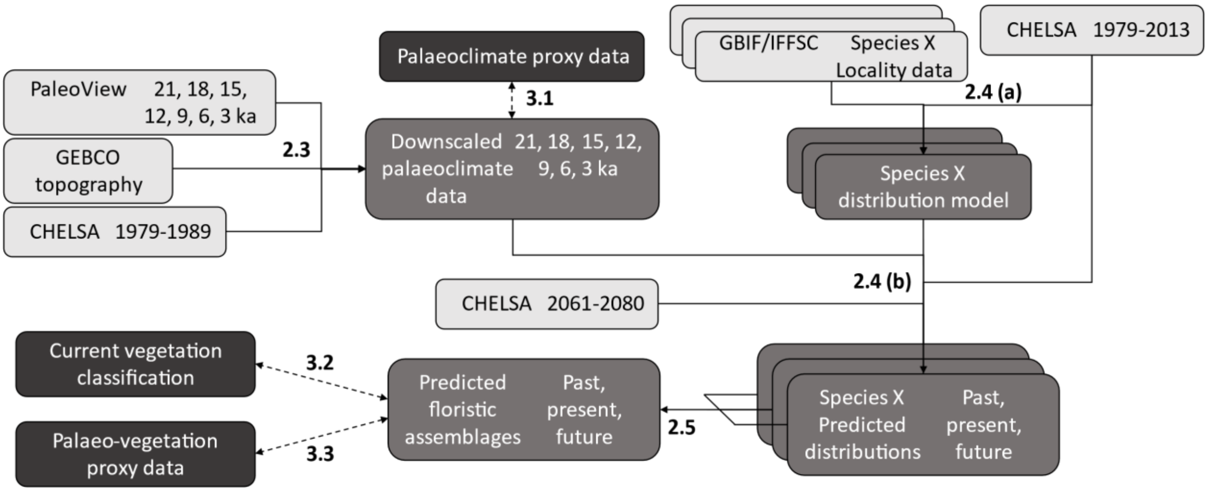


Fig. 2: conceptual overview of this study showing input data (light grey), generated outputs (mid grey), and data for model intercomparisons (dark grey). Segment labels highlight where in the text

relevant sections are discussed. For data generation methods (solid lines): palaeoclimate data downscaling (section 2.3), model fitting and projection (section 2.4 – labelled a and b respectively), combining individual species predictions into floristic assemblages (section 2.5). For model-data intercomparison results (dashed lines): palaeoclimate data and proxies (section 3.1), current mapped and modelled vegetation (section 3.2), and predicted floristic assemblages and palaeo-vegetation proxies (section 3.3).

2.2. Modern ecosystems of the southern Atlantic Forest

Atlantic Rainforest (ARF) is an evergreen subtropical rainforest which grows under constantly hot and humid conditions in a relatively narrow band between the Atlantic coast and the highlands' eastern escarpment. Its wide elevational range (from sea level to >800m) and associated climatic differences drive variations in its composition, with lowland, submontane and montane ARF formations distinguished (Klein, 1975; Lingner et al., 2013b; Uhlmann et al., 2012).

Araucaria Mixed Forest (AMF) occurs inland on the highland plateau almost exclusively above 500m elevation (Hueck, 1953). Characterised by an emergent layer of *Araucaria angustifolia* above an angiosperm-dominated sub-canopy, AMF requires high and constant rainfall and is one of the most marginal ecosystems in the Atlantic Forest, occupying its coldest and highest elevation niches (Neves et al., 2017; Oliveira-Filho et al., 2014; Uhlmann et al., 2012). AMF's floristic mix of warm-adapted tropical and cold-adapted Austral-Antarctic and Andean taxa varies extensively throughout its range in response to a variety of factors (Duarte et al., 2014; Higuchi et al., 2012; Klein, 1975; Oliveira-Filho et al., 2014; Sevegnani et al., 2016).

At the plateau's highest elevations, which exceed 1,800m, AMF forms mosaics with – and eventually gives way to – natural highland grasslands called Campos. One of the very few herbaceous ecosystems in the Atlantic Forest biome, Campos are highly diverse, though less well studied, appreciated or protected than the surrounding forests (Andrade et al., 2019, 2016; Iganci et al., 2011; Overbeck et al., 2007). They have occupied parts of the highlands for more than 40,000 years, with relatively steady forest encroachment over the last 4,000 years (Behling et al., 2004; Dümig et al., 2008; Silva and Anand, 2011). These ecotones are maintained by natural or anthropogenic fire and grazing, and in the absence of such disturbance the conversion of Campos to forest can be rapid (Jeske-Pieruschka et al., 2010; Müller et al., 2012; Oliveira and Pillar, 2005; Sühs et al., 2020).

Campos share the highest and coldest parts of the plateau with Cloud Forest, especially along the escarpment's upper edge where orographic fog is common (Falkenberg and Voltolini, 1993). These forests contain a mix of cold-adapted species from both AMF and ARF, but despite being floristically distinct they are often treated as high-montane expressions of these larger forest formations

(Bertoncello et al., 2011; Falkenberg and Voltolini, 1993; Higuchi et al., 2013; Oliveira-Filho et al., 2014; Scheer et al., 2011).

The Atlantic Forest's westernmost ecosystem is Seasonally Deciduous Forest (SDF), which extends across Brazil's borders into north-eastern Argentina and eastern Paraguay as well as along lower elevations to the south of the highlands. These forests experience similarly high average temperatures and precipitation to ARF but greater temperature seasonality, with more frequent frosts (6.5-10.4 days per year on average) (Gasper et al., 2012). In the south, canopy trees shed their leaves in response to winter's low temperatures and shorter photoperiod, though SDF's understorey is largely evergreen (Gasper et al., 2012; Klein, 1975). At the higher elevations of its range (800-900m) the forest incorporates floristic elements from lower-elevation AMF – indeed, the two ecosystems can be considered different expressions of a similar seasonal forest flora (Oliveira-Filho et al., 2014).

2.3. Climate data

Present-day (average of 1979-2013) and future (average of 2061-2080, termed '2070s') gridded climate datasets were downloaded from CHELSA (Karger et al., 2017b, 2017a). Our future data uses the RCP8.5 emissions scenario (worst-case business-as-usual) from the CCSM4 general circulation model (GCM), as this has been found to be among the best-performing GCMs for our study region and Latin America more broadly (Hidalgo and Alfaro, 2015; Lovino et al., 2018; Yin et al., 2013), and is also closely related to CCSM3, the GCM which underpins our palaeoclimate dataset. These palaeoclimate data come from PaleoView, a tool for querying the TRaCE21ka transient climate simulation at up to decadal temporal resolution (Fordham et al., 2018, 2017).

We generated gridded monthly precipitation and temperature (mean, maximum and minimum) data from PaleoView for seven past time slices: 21,000, 18,000, 15,000, 12,000, 9,000, 6,000 and 3,000 years BP. We used the delta change method to downscale these data from 2.5° (PaleoView's resolution) to 30" (ca. 800m, the resolution of CHELSA climate data), with local lapse rate modifications for temperature variables (see Supplementary Methods). The region's changing sea levels from the LGM to present were incorporated by adjusting elevation and bathymetry data from the GEBCO project (Weatherall et al., 2015) by -30m (9,000 BP), -50m (12,000 BP), -90m (15,000 BP), -100m (18,000 BP) and -130m (21,000 BP) relative to present (Cooper et al., 2018; de Mahiques et al., 2010). Climatic and ecological predictions for exposed shelf areas should be treated with greater caution than areas which were never submerged, as CHELSA data is only validated over current land areas and was spatially extrapolated for precipitation (Lorenz et al., 2016).

The Köppen-Geiger scheme classifies the world's climate into distinct, ecologically relevant zones; we applied this classification (as implemented by Alvares et al., 2013; Beck et al., 2018; Peel et al., 2007) to our present, future and downscaled past climate data to provide a broad-scale overview of the changing conditions in our study area through time.

2.4. Species distribution modelling

Best practice in species distribution modelling advocates restricting input variables to those which are ecologically relevant and weakly correlated with one another (Fourcade et al., 2017). We selected the following bioclimatic variables (see Supplementary Methods), which describe the general trends, extremes and variability of temperature and precipitation: Bio2 (mean diurnal temperature range), Bio3 (isothermality), Bio4 (temperature seasonality), Bio5 (maximum temperature of the warmest month), Bio6 (minimum temperature of the coldest month), Bio8 (average temperature of the wettest quarter), Bio9 (average temperature of the driest quarter), Bio12 (annual precipitation), Bio15 (precipitation seasonality), Bio17 (precipitation of the driest quarter).

We selected six key species from each of Seasonally Deciduous Forest, Araucaria Mixed Forest, Campos, Cloud Forest, and Atlantic Rainforest, according to their ecological importance in the ecosystems' different communities (Andrade et al., 2019; Bertoncello et al., 2011; Klein, 1975; Lingner et al., 2013a; Meyer et al., 2013; Schorn et al., 2014, 2012) and likely visibility in fossil pollen records. However, the dominance and diversity of Poaceae and Asteraceae species in Campos, combined with pollen's relatively low taxonomic resolution (particularly for Poaceae), means that our selected Campos taxa cannot be readily identified in the pollen record. Similarly, the lack of palaeoecological research into southern Brazil's SDF means its taxa are not often identified in fossil pollen studies.

Species (abbreviation code; family)	**SDF**	**AMF**			**CAM**	**CLD**	**ARF**			**Fossil pollen**
		low	**mid**	**high**			**high**	**mid**	**low**	
Alchornea triplinervia (Alctri; Euphorbiaceae)							Y	Y	Y	Y
Apuleia leiocarpa (Apulei; Fabaceae)	Y									
Araucaria angustifolia (Araang; Araucariaceae)		Y	Y	Y						Y
Calophyllum brasiliense (Calbra; Calophyllaceae)									Y	

Cecropia glaziovii (Cecgla; Urticaceae)								Y		Y
Cedrela fissilis (Cedfis; Meliaceae)	Y	(Y)						(Y)		
Clethra scabra (Clesca; Clethraceae)		Y	Y	Y						Y
Cupania vernalis (Cupver; Sapindaceae)	Y	(Y)	(Y)					(Y)		
Danthonia secundiflora (= *D. montana*) (Dansec; Poaceae)					Y					
Dicksonia sellowiana (Dicsel; Cyatheaceae)		Y	Y	Y			(Y)			Y
Drimys brasiliensis (Dribra; Winteraceae)			(Y)	Y		Y				Y
Eragrostis polytricha (Erapol; Poaceae)					Y					
Euterpe edulis (Eutedu; Arecaceae)							(Y)	Y	Y	
Hypochaeris lutea (Hyplut; Asteraceae)					Y					
Ilex microdonta (Ilemic; Aquifoliaceae)						Y				Y
Lithraea brasiliensis (Litbra; Anacardiaceae)		Y	Y							Y
Luehea divaricata (Luediv; Malvaceae)	Y									(Y)
Matayba elaeagnoides (Matela; Sapindaceae)	Y	Y	Y							Y
Mikania decumbens (Mikdec; Asteraceae)					Y					
Mimosa scabrella (Mimsca; Fabaceae)			(Y)	Y		(Y)				Y

Myrocarpus frondosus (Myrfro; Fabaceae)	Y								
Ocotea catharinensis (Ococat; Lauraceae)					Y	Y	(Y)		
Ocotea puberula (Ocopub; Lauraceae)	Y	Y							
Podocarpus lambertii (Podlam; Podocarpaceae)			Y		Y				Y
Podocarpus sellowii (Podsel; Podocarpaceae)					Y				Y
Schizachyrium tenerum (Schten; Poaceae)				Y					
Sloanea guianensis (Slogui; Elaeocarpaceae)							Y	Y	(Y)
Trifolium riograndense (Tririo; Fabaceae)				Y					
Weinmannia humilis (Weihum; Cunoniaceae)			Y		Y				Y
Weinmannia paulliniifolia (Weipau; Cunoniaceae)			(Y)		Y	(Y)			Y

Table 1: Modelled species and their importance in the ecosystems of southern Brazil's Atlantic Forest (SDF = Seasonally Deciduous Forest, AMF = Araucaria Mixed Forest, CAM = Campos, CLD = Cloud Forest, ARF = Atlantic Rainforest) (from Andrade et al., 2019; Bertoncello et al., 2011; Klein, 1975; Lingner et al., 2013a; Meyer et al., 2013; Schorn et al., 2014, 2012). *Fossil pollen importance generalised from pollen taxa (genus level or below) in published proxy sites listed in Table S2. 'Y' indicates very high importance/frequent presence, and '(Y)' indicates somewhat high importance/frequent presence.*

Locality data for these species were drawn from two sources: the Santa Catarina Forest Floristic Inventory (IFFSC) (Vibrans et al., 2020, 2010), and the Global Biodiversity Information Facility for records outside Santa Catarina (https://doi.org/10.15468/dl.0l64p1, https://doi.org/10.15468/dl.o97owq, https://doi.org/10.15468/dl.nxy2cp). GBIF records were taken from 15-45° S and 67.5-35°W, where present-day conditions generally encompass those experienced by our study area over the last 21,000 years, then coordinates were cleaned and thinned. Because true absences were only available from the IFFSC, which covers only a subset of the geographic and climatic space our models were trained on and lacks data on Campos species, we added 1,000 randomly located pseudo-absence points for each species.

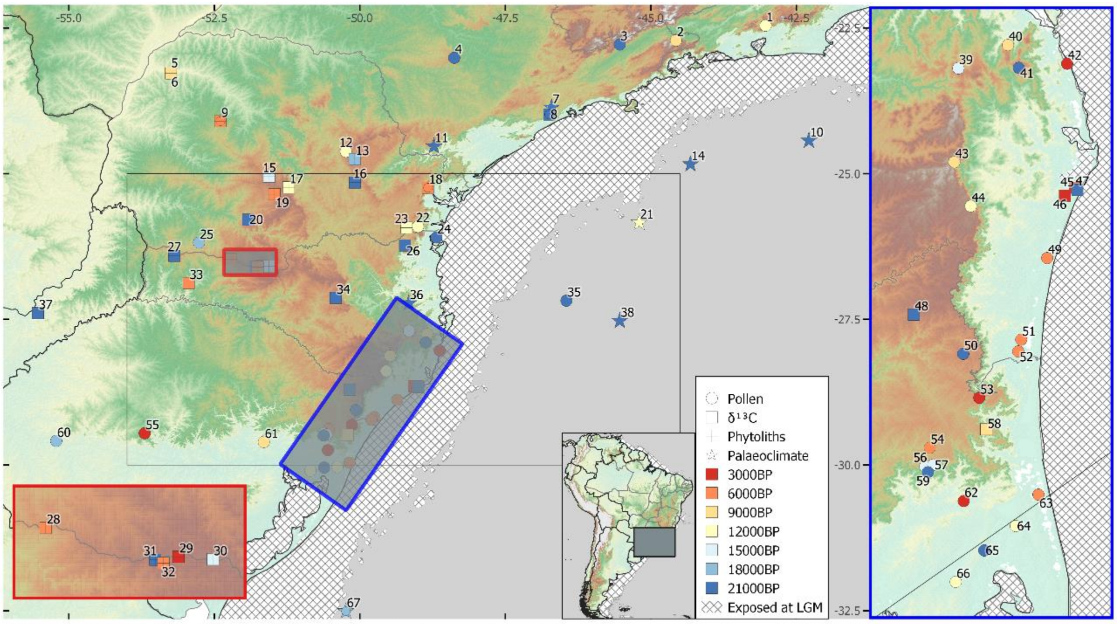
Modelling used the package ‘biomod2’ in R v3.5 (R Core Team, 2018; Thuiller et al., 2016). For each species a randomly selected 25% of the location data was set aside for model evaluation, with the remaining 75% used for training and cross-validating the models. We used an ensemble modelling approach built from seven individual modelling algorithms (see Supplementary Methods). For each species, each algorithm was run ten times and evaluated using the metrics AUC (area under the receiver operating curve) and TSS (true skill statistic) (Allouche et al., 2006). These evaluation scores were ranked and their ranks summed, with a species’ ten top-ranked models combined into an ensemble prediction, which was projected to the past and future time slices. If more than one model run tied for the tenth-highest position, the ensemble was produced from more than ten runs (Table S1).

2.5. Floristic assemblage analysis

‘Stacking’ our models’ projections across all 30 species and nine time slices produced 43,023 unique combinations of species presence and absence. These combinations were aggregated to 34 potential floristic assemblages using hierarchical clustering with the R package ‘vegan’ (Oksanen et al., 2019) – see supplementary methods for further details. Potential assemblages/communities which never occupy ≥5% of any time slice’s land area were excluded from further analysis (fig. S2). Assemblages are characterised by the prevalence of the modelled species within them, averaged across all time slices and ranging from 0 (absent from all pixels of an assemblage) to 1 (present in all the assemblage’s pixels; see fig. 4).

2.6. Palaeo-data - model comparison

To compare our modelled predictions against palaeoecological data we compiled a comprehensive list of previously studied sites, drawing on the Latin American Pollen Database (Flantua et al., 2015), the Temperature 12k Database (Kaufman et al., 2020), Smith & Mayle (2017), and extensive literature searches (see Supplementary Methods). The final list (Table S2 and Fig. 3) comprises 67 sites (47 of them within our study area), including eight independent palaeoclimate archives (six for temperature and two for precipitation). Selected sites outside our study area are included to provide a broader regional context for patterns of vegetation change and to help interpret records within our study area. This compares favourably with the 110 sites used across lowland tropical and subtropical South America by Smith & Mayle (2017) and greatly exceeds the density used as controls in other past modelling studies in the region. We generated new age-depth models for all pollen sites using the R package ‘rbacon’ (Blaauw et al., 2020; Blaauw and Christen, 2011); age-depth models were generally not created for soil profiles (see Supplementary Methods for further information). Fossil pollen data are summarised as percentages of forest and grassland pollen, and soil carbon isotope values are generalised following Silva & Anand (2011).



1: Serra dos Orgãos | 2: Serra da Bocaina | 3: Morro de Itapeva | 4: Serra de Botucatu | 5: Terraço Ivaí | 6: Trincheira Reserva | 7: Colônia | 8: Curucutu | 9: Água dos Papagaios | 10: SAN-76 | 11: Santana St8 | 12: Serra Campos Gerais | 13: Iapó River | 14: NAP 63-1 | 15: Turvo | 16: Ponta Grossa | 17: Aroeiras | 18: Caratuva Peak 2 | 19: Guarapuava | 20: Reserva do Iguaçu | 21: LaPAS-KF02 | 22: Serra do Araçatuba | 23: Tijucas do Sul | 24: Volta Velha | 25: Buriti | 26: Cerro do Touro Watershed | 27: Campo Erê | 28: Mata Preta | 29: Coxilhão | 30: Hs1 | 31: Hs17 | 32: Hs13 | 33: Xanxerê | 34: Canoas Ponte Alta do Norte | 35: GeoB2107-3 | 36: Botuverá Bt2 | 37: Obera | 38: 36GGC | 39: Serra da Boa Vista | 40: Tabuleiro Summit | 41: Ciama 2 | 42: Garopaba | 43: Morro da Igreja | 44: Serra do Rio Rastro | 45: Riachinho Valley | 46: Sangão | 47: Figueirinha Lake | 48: São José dos Ausentes | 49: Campo Mãe Luzia | 50: Cambará do Sul | 51: Santa Rosa do Sul | 52: São João do Sul | 53: Banhado Amarelo | 54: Fazenda do Pinto | 55: São Martinho da Serra | 56: Alpes de São Francisco 1 | 57: Rincão das Cabritas | 58: CPCN Pro Mata | 59: Alpes de São Francisco 2 | 60: São Francisco de Assis | 61: Serra Velha | 62: Santo Antônio da Patrulha | 63: Tramandaí Lagoon | 64: Passinhos | 65: Barrocadas | 66: Águas Claras | 67: GeoB6211-2

Fig. 3: Map showing palaeo-data sites included in this study. For further details on the sites, see table S2.

3. Results

3.1. Palaeoclimate data validation

Our downscaled palaeoclimate data broadly agree with proxies of past temperature and precipitation (Figs. S3-S7). The LGM (21,000-18,000 BP) is reconstructed with higher and more seasonal precipitation than the present, especially in the west of our study area, and mostly 3-4°C cooler. This aligns with speleothem evidence from Botuverá and Santana caves (Cruz et al., 2007, 2006, 2005), as well as proxies of air and sea surface temperatures from Colônia and marine cores (Carlson et al., 2008; Chiessi et al., 2015, 2014; Dauner et al., 2019; Pivel et al., 2013; Rodríguez-Zorro et al., 2020; Toledo et al., 2007). Conditions at 15,000 BP are transitional between this LGM climate and a markedly different early Holocene.

At 12,000 BP, much of our study area was somewhat drier and more seasonal than the present; the north-east was 1-2°C cooler than present and the south up to 1°C warmer, though most areas were within 1°C of modern average temperatures. Proxy evidence from Botuverá and Santana supports the early Holocene (12,000 – 9,000 BP) being the driest in the study period, with the lowest contributions from the summer monsoon. Subsequent gradual and relatively minor increases in precipitation in the proxy records are reflected in our downscaled data. Temperature proxies generally record 12,000 BP as being similar to, or warmer than, the preceding time slices; several also show slight increases in temperatures through the Holocene which are less clear in our downscaled data.

Our future scenario (2070, RCP8.5) has slightly higher precipitation than the present, though still less than experienced during the LGM, and significantly higher temperatures (2-3.5°C warmer) than at any other modelled point.

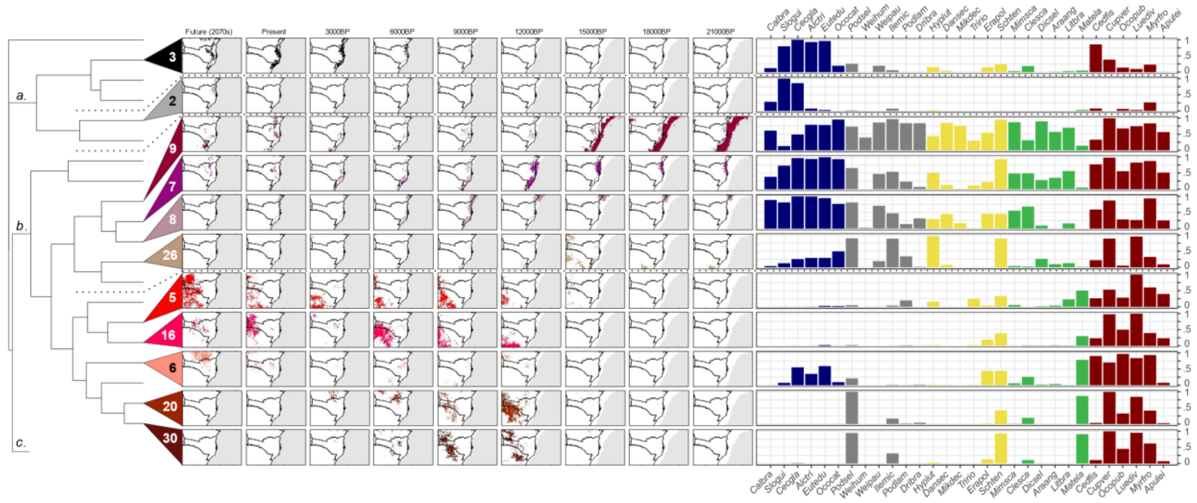
The Köppen-Geiger climate classification system (Fig. S8) shows that southern Brazil's highlands have retained a subtropical climate with warm summers and no dry season since the LGM. This Cfb climate type covered almost all of southern Brazil's current land area at the LGM. Increasing temperatures since then have seen Cfa (hot summers) progressively replacing Cfb from the east, south and west of our study area. Cfb's present extent is the lowest in the studied period, and its near-total replacement by the 2070s under a high-emissions scenario is its largest reduction since at least the LGM. Relatively small areas of tropical rainforest climate (Af) have been found along northern coastal areas since 15,000 BP, and are predicted to extend significantly to the south (and also develop in the north-west) later in the 21st Century.

3.2. Modelled species and modern-day ecosystems

The 30 key species modelled here effectively characterise the main ecosystems of southern Brazil's Atlantic Forest; only the south-western corner of our study area, which is not part of the biome, had poor species coverage in the present (Fig. 1, Figs. S9-S10). Several species transcend ecosystem boundaries (e.g. *Ocotea puberula* and *Matayba elaeagnoides* in Seasonally Deciduous Forest and Araucaria Mixed Forest, and *Cedrela fissilis* in parts of these and Atlantic Rainforest), reflecting the compositional gradients between the region's different forests (Table 1, Fig. S9) (Bergamin et al., 2017; Duarte et al., 2014; Oliveira-Filho et al., 2014; Oliveira-Filho and Fontes, 2000). Most high-elevation areas are currently predicted to be suitable for combinations of AMF, Campos and Cloud Forest species; these ecosystems' modern boundaries are not clearly delineated in their constituent species' distributions.

The stability of species associations – with one another and with their nominal ecosystem (Table 1) – differs between ecosystems and time slices. For instance, important ARF species tend to co-occur from the LGM to the present, where they are rarely found outside ARF areas, though non-ARF species sometimes overlap their distributions. By contrast, AMF's composition is more variable across its modern range – it contains significant floristic gradients (Duarte et al., 2014; Oliveira-Filho et al., 2014) – and, accordingly, its species associations are less stable through time (Figs. S9, S11).

The clustering analysis identifies 34 potential floristic assemblages, divisible into three broad groups, which encompass these different expressions of our target ecosystems (Fig. 4): the small cluster *a* that aligns closely with modern-day ARF (assemblages 3 and 2); cluster *b*, with one subsection dominated by mixtures of different forest and Campos species like those found currently on the highlands' escarpment slopes (assemblages 9, 7, 8 and 26) and another by SDF species (assemblages 5, 16, 6, 20 and 30); and cluster *c*, with subsections dominated by AMF/SDF/Campos species (assemblages 25, 27, 17 and 24), Campos and Cloud Forest (15 and 29), AMF/Campos/Cloud Forest and some SDF (14, 13 and 33), and SDF/Campos (31 and 34).



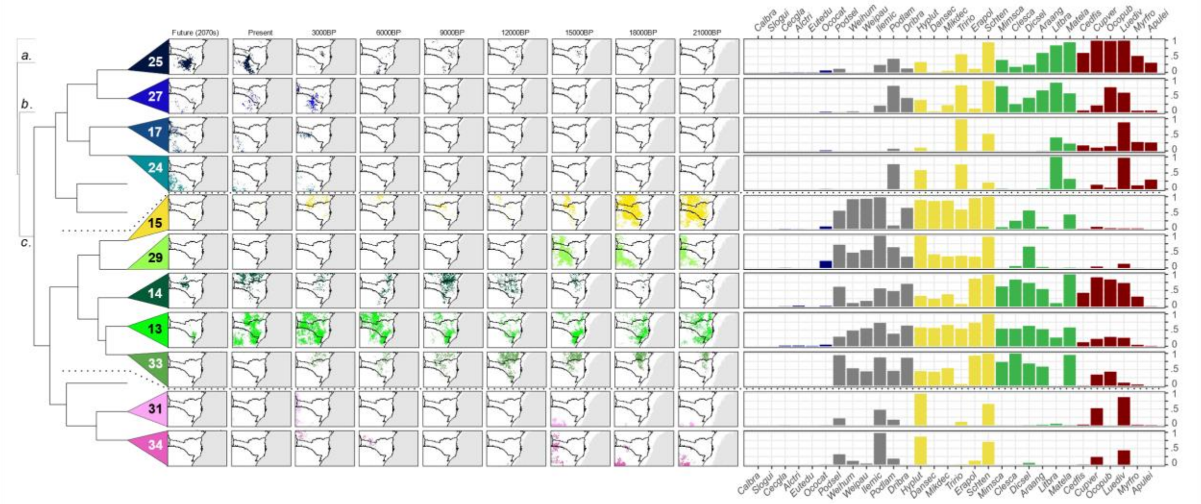


Fig. 4: relationships (left; see also fig. S2), distributions (centre; see also fig. 6), and floristic compositions (right; each species' average predicted prevalence) of predicted assemblages used in this study (top, clusters a and b; bottom, cluster c). The right-most panel shows species' average predicted prevalence in each assemblage, using species' six-letter codes from table 1 and colours from the ecosystems in which each species is currently most important (see table 1 and fig. 1). Dendrogram branches without additional detail represent assemblages which never reach 5% of the land area in any time slice and which are excluded from further analysis (see fig. S2).

The relationships between these cluster-derived floristic assemblages and the southern Atlantic Forest's ecosystems are evident from comparisons with Brazil's official vegetation map (IBGE, 2012) (Fig. 5). This shows that, while the associations are generally accurate, cluster *c*'s AMF/Campos/Cloud Forest assemblages occupy only part of their expected extent in the east and (especially) the west. A species-level analysis suggests different causes in each area (Fig. S9). In the east this appears to be due to ARF species such as *Alchornea triplinervia* co-occurring with AMF, Campos and Cloud Forest taxa at higher-elevation areas, forming the mixed-ecosystem assemblage 9. In the west, by contrast, the main cause is the predicted absence of typical AMF species (except *Matayba elaeagnoides*), without which these areas' coverage with SDF and low-elevation AMF species (*M. elaeagnoides, Cedrela fissilis, Cupania vernalis, Luehea divaricata, Ocotea puberula*) lead to their classification as SDF-like assemblages 5, 16 and 6. Modern ecotonal areas combining SDF and AMF species are best represented by assemblages 25 and 14 in the south and north of our study area, respectively – both found considerably uphill and to the east of the official boundary between SDF and AMF.

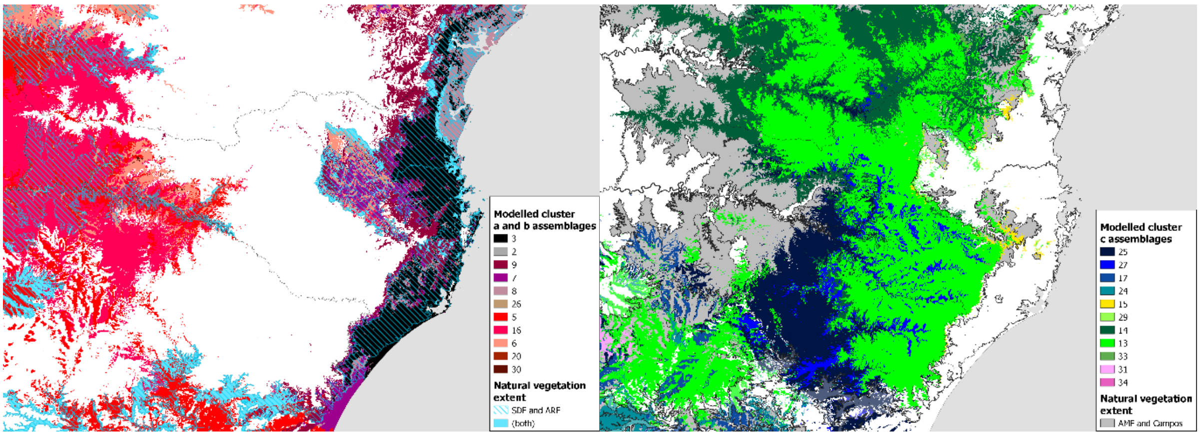


Fig. 5: overlay maps of modelled floristic assemblages and official vegetation (IBGE, 2012; see Fig. 1). Left: assemblages from clusters a and b compared with SDF and ARF (blue). Right: assemblages from cluster c compared with grassland and AMF (dark grey). See Fig. S12 for ecotonal areas and comparison with the future scenario.

3.3. Changes through time and proxy comparison

Our modelling suggests that the southern Atlantic Forest's ecosystems have changed significantly in both distribution and composition over the last 21,000 years, and are predicted to experience exceptionally drastic changes as a result of changing conditions over the coming decades (Fig. 6).

3.3.1. Last Glacial Maximum (21,000 – 18,000 BP)

Between 21,000 and 18,000 BP, the highlands were dominated by cold-adapted floristic assemblages from cluster *c*, with relatively slight differences between the periods. Assemblages 15 and 29 (Campos and Cloud Forest species) occupy most of the centre, south and west of the plateau; assemblages 13 and 33 (which include more AMF species) are found more to the highlands' east, especially at 18,000 BP. The north of the plateau transitions from assemblage 13 to 15 between the time slices, with the former assemblage extending into the southern part of what today is Santa Catarina's coastal plain. Most of our modelled tree species, as well as several Campos herbs, are predicted to have occurred on continental shelf areas exposed by sea levels 130m lower than present. This combination forms assemblages 9 (which covers almost all of the continental shelf), 7 and 8: cold-adapted taxa are less prevalent in the latter two assemblages, which are found along and close to the present-day northern coastal plains.

Where these modelled assemblages are found in the present day (generally on the plateau and its eastern escarpment), much of their extent is forested. However, this does not appear to have been the case at the LGM as grassland proxies generally dominate, though phytolith records do suggest some areas that might have had higher tree cover. Half or more of the phytoliths at Iapó River (Kalinovski et al., 2016) around 18,000 BP come from woody plants (though the site's $\delta^{13}C$ signature is C4-dominated), and some samples from approximately the same time in Campo Erê (Cecchet, 2015) have modest contributions of eudicot and palm phytoliths, though precise ages and identifications are not available in the latter record. Campo Erê is also one of three LGM sites in our study area (with São José dos Ausentes (Pereira, 2017) and Cerro do Touro Watershed (de Oliveira et al., 2008)) whose $\delta^{13}C$ values indicate a mixture of C3- and C4-photosynthesising vegetation, though only Obera (Zech et al., 2009) and Curucutu (Pessenda et al., 2009), respectively to the west and north of our study area, have C3-majority contributions.

The highest values for forest pollen are found in Volta Velha (14%, 21,000 BP; Behling and Negrelle, 2001), where Myrtaceae and Melastomataceae dominate, and GeoB2107-3 (22%, 18,000 BP; Gu et al., 2017), with *Alchornea, Podocarpus, Araucaria* (at 21,000 BP) and *Myrsine* (at 18,000 BP) the latter's main components. These sites' investigators suggest this indicates a mosaic of subtropical forest patches with grasslands on the lowlands (Behling and Negrelle, 2001; Gu et al., 2017), a suggestion supported by proxy evidence from Curucutu (Pessenda et al., 2009), north of our study area. At 21,000 BP, this site had a similar forest pollen proportion (17%) and composition (mainly Myrtaceae and Melastomataceae-Combretaceae, with some *Alchornea*) to Volta Velha and GeoB2107; the core's $\delta^{13}C$ values show that the site was dominated by C3 vegetation, and nine other nearby profiles show mixes of C3 and C4 contributions (Pessenda et al., 2009). Our predicted assemblages on the exposed continental shelf and modern-day lowlands could have been expressed as such a grassland-forest mosaic, its precise configuration dictated by non-climatic (e.g. topographic) conditions. A similar physiognomy was likely found on the highlands around the LGM, with Campos dominating and AMF and/or Cloud Forest species probably confined to rare, small patches – at least in the highlands' south-east where long fossil pollen records exist (Behling et al., 2004; Leonhardt and Lorscheitter, 2010). The higher contribution of *Podocarpus* and *Araucaria* pollen to GeoB2107's LGM pollen spectrum suggests AMF forest elements were more common further north or on the continental shelf (Gu et al., 2017), which may align with the early phytolith record from Iapó River (Kalinovski et al., 2016).

3.3.2. Late Glacial Period (15,000 BP)

Although floristic assemblages from the cold-adapted cluster *c* continue to dominate the highlands, and components of cluster *b* the coastal region, there are notable compositional changes in most areas from the LGM to the Late Glacial. The range shifts that underpin these are reductions for many of the most cold-adapted species (Cloud Forest and Campos) and expansions for more warm-adapted SDF taxa, with most AMF and ARF species relatively stable over the time period. The main exceptions to these trends are a south-western expansion for *Podocarpus sellowii* and an eastward consolidation for *Dicksonia sellowiana,* though the potential ranges of several Campos, Cloud Forest and SDF species experience little change from the LGM. At 15,000 BP there is an increased extent of assemblages 31 and 34, which expand north and west from their LGM locations in low-elevation areas at our study area's southern limits and part of the Uruguay River valley. Rather than being true reflections of probable communities, however, these assemblages are more likely to denote areas that are suitable for few of our modelled species (Fig. S10).

Most of the predicted changes between the LGM and Late Glacial occur in areas not covered by palaeo-data sites, making it difficult to discern their accuracy. Most sites in our study area do show modest increases in forest pollen between 18,000 and 15,000 BP, in line with predictions of more range expansions for forest species than herbs, though fossil pollen from the growing cluster of south-eastern plateau sites remains ≥90% grassland taxa. The largest increases in forest pollen are found in GeoB2107 and Curucutu, reaching 33% of the total in each. GeoB2107's arboreal pollen also becomes more diverse, with notable increases of Moraceae/Urticaceae, Melastomataceae and

Celtis, while previously established taxa such as *Alchornea, Araucaria* and *Podocarpus* are maintained. This might support the predicted development of assemblage 7 at the expense of assemblage 9 on the north-central continental shelf: the former is more dominated by warm-adapted tropical trees, with cold-adapted Campos, Cloud Forest and AMF species less prevalent than in assemblage 9. A notable proxy site which first covers the 15,000 BP time slice is Buriti (Bertoldo et al., 2014): at this time period, 91% of Buriti's pollen comes from tree taxa – a proportion far higher than any other site at this period – with *Araucaria* (ca. 20%), *Ilex* and *Podocarpus* (15-20%) the main contributors. This would suggest that at least some western areas in our study area – around assemblages 29, 26 and 34 – had AMF-like forest cover at 15,000 BP.

3.3.3. Early Holocene (12,000 – 9,000 BP)

The change between 15,000 BP and 12,000 BP, the transition from the Late Glacial to the Holocene, is the greatest among any of our past time slices, especially in our study area's south and west. Here, areas previously characterised by the cold-adapted floristic assemblage 29 undergo significant compositional changes, becoming the largely novel SDF-like assemblages 20 and 30, with areas of modern-day SDF assemblages 5, 16 and 6. This change is broadly driven by this area's loss of formerly widespread cold-adapted taxa (*Ilex microdonta, Hypochaeris lutea* and *Schizachyrium tenerum*), and the expansion into it of SDF/lowland AMF species (mainly *Matayba elaeagnoides, Cupania vernalis* and *Luehea divaricata*). With some changes between these assemblages, this band of more warm-adapted vegetation remains until 9,000 BP.

Unfortunately, the dearth of palaeoecological records covering this period and area mean there is sparse evidence against which to assess our model predictions. In its northern reaches, Buriti – the only site available at 12,000 BP – experiences large increases in Asteraceae pollen that reduce its forest pollen from 91% to 65%, then 55% at 9,000 BP, suggesting an increasingly open landscape. Buriti's forest pollen composition in the early Holocene is still mostly *Araucaria* and *Ilex,* though with less *Podocarpus* than previously and more *Alchornea,* Arecaceae*, Hieronyma* and *Luehea* (all warm-adapted taxa). Notably, a stable co-occurrence of *Luehea* and *Podocarpus* pollen (ca. 5-10% each) begins shortly after 9,000 BP, potentially matching the predicted presence of assemblages 20 and 30, in which *L. divaricata* and *P. sellowii* are prevalent. In the area's south-east, Serra Velha's record (Leal and Lorscheitter, 2007) starts around 11,000 BP as ca. 95% grassland pollen, but forest pollen from early-successional tropical trees accounts for 42% of the total by 9,000 BP. Though its composition and forest-grassland trajectory differ from Buriti's, Serra Velha too appears to have been found in a generally open environment. Finally, in Campo Erê, at the north-western edge of the area of rapid change, several phytolith morphotypes experience abrupt changes around a sample dated to 8,000 BP, suggesting the existence (but not the nature) of significant changes early in the Holocene.

Further east in the early Holocene, our modelling suggests the incremental loss of more cold-adapted species along the coastal lowlands. This is best captured by the pollen record of Volta Velha (Behling and Negrelle, 2001), which sees drastic increases in forest pollen between 15,000 BP and 12,000 BP due to sharp reductions in Campos (Poaceae) pollen and the emergence of a forest pollen assemblage dominated by generally tropical Arecaceae, *Alchornea* and Myrtaceae pollen with *Myrsine* and Moraceae/Urticaceae. Serra da Boa Vista (Behling, 1995) records an increase in ARF-type pollen, though coastal cores at our study area's south do not, remaining grassland-dominated. While GeoB2107's arboreal pollen sum changes little overall, there are changes in its composition, with *Alchornea,* Moraceae/Urticaceae and Arecaceae all experiencing sustained increases.

The cold-adapted assemblages of cluster *c* also experience significant changes between the late glacial and early Holocene. Here again, however, few palaeoecological sites can test these predictions. Phytoliths and soil carbon isotopes at Aroeiras (Silva, 2018), Guarapuava (Calegari, 2008) and another nearby site (Silva et al., 2016; no precise location) suggest the presence of woody AMF-like vegetation in the early Holocene, which subsequently declined. Further soil profiles at CPCN Pro Mata (Dümig et al., 2008; Silva and Anand, 2011) show that smaller-than-modern forest blocks were also found in the highlands' south-east by 9,000 BP, but any changes in their composition are invisible in the region's grassland-dominated pollen records. Further north, there is little change in the grassland-dominated pollen record from Serra do Aracatuba (Behling, 2006), but a short buried peat sample near the Cerro do Touro Watershed (de Oliveira et al., 2008) shows a 30% decline in Campos pollen within a few centuries of 12,000 BP as *Weinmannia,* Myrtaceae, *Myrsine* and *Dicksonia sellowiana* pollen increase. Combined with changes in AMF taxa from GeoB2107 (*Araucaria, Schinus/Lithraea, Podocarpus* and *Myrsine* all respond differently), this may provide general support for predicted compositional changes in highland vegetation through the early Holocene, though forest coverage apparently remained patchy.

3.3.4. Mid-Holocene (6,000 BP)

At the mid-Holocene (6,000 BP), many parts of the study area – including much of its west – are poorly characterised by our modelled species (Fig. S10), most of which experience reductions in their predicted extents compared to 9,000 BP (Fig. 6). For this reason, increased caution is required when interpreting vegetation changes in these areas. Many areas designated as assemblages 20 and 30 in the early Holocene become assemblages 16 (SDF-like) or 13 (AMF/Campos-like), depending largely on changes to the distributions of *Matayba elaeagnoides* and *Podocarpus sellowii.* Assemblage 20 reappears north-west of the Itajaí valley, however, replacing the AMF/SDF-like assemblage 14 as the location becomes unsuitable for several Campos, AMF and Cloud Forest species. Similar but less drastic changes convert the Campos/Cloud Forest-like assemblage 15 to the more AMF-like assemblage 13 in our study area's centre. Changes are somewhat less marked along the coastal lowlands, where sea-levels reach essentially modern levels – small compositional changes happen in the south and the central region records the first significant presence of assemblage 3, modern ARF's best representative.

Most palaeo-proxy sites in the region's west are dominated by grassland/C4 signals at the mid-Holocene, apart from Trincheira Reserva (Alcantara dos Santos, 2013) to the north-west, where phytoliths and $\delta^{13}C$ records show dominant woody C3 vegetation, and Buriti, where forest pollen increases to make up 70% of the total. As before, there is compositional change in Buriti's arboreal pollen with *Araucaria*'s contribution decreasing, being overtaken by *Alchornea*. There are also increases in *Dicksonia sellowiana* spores and pollen from *Drimys, Podocarpus* and *Luehea*, with *Sloanea* occurring at 6,000 BP for the first time in several millennia. This combination of AMF and more warm-adapted tropical taxa may suggest a no-analogue forest assemblage at Buriti in the mid-Holocene; although our modelled species do not cover the location well at this period, this could support our prediction of the site occurring between floristic assemblages resembling tropical forest and AMF 6,000 years ago.

Further east, most sites show increases in forest pollen. This is particularly notable at the high elevations in our study area's centre-east at Ciama 2, Tabuleiro Summit and Serra da Boa Vista (Behling, 1995; Behling and de Oliveira, 2018; Jeske-Pieruschka et al., 2013). Sites in the southern coastal lowlands show heterogeneous mixtures of persistently dominant grassland (Águas Claras, Bauermann, 2003; Santa Rosa do Sul, Cancelli, 2012; Passinhos, Macedo et al., 2007) and expanded forest pollen (São João do Sul, Cancelli, 2012; Tramandaí Lagoon, Lorscheitter and Dillenburg, 1998), mostly from tropical taxa. Serra Velha, further inland, is the exception to this pattern, with its forest pollen proportion dropping from 42% at 9,000 BP to 15% at 6,000 BP. Our models predict tropical forest developing over this period, so while some of this patchiness may be due to fluctuating sea levels influencing coastal vegetation or sites' different catchment sizes, it may also show that coastal forest development in our study area's south was slower and/or later than predicted.

On the plateau's eastern edge, smaller expansions of forest pollen can be seen in most cores between 9,000 BP and 6,000 BP; in CPCN Pro Mata's soil pits forest borders advance by up to 20m and today's large woodland patches first receive increased C3-carbon input (Silva and Anand, 2011). With minimal change in Serra Campos Gerais (Behling, 1997a) or in GeoB2107's AMF taxa, it is possible that the plateau's vegetation changed less between 9,000 and 6,000 BP than predicted, though with no sites in the most changeable area of modelled cluster *c* assemblages it is impossible to be certain.

3.3.5. Late Holocene (3,000 BP)

At 3,000 BP, western parts of our study area are again poorly covered by our modelled species; further east, however, predicted assemblages on the plateau and coastal plain begin to more closely resemble those of the present day.

The south-west of our study area is covered by a combination of assemblages, with extensive assemblage 5 (SDF-like in the present, but with *Podocarpus lambertii, Schizachyrium tenerum* and *Luehea divaricata* most prevalent here), some AMF/Campos-like assemblage 13, and other areas poorly characterised (assemblage 31 and other rarer groupings). The only palaeo-proxy record within this region, São Martinho da Serra (Bauermann et al., 2008) is dominated by herbaceous pollen; Serra Velha, at its eastern end, becomes dominated by tree pollen, much of it unidentified but with major contributions from Myrtaceae and *Alchornea*. The north-west is classed as assemblages 31 and 34, here predicted to be a mixture of Campos and SDF species, with *Ilex microdonta* (Cloud Forest) and *Araucaria angustifolia* (AMF) in some areas. Buriti, sited between these assemblages and AMF/Campos-like assemblage 13, records high levels of forest pollen – mainly *Ilex* (*Araucaria* and *Alchornea* experience temporary lows at 3,000 BP) with a continued mixture of cold-adapted (*Symplocos, Podocarpus*) and warm-adapted (*Luehea, Hieronyma*) trees – which may corroborate the unusual combination of taxa modelled for the site.

Across the rest of the plateau, our models predict a consolidation and expansion of assemblages associated with cold-adapted taxa. Assemblages 13 and 27, which describe present-day AMF and Campos areas, cover much of the highlands, including parts of western Santa Catarina state and north-western Rio Grande do Sul which are now SDF. Assemblage 15, dominated by Cloud forest and Campos species, also expands to cover its largest extent since 18,000 BP, concentrated at high elevations along the escarpment and in areas of modern-day Campos in south-central Paraná state. Soil profiles in these latter areas record C4-dominated vegetation for this period, as they had for 6,000 BP, despite the region's only pollen record (Buriti) continuing to be forest-dominated. Further east, palaeo-proxy records show increasing contributions from forest taxa compared to the mid-Holocene. This expansion of AMF over Campos is recorded between 3,000 and 4,000 BP in many sites at the highlands' southern edge, as well as in others north of our study area (Behling, 1997b, 1995; Behling et al., 2004; Bissa and de Toledo, 2015; Jeske-Pieruschka and Behling, 2012; Leonhardt and Lorscheitter, 2010; Scherer and Lorscheitter, 2014). Some of these sites also record a subsequent expansion of AMF around 1,000 BP (Behling, 2006; Behling et al., 2004; Leonhardt and Lorscheitter, 2010; Scherer and Lorscheitter, 2014), so many plateau proxy sites' surroundings were probably more open at 3,000 BP than in the present. Notably, however, given its likely regional catchment, the marine core GeoB2107 records little change in the relative proportions of forest and grassland pollen between 6,000 and 3,000 BP, though forest pollen (notably *Araucaria*) does increase subsequently.

In the late Holocene, most of the coastal region becomes covered by assemblages 3 and 7, primarily differentiated here by the distributions of *Myrocarpus frondosus* and *Ocotea catharinensis*. Accordingly, most pollen cores from the coastal lowlands see increasing forest pollen proportions, generally dominated by combinations of Myrtaceae, Arecaceae and *Myrsine* (and, to a lesser extent, *Ilex* and *Alchornea*), likely reflecting developing ARF vegetation. This development was unlikely to have been complete, however, as in almost every case these coastal sites record less forest pollen at 3,000 BP than they do in the present day, suggesting that – like the plateau sites – their surrounding landscapes were then more open than now. In the central coastal mountains *Weinmannia* (with Myrtaceae) dominates forest pollen assemblages at this time, whose trajectories differ between each site from the mid-Holocene to 3,000 BP, and again to the present. Although our predictions accurately place these sites at the intersection of tropical and more cold-adapted floristic assemblages, their nuances – likely caused by local topography-weather system interactions (Behling and de Oliveira, 2018) – are not fully captured.

3.3.6. Future (2070s)

By the late 21st Century, under a pessimistic carbon emissions scenario, the distributions and compositions of our modelled ecosystems are predicted to be strikingly different to their present and past. Species generally shift to higher elevations, with increasing numbers of lowland tropical trees gaining wider footholds in adjacent highland areas – especially ARF species in the northeast and SDF species across the region's centre and west. These uphill expansions lead some species to vacate their present ranges' lower elevations, resulting in (near-)novel assemblages being left behind. More cold-adapted AMF, Campos and Cloud Forest species – already found at our study area's highest elevations – tend to experience drastic losses from areas that are presently suitable, and few spread into new, previously unsuitable locations.

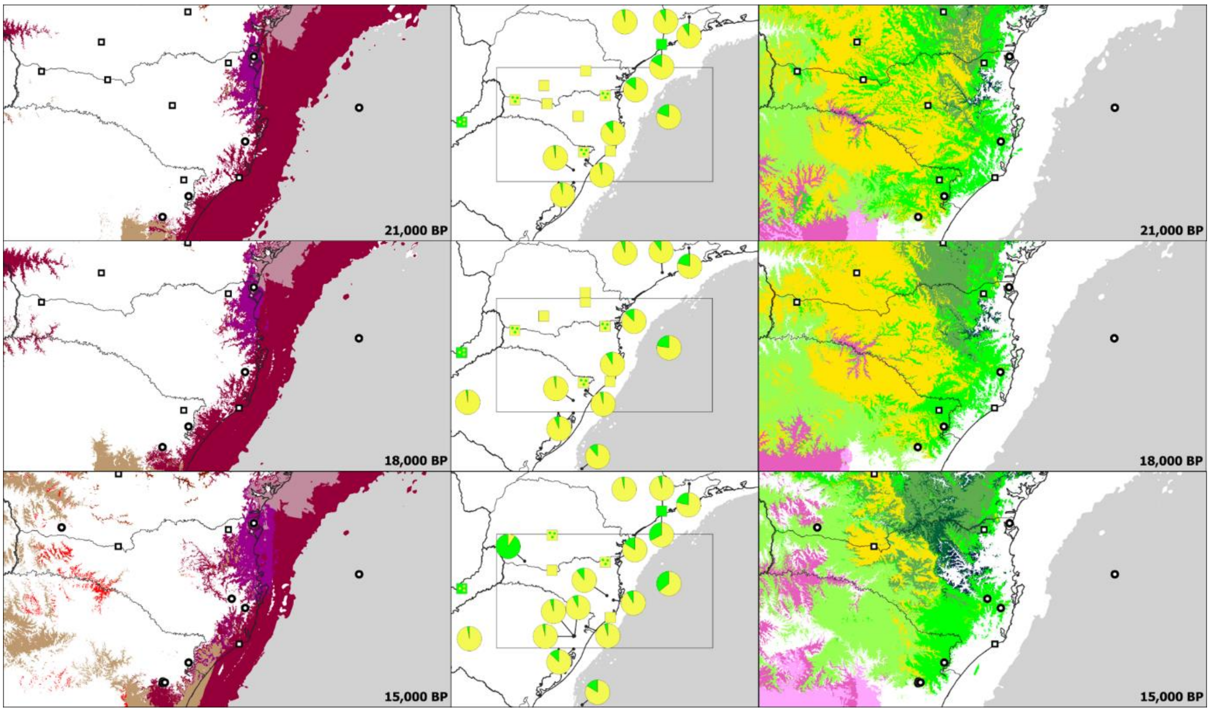
In our study area's west, assemblages 17 and 24, presently rare and scattered in the southwest, become widespread. Assemblage 24, the more southerly of the two, is characterised by a mixture of SDF and AMF/SDF species, with some presence of the few cold-adapted species to experience westward range expansions (*Podocarpus lambertii*, *Trifolium riograndense* and *Hypochaeris lutea*).

Fewer species characterise assemblage 17, found along parts of the Uruguay and Iguazu river valleys, and, still further to the north-west, other parts of the Iguazu valley are predicted to be unsuitable for all our modelled species by the 2070s. These assemblages are interspersed with the SDF-like assemblage 5, dominated here by *Luehea divaricata* and other SDF species with some *Lithraea brasiliensis* and *Matayba elaeagnoides*, which occupies large parts of present-day AMF/SDF ecotones.

Across the northern part of our study area, the only species of AMF, Campos and Cloud forest which largely maintains its range is *M. elaeagnoides*; most others are predominantly or completely lost from this region, but much less change is predicted for the area's shared SDF/AMF species. Combined with northward expansions of *Myrocarpus frondosus* (SDF), *Euterpe edulis, Cecropia glaziovii* and (to a lesser extent) *Alchornea triplinervia* (all ARF), our study region's north becomes classified as assemblage 6, presently a relatively rare grouping found around AMF's ecotones with SDF and ARF.

The loss of climatically suitable habitat for AMF, Campos and Cloud forest species across our study area's northern region leads to a dramatic retraction in the area covered by their associated assemblages. Assemblage 13 covers a smaller area in the 2070s than in any other modelled time slice, becoming confined to the highest elevations in our study area's centre and south-east. Most present-day AMF and Campos areas become characterised by assemblages which today mark ecotones with SDF – assemblages 14 in the centre and 25 in the south, with *Araucaria angustifolia* largely restricted to the latter. The plateau's south-easternmost part, which today is assemblage 13, becomes assemblage 9 as highland species' ranges contract and species more common in (or shared with) ARF and SDF expand.

ARF species showcase the interspecific variability in responses to the changing climate. *Cecropia glaziovii* and *Sloanea guianensis* retain their current range as well as expanding to higher elevations; *Alchornea triplinervia* and *Euterpe edulis,* by contrast, shift away from the coast as both leading and trailing edges of their ranges shift uphill. *Ocotea catharinensis*'s range already occupies high elevations and changes little in the north, is reduced in the centre of our study area (where the mountains are more isolated), and expands a little in the south; *Calophyllum brasiliense* spreads considerably to the south, but its elevational distribution changes little. Overall this means that assemblage 3, typical of modern-day ARF, covers a similar extent in the 2070s to the present day, but at a higher elevational band, partly replacing assemblage 9 (escarpment forest). This in turn creates space for novel or rare cluster *a* (ARF-like) assemblages, which appear along the coast (e.g. assemblage 2) and in parts of the Itajaí valley.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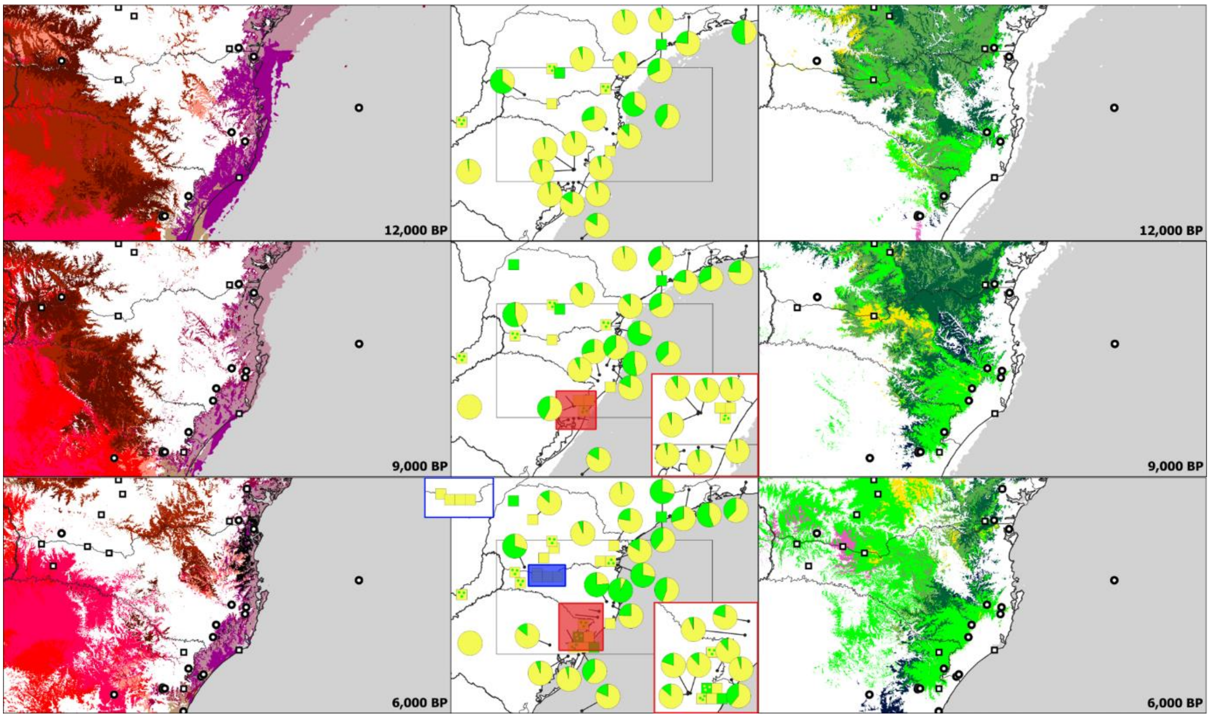
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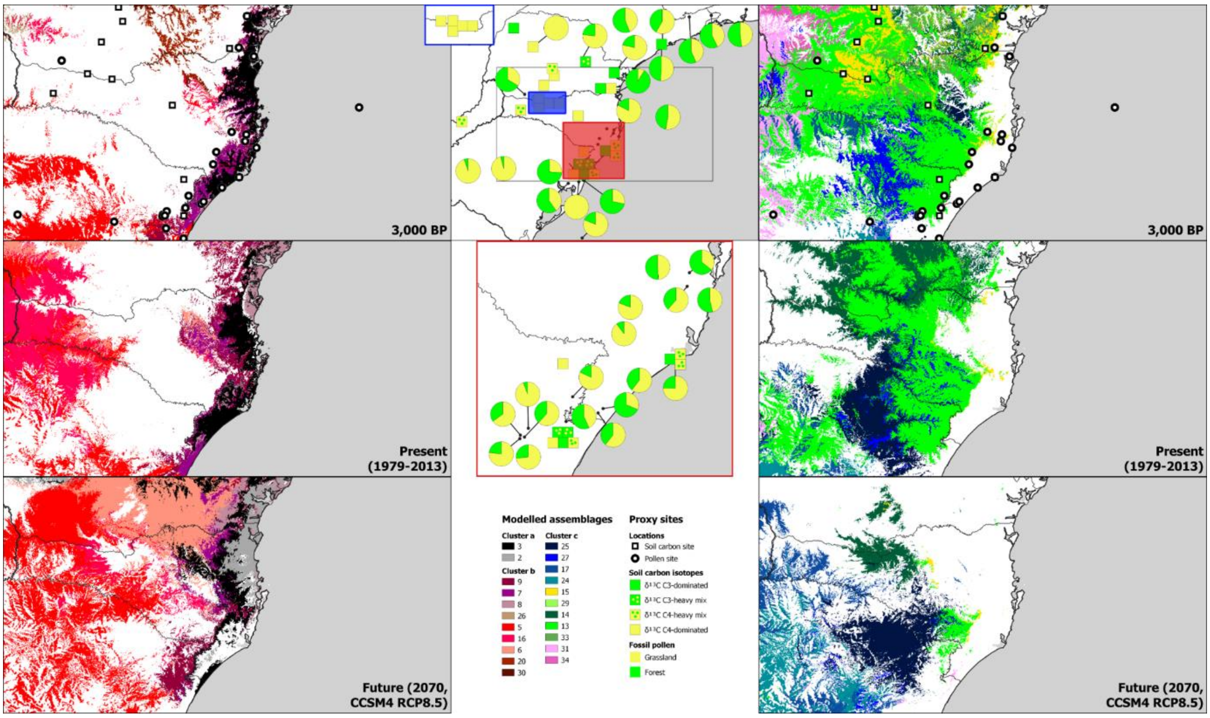

Fig. 6: predicted floristic assemblages (clusters a and b, left, and cluster c, right) and palaeo-proxy values (centre) for our study area through time. For maps of individual assemblages, see Fig. 4 or Supplementary Information.

3.4. Long-term context for present and future floristic assemblages

When have locations previously been occupied by plant assemblages most like those of the modern day? Our results show that the southern Atlantic Forest's different ecosystems find their closest analogues at different times over the last 21,000 years (Fig. 7). In the west, modern plant assemblages in some SDF areas are most similar to those found in the mid-Holocene (6,000 BP) and others to those of the early Holocene (12,000-9,000 BP), but all are very unlike floristic assemblages found in these areas during the LGM and Late Glacial (before 15,000 BP). By contrast, closely related assemblages have occupied the highlands from at least the LGM through to the present. Areas in the north had floristic assemblages most like the present day at various points through the Holocene, though in the southern part of the highlands the closest match is found 3,000 years ago. Notably, the highest elevations have experienced very little compositional change over the last 21,000 years. The present-day coastal assemblages are largely closest to those found 3,000 BP, though some areas in the north and in the Itajaí valley have closer matches earlier in the Holocene.

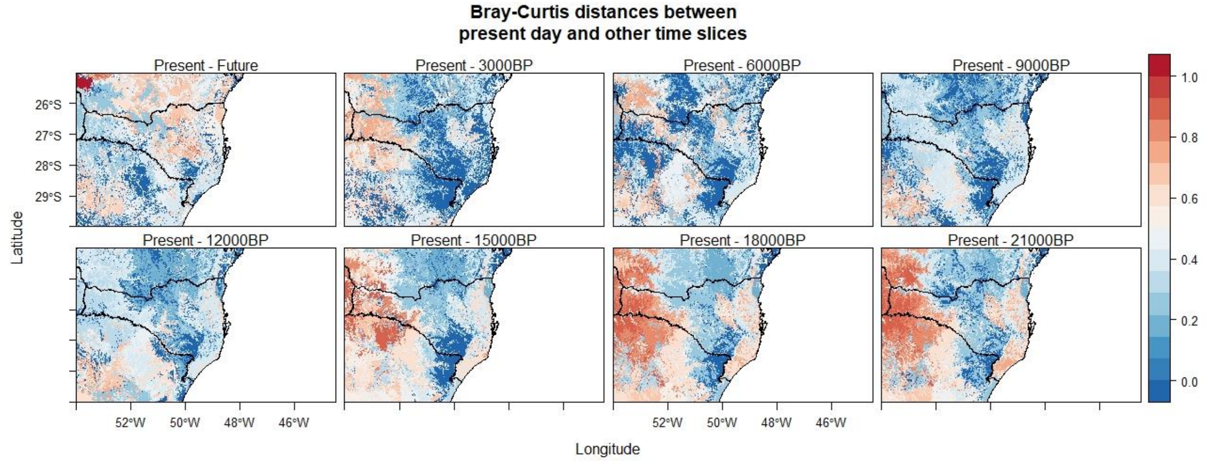

Fig. 7: the (dis)similarity of present-day floristic assemblages to those of past and future time slices – red denotes assemblages which are more dissimilar and blue those which are more similar.

Our results also show that, without reductions in greenhouse gas emissions, by the 2070s much of the southern Atlantic Forest will have – or at least will be on track to have – very different floristic composition to any experienced since at least the LGM (Fig. 8). Close local analogues for future assemblages can only really be found for ecosystems at the highest elevations; in some western and south-western areas the early and mid-Holocene (9,000-6,000 BP) provides some relatively close matches for future assemblages. By contrast, more than 48,000 km^2 of assemblages predicted to arise across our study area's north and east are highly dissimilar (Bray-Curtis score above 0.5) to those modelled for those areas in any other time slice, including the present day.

More than 102,000 km^2 of our study area is predicted to experience greater floristic change between the present day and the high-emissions future scenario than in any other 3,000-year interval modelled here (Fig. 9, Table S3). By comparison, deglacial warming during the last glacial-Holocene transition (15,000 – 12,000 BP) brought the greatest vegetation change to over 105,000 km^2; around 15% of that area would experience even greater floristic change over the coming decades in a high-emissions 21st Century (Table S3). Notably, the spatial distribution of vegetation changes during the 21st-Century and glacial-Holocene transition differ: climate change associated with the onset of the Holocene affected vegetation in the south and western parts of our study area significantly, whereas future climate changes are predicted to have their greatest impact on vegetation in northern and eastern regions which have otherwise experienced relatively little change since the LGM (Figs. 9, S13-14).

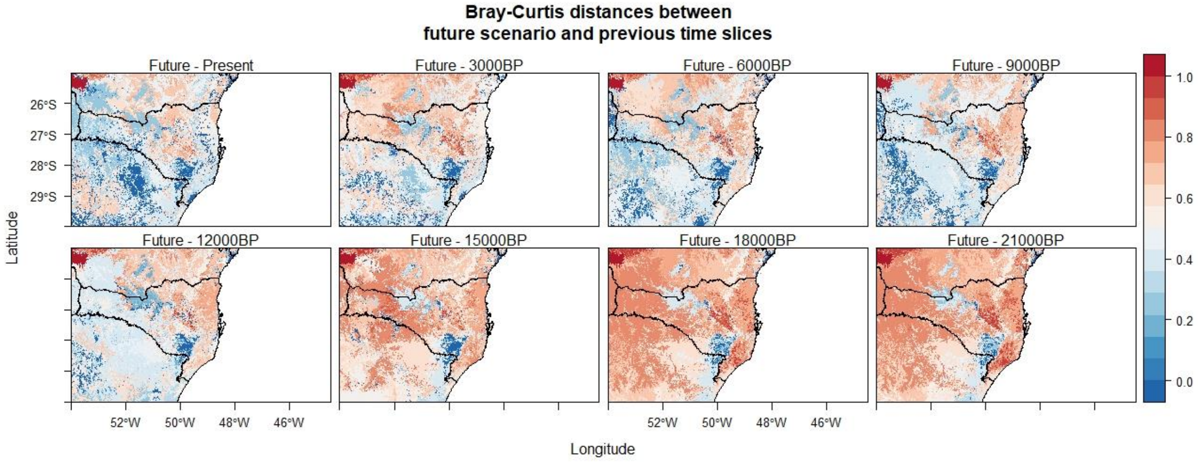

Fig. 8: The (dis)similarity of future floristic assemblages to those of past and present time slices – red denotes assemblages which are more dissimilar and blue those which are more similar.

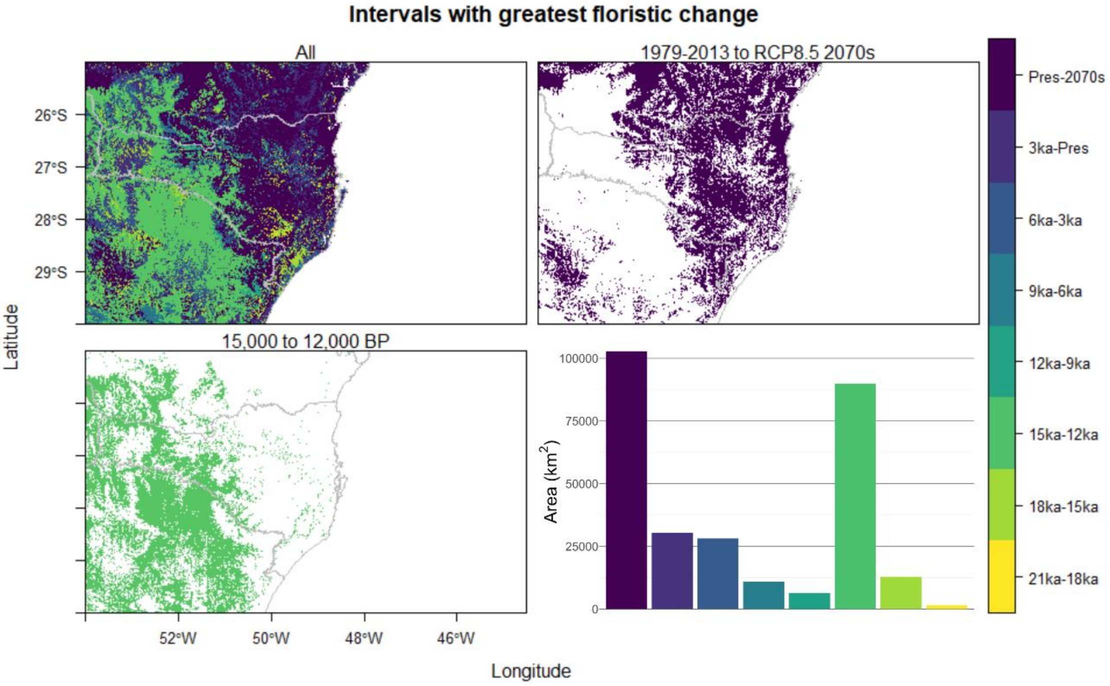

Fig. 9: Between-time slice intervals during which the greatest floristic change is predicted. For figures underpinning column chart, see Table S3. For past time slices only (i.e. excluding the future scenario), see Fig. S13. For change between all intervals, see Fig. S14.

4. Discussion

Our study demonstrates the value of combining species-level distribution modelling with a granular synthesis of palaeovegetation-proxy evidence to better understand how plant species in Brazil’s southern Atlantic Forest have responded to climate changes since the LGM. The results generated show that our downscaled climate data and predicted species distributions are broadly aligned with independent proxy evidence, and provide a number of important novel insights into the past and future of southern Brazil's Atlantic Forest.

4.1. Plant community change since the LGM

Our results highlight the importance of considering ecosystems' compositional changes alongside shifts in distribution – especially in the southern Atlantic Forest's variable ecosystems. At an aggregate (e.g. cluster *a, b, c*) level, our findings confirm expectations based upon previously published fossil pollen data and modelling studies (Arruda et al., 2017; Bauermann, 2003; Behling et al., 2004; Bergamin et al., 2019; Costa et al., 2017): cold-adapted floristic assemblages have occupied most of the highlands for most of the last 21,000 years, with their wider LGM extent reduced by the early Holocene; large areas of more warm-adapted and seasonal communities emerged at lower elevations in the south and west around 12,000 years ago before receding in the late Holocene; and the full development of coastal tropical forest only occurred in the last few thousand years. However, our approach provides unique insights into the floristic changes within these broad-scale vegetation shifts by providing significantly enhanced spatial and taxonomic (species-level) resolution (Fig. 6). Our modelling results show that highland LGM assemblages were not floristically uniform across the plateau – vegetation in western highland areas was compositionally closer to modern Campos and Cloud Forest, while more Araucaria Mixed Forest elements occurred in eastern highland areas. Our evidence suggests that the eastern plateau and coastal plain experienced no ecosystem- (i.e. cluster-) level turnover over the last 21,000 years, but rather underwent numerous subtle compositional shifts.

Our species-level modelling approach provides important new insights into Holocene plant communities that were unlike any currently known from the region. Although no-analogue Quaternary floristic assemblages have been inferred from previously published fossil pollen studies elsewhere in the neotropics, including Brazil's Cerrado biome and the central sector of the Atlantic Forest biome to the north (De Oliveira, 1992; De Oliveira et al., 2020; Francisquini et al., 2020; Horák-Terra et al., 2020; Raczka et al., 2013), the taxonomic limitations of pollen analysis, combined with the paucity of sites, mean their full nature, extent, and presence in southern Brazil have not previously been ascertained. Our palaeo SDM results provide the first evidence that significant species turnover in Brazil's southern Atlantic Forest in the early Holocene (12,000-9,000 BP) – most notably across the plateau's (south-)west sector – created novel plant communities without modern analogue. However, the absence of existing palaeovegetation data sites from much of our study area makes these predictions hard to verify. Buriti (Bertoldo et al., 2014), at the modelled assemblages' northern edge, does provide some support for this early Holocene no-analogue plant community hypothesis, recording high levels of Asteraceae pollen and an unusual mixture of cold- and warm-adapted trees (*Araucaria, Ilex, Hieronyma, Luehea*) at this period. Other sites (Jeske-Pieruschka and Behling, 2012; Leal and Lorscheitter, 2007; Leonhardt and Lorscheitter, 2010; Scherer and Lorscheitter, 2014) at the opposite ends of this putative non-analogue community differ from Buriti and one another, suggesting that floristic composition was not homogeneous across this region. More fossil pollen records are therefore needed to more rigorously test the accuracy of these findings and confirm, clarify or refute the model predictions.

The importance of redoubled proxy-based palaeoecological investigations on southern Brazil's plateau is further emphasised by our finding that most highland fossil pollen sites occur in the most historically stable areas. Recording long periods of continuous grassland, these records do not show notable compositional changes – in part, this may be a function of low taxonomic resolution in herbaceous pollen and the rarity of pollen from (systematically under-represented) forest taxa (Bush, 1995; Cárdenas et al., 2019; Guarinello de Oliveira Portes et al., 2020; Jan et al., 2015; Schüler and Behling, 2011a, 2011b). These sites along the plateau's south-eastern edge have been used to characterise the highlands as largely or entirely treeless from the LGM to the late Holocene (e.g. Behling, 2002, 1998; Bergamin et al., 2019; Lauterjung et al., 2018), an extrapolation that our modelling and palaeo-data synthesis shows to be over-simplistic. As with Arruda et al.'s (2017) ecosystem-level models, we find that AMF-like assemblages could have been found across much of the AMF's current range since the LGM (Fig. 6), and proxy sites frequently omitted from other syntheses attest to AMF taxa and/or forest areas on the highlands before the late Holocene (Bertoldo et al., 2014; de Oliveira et al., 2008; Gu et al., 2017; Silva and Anand, 2011). Our results highlight areas that could be investigated by proxy-based palaeoecological study to test these predictions of compositional change amid long-term ecosystem-level persistence, such as central or north-eastern Santa Catarina and south-eastern Paraná states. Understanding whether and how modelled vegetation changes in these regions are represented in palaeoecological data (and *vice versa*) will improve our understanding of the southern Atlantic Forest's multi-millennial-scale plant community dynamics, their underlying drivers, and these techniques' complementary roles in driving these investigations.

4.2. Grassland-forest mosaics across space and time

The palaeoecological value of model-data comparisons for understanding the biogeographic history of the Atlantic Forest can be effectively illustrated with Araucaria Mixed Forest and Campos. Millennial-scale interplay between these ecosystems is generally attributed to rainfall and/or temperature changes (Behling, 2002; Behling et al., 2004), but our analysis shows that SDMs of their constituent species cannot distinguish the two ecosystems in the present, suggesting significant overlap between their climatic niches and therefore that non-climatic factors dictate their boundaries. This corroborates other published modelling studies (Barros et al., 2015; Bergamin et al., 2019; Costa et al., 2017; Maksic et al., 2019; Wilson et al., 2019), as well as contemporary and palaeoecological observations of AMF expanding over Campos in the absence of fire and/or grazing (Behling, 2002; Behling and Pillar, 2007; Dümig et al., 2008; Müller et al., 2012; Oliveira and Pillar, 2005; Silva and Anand, 2011; Sühs et al., 2020). One consequence of this difficulty in differentiating forest and grassland in our SDMs is that, where predicted past assemblages include both herb and tree species, their actual physiognomy is unclear. Our LGM (21,000-18,000 BP) data are a case in point: at this time, most palaeo-data sites in our study area record pollen, soil stable-carbon isotope and phytolith evidence for dominant grasslands, barely differing between modelled assemblages 9 (modern escarpment forests), 15 (Campos/Cloud Forest) and 13 (which encompasses both Campos and AMF; Fig. 6). Which non-climatic factors might explain why these LGM plant assemblages were grasslands rather than forests (as large parts are today)?

There is little evidence that fire restricted forest species' distributions at the (cold, generally wet) LGM; although only three microcharcoal records cover the period (Behling, 1997b; Behling et al., 2004; Jeske-Pieruschka et al., 2013), fire does not appear to have been common across the highlands. As yet, there is also no evidence that herbivory played a role, despite their importance in controlling modern AMF-Campos ecotones: although southern Brazil's herbivorous megafauna persisted into the early Holocene (Asevedo et al., 2020; Lopes and Buchmann, 2011; Raczka et al., 2018), proxies indicative of megafauna, such as *Sporormiella* spores, have not yet been examined in the region. It is likely, however, that the LGM's reduced atmospheric CO_2 concentrations (ca. 190 ppm) would have disproportionately stressed C3-photosynthesising plants, conferring a competitive advantage to C4-photosynthesisers and potentially confining woody vegetation to moister microclimates such as river valleys (Gerhart and Ward, 2010; Montade et al., 2019; Pivel et al., 2010; Svenning et al., 2011). Our evidence suggests that these non-climatic factors may explain southern Brazil's extensive LGM grasslands better than climatic determinants (e.g. extremely cold temperatures or long dry seasons, cf. Behling, 2002; Behling et al., 2004), and so require greater consideration and direct investigation.

One consequence of non-climatic influences on vegetation physiognomy is that modelled assemblages may have manifested quite differently in the past than in the present (e.g. assemblages 9, 15 and 13, detailed above). At the LGM and subsequently, many plant communities predicted to have co-occurring herbaceous and tree taxa may have been grassland landscapes with embedded forest (micro)refugia. Such formations have previously been inferred in southern Brazil from modelling (Barros et al., 2015; Costa et al., 2017; Stefenon et al., 2019), palynology (Behling et al., 2004; de Oliveira et al., 2008; Ledru et al., 2016, 2007) and phylogeography (Auler et al., 2002; de Sousa et al., 2020; Lauterjung et al., 2018; Ledru et al., 2007; Stefenon et al., 2019, 2008, 2007). Direct evidence can also be observed in our synthesised palaeo-proxy sites: a valley's base sheltering more woody vegetation than its head during the Last Glacial (Paisani et al., 2019); 7,500 years of forest and grassland respectively occupying opposing sheltered and exposed aspects of valley slopes (Robinson et al., 2018); and 15,000 years of continuous forest pollen in Buriti's topographic depression, while surrounding soil profiles show grasslands (Bertoldo et al., 2014). The buffering effect of small-scale topography (beyond our climate data's spatial resolution) may also have permitted species to persist in apparently unsuitable areas – Buriti records *Araucaria angustifolia* pollen 15,000 years ago, for instance, when our SDMs suggest it should have been absent (though this could also be because each sediment subsample covers a longer period than our palaeoclimate time slices). Refugia such as these will have played important roles in AMF's late-Holocene expansion across the plateau, and explain the development of *A. angustifolia's* western populations more parsimoniously than long-distance human-mediated dispersal in the late Holocene (cf. Lauterjung et al., 2018).

Compared to the plateau, inferring past vegetation physiognomies from meso-scale SDM predictions and finer-scale topographic data is much more difficult for the coastal lowlands, where detailed palaeo-topography is poorly known, due to submerged LGM coastlines. The prevalence of grassland pollen (and the near-absence of tropical forest pollen) in coastal proxy sites between the LGM and early Holocene has led some to suggest that grasslands replaced Atlantic Rainforest wholesale, with tropical tree species' southern limits found several hundred kilometres further north than at present (Bauermann, 2003; Behling, 2002; Behling and Negrelle, 2001) – a Pleistocene 'Forest Refuge Hypothesis' supported by early palaeo-distribution modelling (Carnaval and Moritz, 2008). However, a subsequent 'Atlantis Forest Hypothesis' argues that continental shelf exposed by lower LGM sea-levels could have supported large areas of forest (Leite et al., 2016). Our modelling and palaeo-data synthesis support an intermediate scenario of subtropical forest patches in a matrix of cold-adapted grassland/Campos (Bauermann, 2003; Behling and Negrelle, 2001; Gu et al., 2017). Our results suggest that the coastal lowlands and continental shelf had temperatures and rainfall suitable for both tropical trees (cf. Leite et al., 2016) and highland Campos species (cf. Behling and Negrelle, 2001), but available palaeoecological records show much more herb than forest pollen (Bauermann, 2003; Behling and Negrelle, 2001; Carvalho do Amaral et al., 2012; Gu et al., 2017), indicating that non-climatic factors likely dictated the distribution of these patches as they did with AMF and Campos on the highlands. However, without detailed topographic data for the presently submerged

LGM coastal area, the precise spatial configuration of this LGM vegetation mosaic cannot be determined.

4.3. Context for a high-emissions future

Our results allow predicted 21st-Century changes in ecosystems' distribution and composition to be placed in a wider temporal context, highlighting just how drastic they could be. Having been stable for millennia (Figs. 6-7; Arruda et al., 2017; Costa et al., 2017), for more than 100,000 km^2 of our southern Atlantic Forest study area the coming decades may bring more dramatic climatic and floristic change than has occurred at any time since the LGM (Figs. 6, 9, S5-S8, S14, Table S3). This is especially true across highland areas from central Santa Catarina to southern Paraná, which stand to lose most of the AMF, Campos and Cloud Forest species that have been present on the highlands since before the LGM (Figs. 6, S9, S12; Behling et al., 2004). Our modelling suggests that these future changes in species' distributions will likely lead to the development of numerous plant communities with few or no analogues in the present – and, in some cases, the past (Figs. 8, S2). Although modelling additional species will no doubt refine SDM characterisations of these assemblages, our modelling results suggest that the predicted loss of many key species may profoundly change the fundamental properties and character of these ecosystems, potentially rendering them more vulnerable to invasive, non-native species.

We also find some indication that these climate change-induced alterations are already underway. In the present day, our models place the lower boundaries of more cold-adapted floristic assemblages at higher elevations than suggested by Brazil's official vegetation classification, and more warm-adapted groups extend higher up (Fig. 5; IBGE, 2012). This could be an artifact of the data used to construct our models, as extensive deforestation in the west of our study area (Fig. 1) has eradicated many climatically suitable localities for some species, which may have led the SDM algorithms to assume conditions are unsuitable for them. The IFFSC's systematic sampling (Vibrans et al., 2020, 2010) should mitigate against this, though, and AMF and SDF species are not similarly affected, being respectively under- and over-predicted. It could also reflect the fact that ecosystems' current potential distributions were likely dictated by pre-industrial climates somewhat different to those of the CHELSA data's present period (1979-2013), which includes recent decades' anthropogenic warming (de Barros Soares et al., 2017; Karger et al., 2017b). This mismatch between 'present day' climate data and when climate conditions were last physiologically relevant may be non-trivial for ecosystems or long-lived tree species, and its impact on SDMs warrants both consideration and research. Taken together, the apparent over-/under-prediction of warm-/cold-adapted species could therefore be a genuine pattern resulting from the inclusion of recent anthropogenic warming in ‘present’ climate data, which is likely to become exacerbated through the 21st century as the magnitude of climate change increases.

4.4. Implications for Conservation

Although our study reveals that southern Brazil’s globally important Atlantic Forest is likely to be severely impacted by future climate change, with major changes in species’ ranges and re-assortment of species into highly novel plant communities, we suggest that our evidence for micro-refugia of forest species under past unfavourable climatic conditions (e.g. the LGM) is cause for cautious optimism about species’ resilience. Our palaeo modelling suggests that, as the atmosphere warms and rainfall patterns change through the 21st Century, those landscape areas whose topography supports microclimates decoupled from these broader, unfavourable climatic trends are more likely to support species that would otherwise be lost (Dobrowski, 2011; Lenoir et al., 2017; McLaughlin et al., 2017; Rull, 2009; Suggitt et al., 2018; Wilson et al., 2019). If protected from habitat loss, these microrefugia can act as holdouts for climatically disadvantaged taxa and, if they can endure long enough, can serve as source populations for future population expansions under more favourable climates (Hannah et al., 2014). Our palaeoecological findings attest to the possibility of such persistence, not only through records of species outside their predicted niche for extended periods (as with *Araucaria* pollen at Buriti; see section 4.2), but also with respect to time lags between climate changes and large-scale vegetation responses (such as ARF’s expansion in the lowlands; see section 3.3.5). These response lags also illustrate why the geographic extent and composition of the southern Atlantic Forest will be unlikely to have changed to the extent predicted by the late 21st century (2070s). Over the coming decades, range shifts, losses and new interspecific associations and interactions will be set in motion, but not necessarily completed. However, the repercussions of anthropogenic climate change will last millennia (Tierney et al., 2020), meaning that these ecosystem changes will become ‘baked in,’ even as more continue to unfold into an ever more uncertain future.

Our palaeoecological insights provide invaluable baselines which can help inform restoration or conservation strategies, but they must be explicitly (and rationally) chosen and many historical baseline landscapes may become unviable under future conditions (Barnosky et al., 2017; Dietl et al., 2015; Loughlin et al., 2018; Rick and Lockwood, 2013; Willis et al., 2010). Under a high-emissions scenario, future floristic assemblages in the southern Atlantic Forest will have few close analogues from the last 21 millennia, possibly favouring ‘taxon-free’ conservation measures – prioritising biodiversity *per se* or ecosystem function, structure or services, rather than the protection or restoration of specific, historically known landscapes (Barnosky et al., 2017). Drastic increases in atmospheric CO_2 concentrations will make structure-preserving measures particularly difficult in

Araucaria Mixed Forest-Campos mosaics – which, in contrast to our LGM reconstruction, will increasingly favour forest over grassland (Fair et al., 2020; McElwain, 2018) – and will also impact the structure, function and biodiversity of the biome's other forests (Esquivel-Muelbert et al., 2019). But regardless of the conservation approaches taken, a key task will be facilitating species' individualistic movements in response to climate changes, including through forest restoration (Rezende et al., 2018; Zwiener et al., 2017). This too will come with challenges, however: increasing landscape connectivity amid anthropogenic climate change may erode endemic-rich marginal habitats and aid biotic homogenisation across the Atlantic Forest (Neves et al., 2017; Zwiener et al., 2018), and risks introducing competitor and antagonist species to populations sheltering in microrefugia (Ashcroft et al., 2012).

4.5. Conclusions

Our findings show the value in combining species-level palaeo-distribution modelling with detailed synthesis of palaeoecological proxy data. The results highlight that 21,000 years of continual species reassortment in response to natural climate changes likely resulted in important (occasionally palynologically silent) compositional changes within southern Atlantic Forest ecosystems, as well as changes to their overall distributions. We demonstrate that different plant communities of this globally-important biodiversity hotspot vary in the degree of species reassortment they underwent in response to climate change since the LGM. Our analyses point to highly novel species assemblages in both the past (in particular, the early Holocene, a period rarely covered in other modelling studies) and future (late 21st century). Our close linkage of palaeo-SDMs and proxy data provides important insights into the biome's vegetation history even at periods that have been well studied, revealing that, at the LGM, low atmospheric CO_2 concentrations (rather than climate) confined (sub)tropical forest to microrefugia among expansive open grasslands across highland plateaus, and that Araucaria forest taxa persisted throughout the Holocene in the west of our study area. Our models highlight a number of promising avenues for future research in southern Brazil, including times and places where significant dynamics might be recorded in as-yet unstudied sedimentary archives. Finally, this study puts into long-term context the magnitude of disruption that unrestrained anthropogenic climate change could bring to parts of the Atlantic Forest over the coming decades. Our findings suggest that the magnitude of plant species' range shifts, and associated floristic turnover, predicted to occur by 2070 due to anthropogenic global warming is likely to have been unparalleled since at least the LGM, 21,000 years ago. We suggest that conservation efforts in the southern Atlantic Forest take account of species reassortment in the face of climate change, enhancing features which enable these distribution changes and protecting areas likely to shelter (micro)refugia, to support species' resilience.

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Author contributions

Conceptualisation: OJW, FEM. Methodology: OJW, RJW. Resources and data curation: OJW, DVL, ACV. Software: OJW. Formal analysis: OJW. Investigation: OJW. Interpretation: OJW, FEM. Supervision: FEM, RJW. Writing: original draft OJW; review and editing OJW, FEM, RJW, DVL, ACV; visualisation OJW.

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Conflicts of interest

The authors have no conflicts of interest to declare.

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