

# *Floristic change in Brazil's southern Atlantic Forest biodiversity hotspot: from the Last Glacial Maximum to the late 21st Century*

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1 Floristic change in Brazil's southern  
2 Atlantic Forest Biodiversity Hotspot: from  
3 the Last Glacial Maximum to the late 21<sup>st</sup>  
4 Century

5 Authors

6 Oliver J. Wilson<sup>a\*</sup>, Francis E. Mayle<sup>a</sup>, Richard J. Walters<sup>b,c</sup>, Débora V. Lingner<sup>d</sup>, Alexander C. Vibrans<sup>d</sup>

7 \* Corresponding author

8 <sup>a</sup> School of Archaeology, Geography and Environmental Science, University of Reading, UK.  
9 University of Reading, Wager Building, Pepper Lane, Whiteknights, Reading, RG6 6EJ, UK.

10 <sup>b</sup> School of Biological Sciences, University of Reading, UK. University of Reading, Health and Life  
11 Sciences Building, Whiteknights, Reading, RG6 6EX, UK.

12 <sup>c</sup> Department of Biology, Lund University, Sweden. Ekologihuset, Sölvegatan 37, 223 62 Lund,  
13 Sweden.

14 <sup>d</sup> Department of Forest Engineering, Universidade Regional de Blumenau, Brazil. Fundação  
15 Universidade Regional de Blumenau, Departamento de Engenharia Florestal, Rua São Paulo, 3250  
16 Itoupava Seca, 89030000 - Blumenau, Santa Catarina, Brasil.

17 Email addresses:

18 OJW: [o.j.wilson@reading.ac.uk](mailto:o.j.wilson@reading.ac.uk)

19 FEM: [f.mayle@reading.ac.uk](mailto:f.mayle@reading.ac.uk)

20 RJW: [richard.walters@biol.lu.se](mailto:richard.walters@biol.lu.se)

21 DVL: [dlingner@furb.br](mailto:dlingner@furb.br)

22 ACV: [acv@furb.br](mailto:acv@furb.br)

## 23 Highlights

- 24 • Combining models and proxy data yields novel insights into past floristic changes
- 25 • 21,000 years of climate-driven species turnover drove frequent community change
- 26 • Early-Holocene no-analogue assemblages found in plateau areas away from proxy sites
- 27 • Non-climatic factors were most likely drivers of LGM forest-grassland structure
- 28 • By the 2070s, S. Brazil could see more floristic change than any time since the LGM

## 29 Abstract

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

## 54 Key words

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

## 57 Abbreviations

58 SDM: species distribution model

59 ARF: Atlantic rainforest

60 AMF: Araucaria mixed forest

61 SDF: seasonally deciduous forest

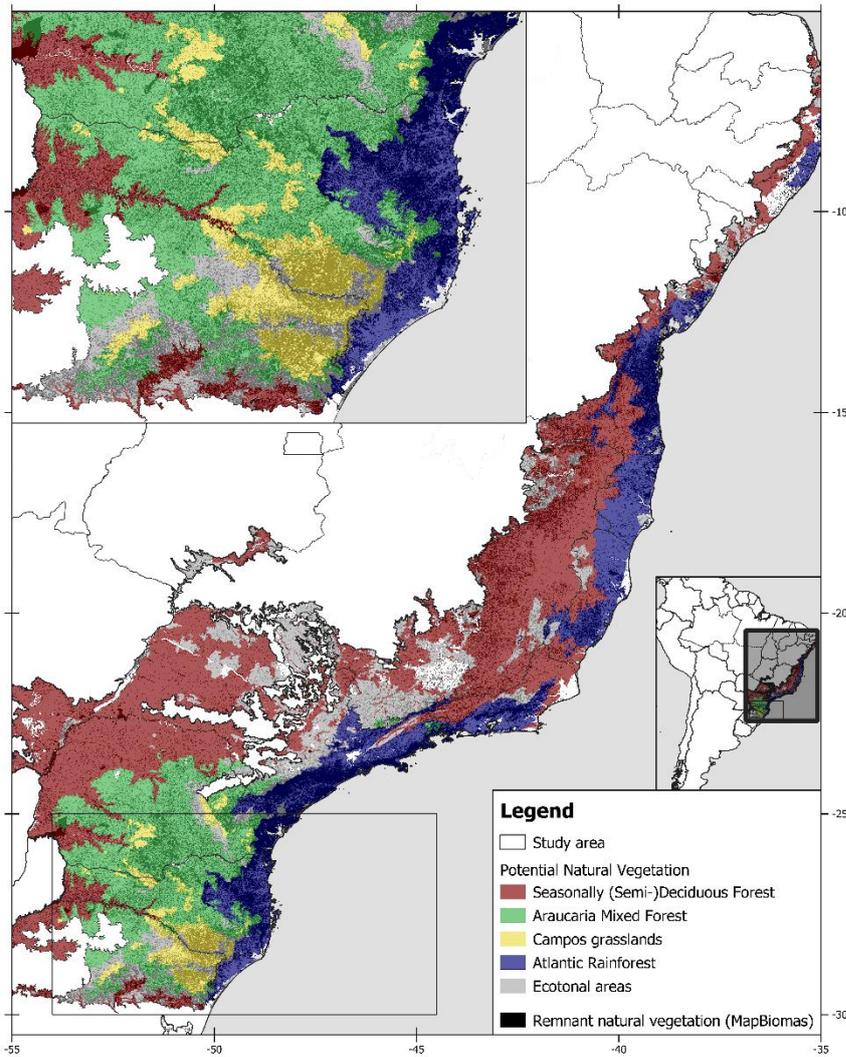
62 LGM: Last Glacial Maximum

## 63 1. Introduction

64 Brazil's Atlantic Forest biome is a global biodiversity hotspot: around one in every fifty species of  
65 vascular plants and non-fish vertebrates on Earth is endemic to this heterogeneous mix of  
66 ecosystems, which stretches over 3,000 km along the country's coast and inland as far as Argentina  
67 and Paraguay (Myers et al., 2000; Neves et al., 2017; Oliveira-Filho and Fontes, 2000; Ribeiro et al.,  
68 2009). This biome is gravely threatened by intense historical and ongoing habitat loss, which has  
69 already removed 84-89% of its natural vegetation (Ferrer-Paris et al., 2019; Ribeiro et al., 2009),  
70 impending anthropogenic climate change (Bergamin et al., 2019; Colombo and Joly, 2010), and the  
71 intersection of the two, which may cause a quarter of the Atlantic Forest's endemic species to be  
72 lost (Bellard et al., 2014; Brown et al., 2020; Wilson et al., 2019).

73 These threats are particularly acute around the Atlantic Forest's subtropical southern limits –  
74 arguably the most heterogeneous part of the biome (Oliveira-Filho et al., 2014), comprising Atlantic  
75 Rainforest *sensu stricto* (ARF, also known as Dense Ombrophilous Forest) along the coast, Araucaria  
76 Mixed Forest (AMF, also known as Mixed Ombrophilous Forest) and Campos grasslands on the  
77 highland plateau, Cloud Forest at the very highest elevations, and Seasonally Deciduous Forest (SDF)  
78 in the west (Fig.1, section 2.2) (IBGE, 2012; Oliveira-Filho and Fontes, 2000). Each of these distinct  
79 and diverse ecosystems is already under threat from habitat conversion: ARF and AMF are  
80 Endangered and SDF is Critically Endangered, with their risk of collapse within 50 years estimated at  
81  $\geq 20\%$  and  $\geq 50\%$  respectively (Ferrer-Paris et al., 2019); 25% of Campos was lost between 1970 and  
82 1996 to timber plantations, agricultural expansion and inappropriate management (Overbeck et al.,  
83 2007). Furthermore, these tropical and subtropical forests and natural grasslands hold significant  
84 populations of more cold-adapted taxa, which are already range-constrained under the present

85 interglacial climate and so at elevated risk from anthropogenic climate change (Bellard et al., 2014;  
86 Carnaval et al., 2014; Ribeiro et al., 2009). Understanding how these ecosystems and their  
87 component species will respond to changing conditions over the coming decades is therefore a key  
88 research priority.



89

90 *Fig. 1: Brazil's Atlantic Forest vegetation (IBGE, 2012) and its natural remnants in 2018 (shaded; Souza et al.,*  
91 *2020); ecosystems not prominent in our study area are not shown in colour.*

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

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

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

121 Although projecting SDMs to past time slices is a potentially powerful way to complement these  
122 data, studies which have attempted this for the southern Atlantic Forest generally share limitations  
123 around their links to proxy records and their taxonomic and temporal coverage. A relatively  
124 restricted subset of the available proxy data tends to be used, with no study using a denser dataset  
125 than Ledo & Colli's (2017) 56 sites across all Amazonia and the Atlantic Forest; Smith & Mayle (2017)  
126 identified 50 proxy sites in south-eastern Brazil alone. Many studies also examine only the LGM  
127 (21,000 BP) and mid-Holocene (6,000 BP), the time slices for which spatialised climate data are most  
128 widely available at ecologically meaningful resolutions (Arruda et al., 2017; Bergamin et al., 2019;  
129 Carnaval and Moritz, 2008; Ledo and Colli, 2017; Porto et al., 2013; Vitorino et al., 2016). Important  
130 as these periods are, southern Brazil's ecosystems responded to a wide array of other conditions in  
131 the intervening millennia which may better illuminate present and potential future distributions or  
132 patterns of diversity (Cruz et al., 2007, 2005; Maksic et al., 2019).

133 Most critically, many palaeo-modelling studies in the Atlantic Forest have examined the distributions  
134 of whole ecosystems or significant parts of the entire biome, treating them as single units with  
135 uniform responses (Arruda et al., 2017; Carnaval et al., 2014; Carnaval and Moritz, 2008; Costa et al.,  
136 2017; Ledo and Colli, 2017). However, palaeoecological data shows that species respond  
137 individualistically to climate changes depending on their niche requirements, which can lead to the  
138 formation of novel floristic assemblages without modern analogues (Davis, 1983; Davis and Shaw,  
139 2001; Mayle et al., 2004; Williams and Jackson, 2007). Although much evidence for this comes from  
140 temperate regions (e.g. Williams et al., 2004), past novel or no-analogue assemblages have been  
141 documented from Amazonia to south-eastern Brazil, generally characterised by the co-occurrence of  
142 cold- and warm-adapted pollen taxa during (late) glacial times (Behling, 1998; Bush et al., 2004;  
143 Colinvaux et al., 2000, 1997; De Oliveira, 1992; De Oliveira et al., 2020; Francisquini et al., 2020;  
144 Haberle and Maslin, 1999; Hermanowski et al., 2012; Horák-Terra et al., 2020; Lima et al., 2018;  
145 Raczka et al., 2013; Whitney et al., 2011). Southern Brazil's forests are characterised by floristic  
146 gradients – each contains significant compositional diversity, and differences between forest types  
147 are generally marked most by gradual species turnover (Bergamin et al., 2017; Brown et al., 2020;  
148 Duarte et al., 2014; Esser et al., 2019; Oliveira-Filho et al., 2014; Oliveira-Filho and Fontes, 2000).  
149 These characteristics mean there is a significant chance that any past or future reassembly of these  
150 communities would be poorly captured by modern-day ecosystem classifications. It is especially  
151 important, therefore, that the effects of past and future climate change on the southern Atlantic  
152 Forest are considered at species level, as these potential 'ecological surprises' (Williams and Jackson,  
153 2007) cannot be examined in ecosystem- or biome-level modelling studies.

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

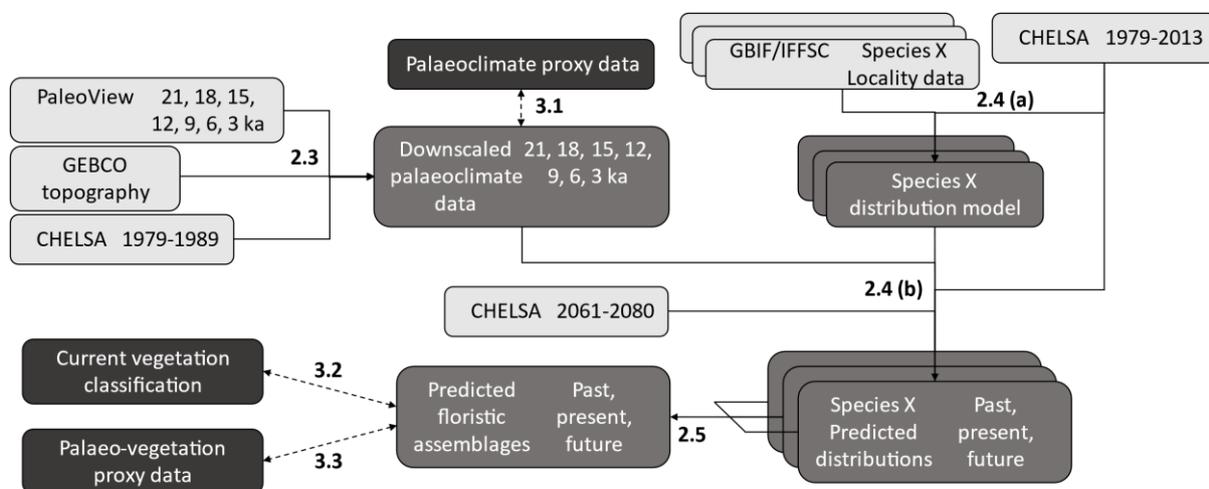


167 2. Methods

168 2.1. Overview

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

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



188  
 189 Fig. 2: conceptual overview of this study showing input data (light grey), generated outputs (mid  
 190 grey), and data for model intercomparisons (dark grey). Segment labels highlight where in the text

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

## 197 2.2. Modern ecosystems of the southern Atlantic Forest

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

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

211 At the plateau's highest elevations, which exceed 1,800m, AMF forms mosaics with – and eventually  
212 gives way to – natural highland grasslands called Campos. One of the very few herbaceous  
213 ecosystems in the Atlantic Forest biome, Campos are highly diverse, though less well studied,  
214 appreciated or protected than the surrounding forests (Andrade et al., 2019, 2016; Iganci et al.,  
215 2011; Overbeck et al., 2007). They have occupied parts of the highlands for more than 40,000 years,  
216 with relatively steady forest encroachment over the last 4,000 years (Behling et al., 2004; Dümig et  
217 al., 2008; Silva and Anand, 2011). These ecotones are maintained by natural or anthropogenic fire  
218 and grazing, and in the absence of such disturbance the conversion of Campos to forest can be rapid  
219 (Jeske-Pieruschka et al., 2010; Müller et al., 2012; Oliveira and Pillar, 2005; Sühs et al., 2020).

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

224 (Bertoncello et al., 2011; Falkenberg and Voltolini, 1993; Higuchi et al., 2013; Oliveira-Filho et al.,  
225 2014; Scheer et al., 2011).

226 The Atlantic Forest's westernmost ecosystem is Seasonally Deciduous Forest (SDF), which extends  
227 across Brazil's borders into north-eastern Argentina and eastern Paraguay as well as along lower  
228 elevations to the south of the highlands. These forests experience similarly high average  
229 temperatures and precipitation to ARF but greater temperature seasonality, with more frequent  
230 frosts (6.5-10.4 days per year on average) (Gasper et al., 2012). In the south, canopy trees shed their  
231 leaves in response to winter's low temperatures and shorter photoperiod, though SDF's understorey  
232 is largely evergreen (Gasper et al., 2012; Klein, 1975). At the higher elevations of its range (800-  
233 900m) the forest incorporates floristic elements from lower-elevation AMF – indeed, the two  
234 ecosystems can be considered different expressions of a similar seasonal forest flora (Oliveira-Filho  
235 et al., 2014).

### 236 2.3. Climate data

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

245 We generated gridded monthly precipitation and temperature (mean, maximum and minimum) data  
246 from PaleoView for seven past time slices: 21,000, 18,000, 15,000, 12,000, 9,000, 6,000 and 3,000  
247 years BP. We used the delta change method to downscale these data from 2.5° (PaleoView's  
248 resolution) to 30" (ca. 800m, the resolution of CHELSA climate data), with local lapse rate  
249 modifications for temperature variables (see Supplementary Methods). The region's changing sea  
250 levels from the LGM to present were incorporated by adjusting elevation and bathymetry data from  
251 the GEBCO project (Weatherall et al., 2015) by -30m (9,000 BP), -50m (12,000 BP), -90m (15,000 BP),  
252 -100m (18,000 BP) and -130m (21,000 BP) relative to present (Cooper et al., 2018; de Mahiques et  
253 al., 2010). Climatic and ecological predictions for exposed shelf areas should be treated with greater  
254 caution than areas which were never submerged, as CHELSA data is only validated over current land  
255 areas and was spatially extrapolated for precipitation (Lorenz et al., 2016).



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

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

279 Table 1: Modelled species and their importance in the ecosystems of southern Brazil's Atlantic Forest (SDF =  
280 Seasonally Deciduous Forest, AMF = Araucaria Mixed Forest, CAM = Campos, CLD = Cloud Forest, ARF = Atlantic  
281 Rainforest) (from Andrade et al., 2019; Bertonecello et al., 2011; Klein, 1975; Lingner et al., 2013a; Meyer et al.,  
282 2013; Schorn et al., 2014, 2012). Fossil pollen importance generalised from pollen taxa (genus level or below) in  
283 published proxy sites listed in Table S2. 'Y' indicates very high importance/frequent presence, and '(Y)' indicates  
284 somewhat high importance/frequent presence.

285 Locality data for these species were drawn from two sources: the Santa Catarina Forest Floristic  
286 Inventory (IFFSC) (Vibrans et al., 2020, 2010), and the Global Biodiversity Information Facility for  
287 records outside Santa Catarina (<https://doi.org/10.15468/dl.0l64p1>,  
288 <https://doi.org/10.15468/dl.o97owg>, <https://doi.org/10.15468/dl.nxy2cp>). GBIF records were taken  
289 from 15-45° S and 67.5-35°W, where present-day conditions generally encompass those experienced  
290 by our study area over the last 21,000 years, then coordinates were cleaned and thinned. Because  
291 true absences were only available from the IFFSC, which covers only a subset of the geographic and  
292 climatic space our models were trained on and lacks data on Campos species, we added 1,000  
293 randomly located pseudo-absence points for each species.

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

## 304 2.5. Floristic assemblage analysis

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

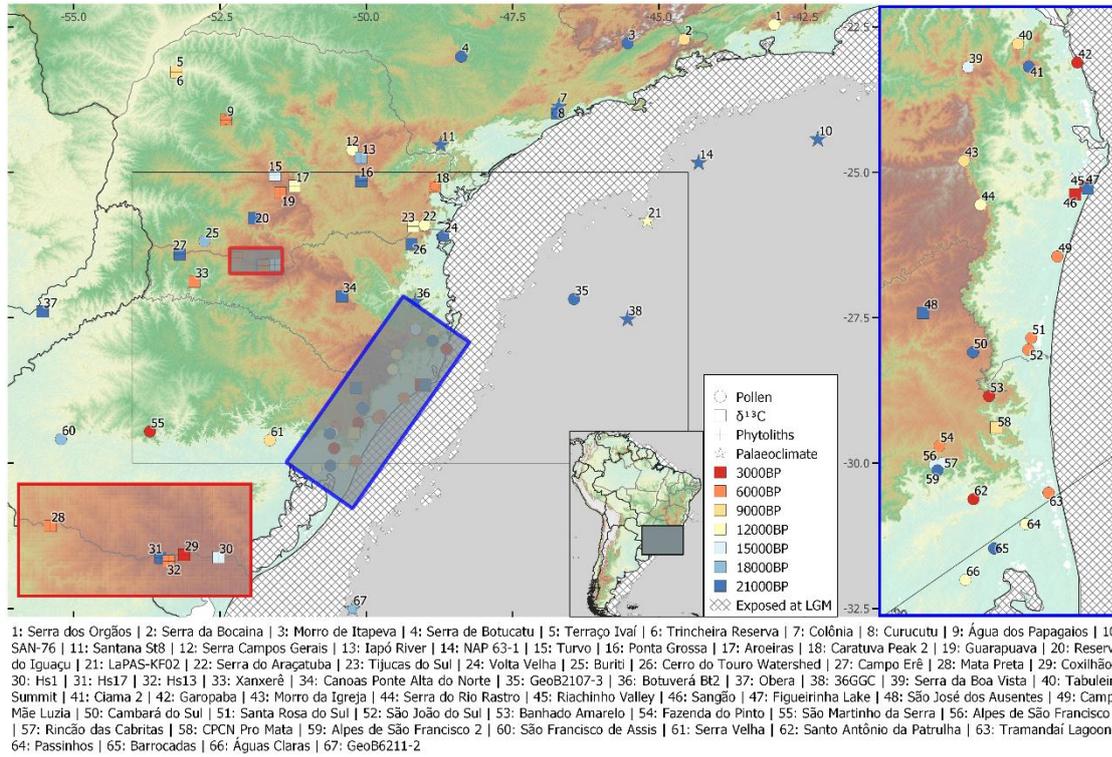
## 313 2.6. Palaeo-data - model comparison

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

326 information). Fossil pollen data are summarised as percentages of forest and grassland pollen, and  
327 soil carbon isotope values are generalised following Silva & Anand (2011).

328

329



330

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

### 332 3. Results

#### 333 3.1. Palaeoclimate data validation

334 Our downscaled palaeoclimate data broadly agree with proxies of past temperature and  
335 precipitation (Figs. S3-S7). The LGM (21,000-18,000 BP) is reconstructed with higher and more  
336 seasonal precipitation than the present, especially in the west of our study area, and mostly 3-4°C  
337 cooler. This aligns with speleothem evidence from Botuverá and Santana caves (Cruz et al., 2007,  
338 2006, 2005), as well as proxies of air and sea surface temperatures from Colônia and marine cores  
339 (Carlson et al., 2008; Chiessi et al., 2015, 2014; Dauner et al., 2019; Pivel et al., 2013; Rodríguez-  
340 Zorro et al., 2020; Toledo et al., 2007). Conditions at 15,000 BP are transitional between this LGM  
341 climate and a markedly different early Holocene.

342 At 12,000 BP, much of our study area was somewhat drier and more seasonal than the present; the  
343 north-east was 1-2°C cooler than present and the south up to 1°C warmer, though most areas were



344 within 1°C of modern average temperatures. Proxy evidence from Botuverá and Santana supports  
345 the early Holocene (12,000 – 9,000 BP) being the driest in the study period, with the lowest  
346 contributions from the summer monsoon. Subsequent gradual and relatively minor increases in  
347 precipitation in the proxy records are reflected in our downscaled data. Temperature proxies  
348 generally record 12,000 BP as being similar to, or warmer than, the preceding time slices; several  
349 also show slight increases in temperatures through the Holocene which are less clear in our  
350 downscaled data.

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

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

### 363 3.2. Modelled species and modern-day ecosystems

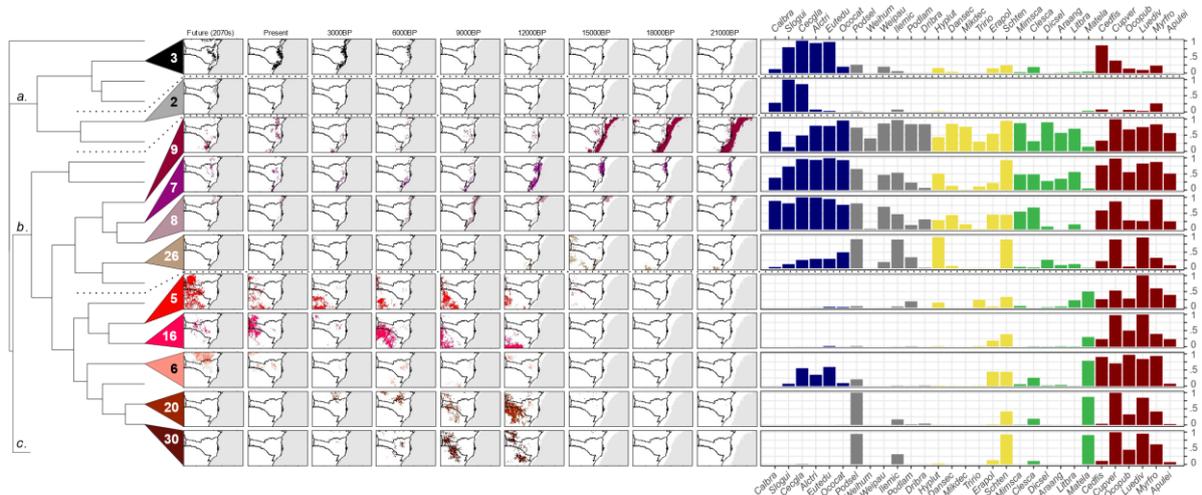
364 The 30 key species modelled here effectively characterise the main ecosystems of southern Brazil's  
365 Atlantic Forest; only the south-western corner of our study area, which is not part of the biome, had  
366 poor species coverage in the present (Fig. 1, Figs. S9-S10). Several species transcend ecosystem  
367 boundaries (e.g. *Ocotea puberula* and *Matayba elaeagnoides* in Seasonally Deciduous Forest and  
368 Araucaria Mixed Forest, and *Cedrela fissilis* in parts of these and Atlantic Rainforest), reflecting the  
369 compositional gradients between the region's different forests (Table 1, Fig. S9) (Bergamin et al.,  
370 2017; Duarte et al., 2014; Oliveira-Filho et al., 2014; Oliveira-Filho and Fontes, 2000). Most high-  
371 elevation areas are currently predicted to be suitable for combinations of AMF, Campos and Cloud  
372 Forest species; these ecosystems' modern boundaries are not clearly delineated in their constituent  
373 species' distributions.

374 The stability of species associations – with one another and with their nominal ecosystem (Table 1) –  
375 differs between ecosystems and time slices. For instance, important ARF species tend to co-occur  
376 from the LGM to the present, where they are rarely found outside ARF areas, though non-ARF

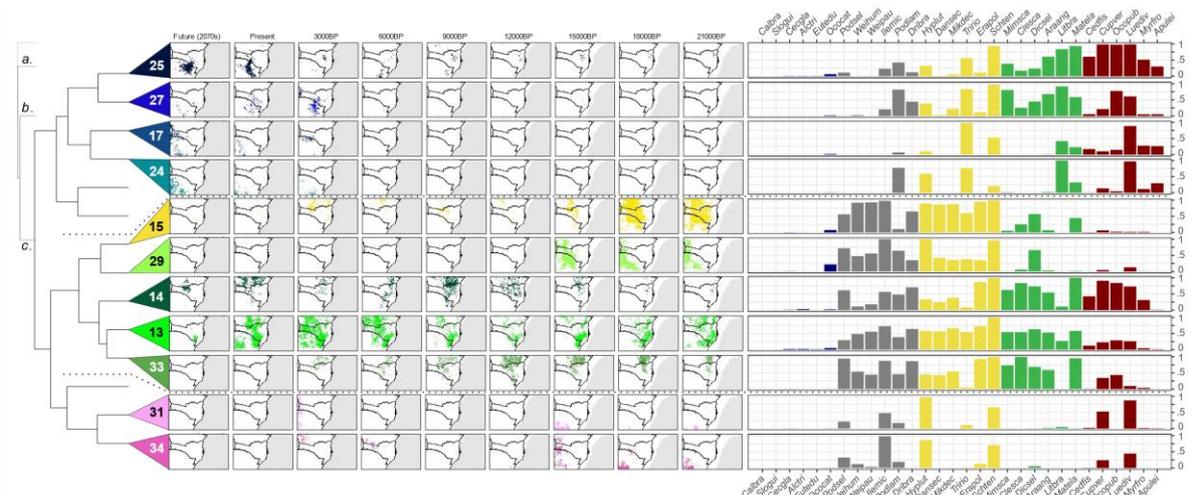
377 species sometimes overlap their distributions. By contrast, AMF's composition is more variable  
 378 across its modern range – it contains significant floristic gradients (Duarte et al., 2014; Oliveira-Filho  
 379 et al., 2014) – and, accordingly, its species associations are less stable through time (Figs. S9, S11).

380 The clustering analysis identifies 34 potential floristic assemblages, divisible into three broad groups,  
 381 which encompass these different expressions of our target ecosystems (Fig. 4): the small cluster *a*  
 382 that aligns closely with modern-day ARF (assemblages 3 and 2); cluster *b*, with one subsection  
 383 dominated by mixtures of different forest and Campos species like those found currently on the  
 384 highlands' escarpment slopes (assemblages 9, 7, 8 and 26) and another by SDF species (assemblages  
 385 5, 16, 6, 20 and 30); and cluster *c*, with subsections dominated by AMF/SDF/Campos species  
 386 (assemblages 25, 27, 17 and 24), Campos and Cloud Forest (15 and 29), AMF/Campos/Cloud Forest  
 387 and some SDF (14, 13 and 33), and SDF/Campos (31 and 34).

388



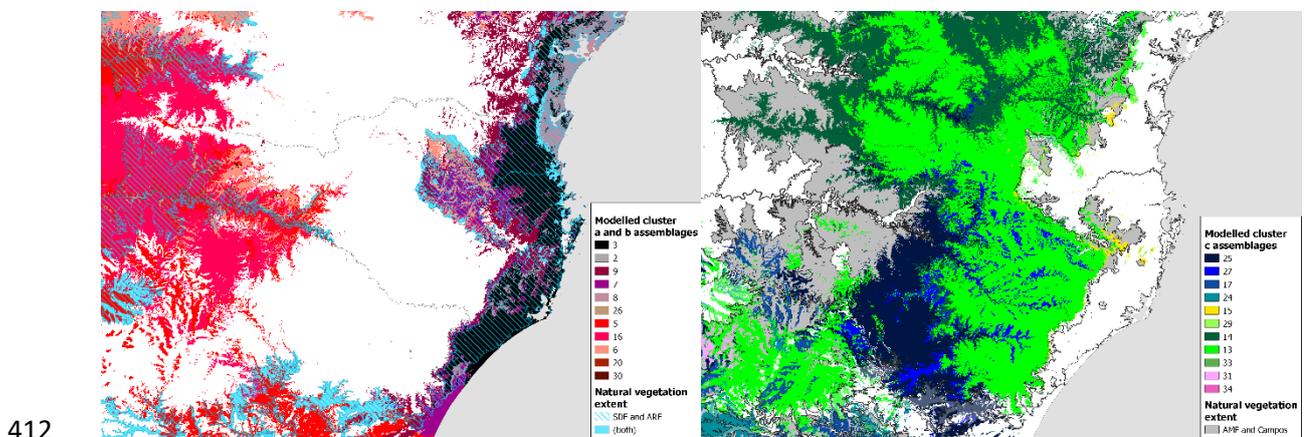
389



390

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

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



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

### 417 3.3. Changes through time and proxy comparison

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

#### 421 3.3.1. Last Glacial Maximum (21,000 – 18,000 BP)

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

433 Where these modelled assemblages are found in the present day (generally on the plateau and its  
434 eastern escarpment), much of their extent is forested. However, this does not appear to have been  
435 the case at the LGM as grassland proxies generally dominate, though phytolith records do suggest  
436 some areas that might have had higher tree cover. Half or more of the phytoliths at Iapó River  
437 (Kalinovski et al., 2016) around 18,000 BP come from woody plants (though the site's  $\delta^{13}\text{C}$  signature  
438 is C4-dominated), and some samples from approximately the same time in Campo Erê (Cecchet,  
439 2015) have modest contributions of eudicot and palm phytoliths, though precise ages and  
440 identifications are not available in the latter record. Campo Erê is also one of three LGM sites in our  
441 study area (with São José dos Ausentes (Pereira, 2017) and Cerro do Touro Watershed (de Oliveira et  
442 al., 2008)) whose  $\delta^{13}\text{C}$  values indicate a mixture of C3- and C4-photosynthesising vegetation, though  
443 only Obera (Zech et al., 2009) and Curucutu (Pessenda et al., 2009), respectively to the west and  
444 north of our study area, have C3-majority contributions.

445 The highest values for forest pollen are found in Volta Velha (14%, 21,000 BP; Behling and Negrelle,  
446 2001), where Myrtaceae and Melastomataceae dominate, and GeoB2107-3 (22%, 18,000 BP; Gu et  
447 al., 2017), with *Alchornea*, *Podocarpus*, *Araucaria* (at 21,000 BP) and *Myrsine* (at 18,000 BP) the  
448 latter's main components. These sites' investigators suggest this indicates a mosaic of subtropical  
449 forest patches with grasslands on the lowlands (Behling and Negrelle, 2001; Gu et al., 2017), a

450 suggestion supported by proxy evidence from Curucutu (Pessenda et al., 2009), north of our study  
451 area. At 21,000 BP, this site had a similar forest pollen proportion (17%) and composition (mainly  
452 Myrtaceae and Melastomataceae-Combretaceae, with some *Alchornea*) to Volta Velha and  
453 GeoB2107; the core's  $\delta^{13}\text{C}$  values show that the site was dominated by C3 vegetation, and nine other  
454 nearby profiles show mixes of C3 and C4 contributions (Pessenda et al., 2009). Our predicted  
455 assemblages on the exposed continental shelf and modern-day lowlands could have been expressed  
456 as such a grassland-forest mosaic, its precise configuration dictated by non-climatic (e.g.  
457 topographic) conditions. A similar physiognomy was likely found on the highlands around the LGM,  
458 with Campos dominating and AMF and/or Cloud Forest species probably confined to rare, small  
459 patches – at least in the highlands' south-east where long fossil pollen records exist (Behling et al.,  
460 2004; Leonhardt and Lorscheitter, 2010). The higher contribution of *Podocarpus* and *Araucaria*  
461 pollen to GeoB2107's LGM pollen spectrum suggests AMF forest elements were more common  
462 further north or on the continental shelf (Gu et al., 2017), which may align with the early phytolith  
463 record from Iapó River (Kalinovski et al., 2016).

#### 464 3.3.2. Late Glacial Period (15,000 BP)

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

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

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

### 493 3.3.3. Early Holocene (12,000 – 9,000 BP)

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

503 Unfortunately, the dearth of palaeoecological records covering this period and area mean there is  
504 sparse evidence against which to assess our model predictions. In its northern reaches, Buriti – the  
505 only site available at 12,000 BP – experiences large increases in Asteraceae pollen that reduce its  
506 forest pollen from 91% to 65%, then 55% at 9,000 BP, suggesting an increasingly open landscape.  
507 Buriti's forest pollen composition in the early Holocene is still mostly *Araucaria* and *Ilex*, though with  
508 less *Podocarpus* than previously and more *Alchornea*, *Arecaceae*, *Hieronyma* and *Luehea* (all warm-  
509 adapted taxa). Notably, a stable co-occurrence of *Luehea* and *Podocarpus* pollen (ca. 5-10% each)  
510 begins shortly after 9,000 BP, potentially matching the predicted presence of assemblages 20 and  
511 30, in which *L. divaricata* and *P. sellowii* are prevalent. In the area's south-east, Serra Velha's record  
512 (Leal and Lorscheitter, 2007) starts around 11,000 BP as ca. 95% grassland pollen, but forest pollen  
513 from early-successional tropical trees accounts for 42% of the total by 9,000 BP. Though its  
514 composition and forest-grassland trajectory differ from Buriti's, Serra Velha too appears to have  
515 been found in a generally open environment. Finally, in Campo Erê, at the north-western edge of the  
516 area of rapid change, several phytolith morphotypes experience abrupt changes around a sample

517 dated to 8,000 BP, suggesting the existence (but not the nature) of significant changes early in the  
518 Holocene.

519 Further east in the early Holocene, our modelling suggests the incremental loss of more cold-  
520 adapted species along the coastal lowlands. This is best captured by the pollen record of Volta Velha  
521 (Behling and Negrelle, 2001), which sees drastic increases in forest pollen between 15,000 BP and  
522 12,000 BP due to sharp reductions in Campos (Poaceae) pollen and the emergence of a forest pollen  
523 assemblage dominated by generally tropical Arecaceae, *Alchornea* and Myrtaceae pollen with  
524 *Myrsine* and Moraceae/Urticaceae. Serra da Boa Vista (Behling, 1995) records an increase in ARF-  
525 type pollen, though coastal cores at our study area's south do not, remaining grassland-dominated.  
526 While GeoB2107's arboreal pollen sum changes little overall, there are changes in its composition,  
527 with *Alchornea*, Moraceae/Urticaceae and Arecaceae all experiencing sustained increases.

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

#### 543 3.3.4. Mid-Holocene (6,000 BP)

544 At the mid-Holocene (6,000 BP), many parts of the study area – including much of its west – are  
545 poorly characterised by our modelled species (Fig. S10), most of which experience reductions in their  
546 predicted extents compared to 9,000 BP (Fig. 6). For this reason, increased caution is required when  
547 interpreting vegetation changes in these areas. Many areas designated as assemblages 20 and 30 in  
548 the early Holocene become assemblages 16 (SDF-like) or 13 (AMF/Campos-like), depending largely  
549 on changes to the distributions of *Matayba elaeagnoides* and *Podocarpus sellowii*. Assemblage 20

550 reappears north-west of the Itajaí valley, however, replacing the AMF/SDF-like assemblage 14 as the  
551 location becomes unsuitable for several Campos, AMF and Cloud Forest species. Similar but less  
552 drastic changes convert the Campos/Cloud Forest-like assemblage 15 to the more AMF-like  
553 assemblage 13 in our study area's centre. Changes are somewhat less marked along the coastal  
554 lowlands, where sea-levels reach essentially modern levels – small compositional changes happen in  
555 the south and the central region records the first significant presence of assemblage 3, modern  
556 ARF's best representative.

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

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

579 On the plateau's eastern edge, smaller expansions of forest pollen can be seen in most cores  
580 between 9,000 BP and 6,000 BP; in CPCN Pro Mata's soil pits forest borders advance by up to 20m  
581 and today's large woodland patches first receive increased C3-carbon input (Silva and Anand, 2011).  
582 With minimal change in Serra Campos Gerais (Behling, 1997a) or in Geob2107's AMF taxa, it is



583 possible that the plateau's vegetation changed less between 9,000 and 6,000 BP than predicted,  
584 though with no sites in the most changeable area of modelled cluster *c* assemblages it is impossible  
585 to be certain.

#### 586 3.3.5. Late Holocene (3,000 BP)

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

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

603 Across the rest of the plateau, our models predict a consolidation and expansion of assemblages  
604 associated with cold-adapted taxa. Assemblages 13 and 27, which describe present-day AMF and  
605 Campos areas, cover much of the highlands, including parts of western Santa Catarina state and  
606 north-western Rio Grande do Sul which are now SDF. Assemblage 15, dominated by Cloud forest and  
607 Campos species, also expands to cover its largest extent since 18,000 BP, concentrated at high  
608 elevations along the escarpment and in areas of modern-day Campos in south-central Paraná state.  
609 Soil profiles in these latter areas record C4-dominated vegetation for this period, as they had for  
610 6,000 BP, despite the region's only pollen record (Buriti) continuing to be forest-dominated. Further  
611 east, palaeo-proxy records show increasing contributions from forest taxa compared to the mid-  
612 Holocene. This expansion of AMF over Campos is recorded between 3,000 and 4,000 BP in many  
613 sites at the highlands' southern edge, as well as in others north of our study area (Behling, 1997b,  
614 1995; Behling et al., 2004; Bissa and de Toledo, 2015; Jeske-Pieruschka and Behling, 2012; Leonhardt  
615 and Lorscheitter, 2010; Scherer and Lorscheitter, 2014). Some of these sites also record a

616 subsequent expansion of AMF around 1,000 BP (Behling, 2006; Behling et al., 2004; Leonhardt and  
617 Lorscheitter, 2010; Scherer and Lorscheitter, 2014), so many plateau proxy sites' surroundings were  
618 probably more open at 3,000 BP than in the present. Notably, however, given its likely regional  
619 catchment, the marine core GeoB2107 records little change in the relative proportions of forest and  
620 grassland pollen between 6,000 and 3,000 BP, though forest pollen (notably *Araucaria*) does  
621 increase subsequently.

622 In the late Holocene, most of the coastal region becomes covered by assemblages 3 and 7, primarily  
623 differentiated here by the distributions of *Myrocarpus frondosus* and *Ocotea catharinensis*.  
624 Accordingly, most pollen cores from the coastal lowlands see increasing forest pollen proportions,  
625 generally dominated by combinations of Myrtaceae, Arecaceae and *Myrsine* (and, to a lesser extent,  
626 *Ilex* and *Alchornea*), likely reflecting developing ARF vegetation. This development was unlikely to  
627 have been complete, however, as in almost every case these coastal sites record less forest pollen at  
628 3,000 BP than they do in the present day, suggesting that – like the plateau sites – their surrounding  
629 landscapes were then more open than now. In the central coastal mountains *Weinmannia* (with  
630 Myrtaceae) dominates forest pollen assemblages at this time, whose trajectories differ between  
631 each site from the mid-Holocene to 3,000 BP, and again to the present. Although our predictions  
632 accurately place these sites at the intersection of tropical and more cold-adapted floristic  
633 assemblages, their nuances – likely caused by local topography-weather system interactions (Behling  
634 and de Oliveira, 2018) – are not fully captured.

### 635 3.3.6. Future (2070s)

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

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

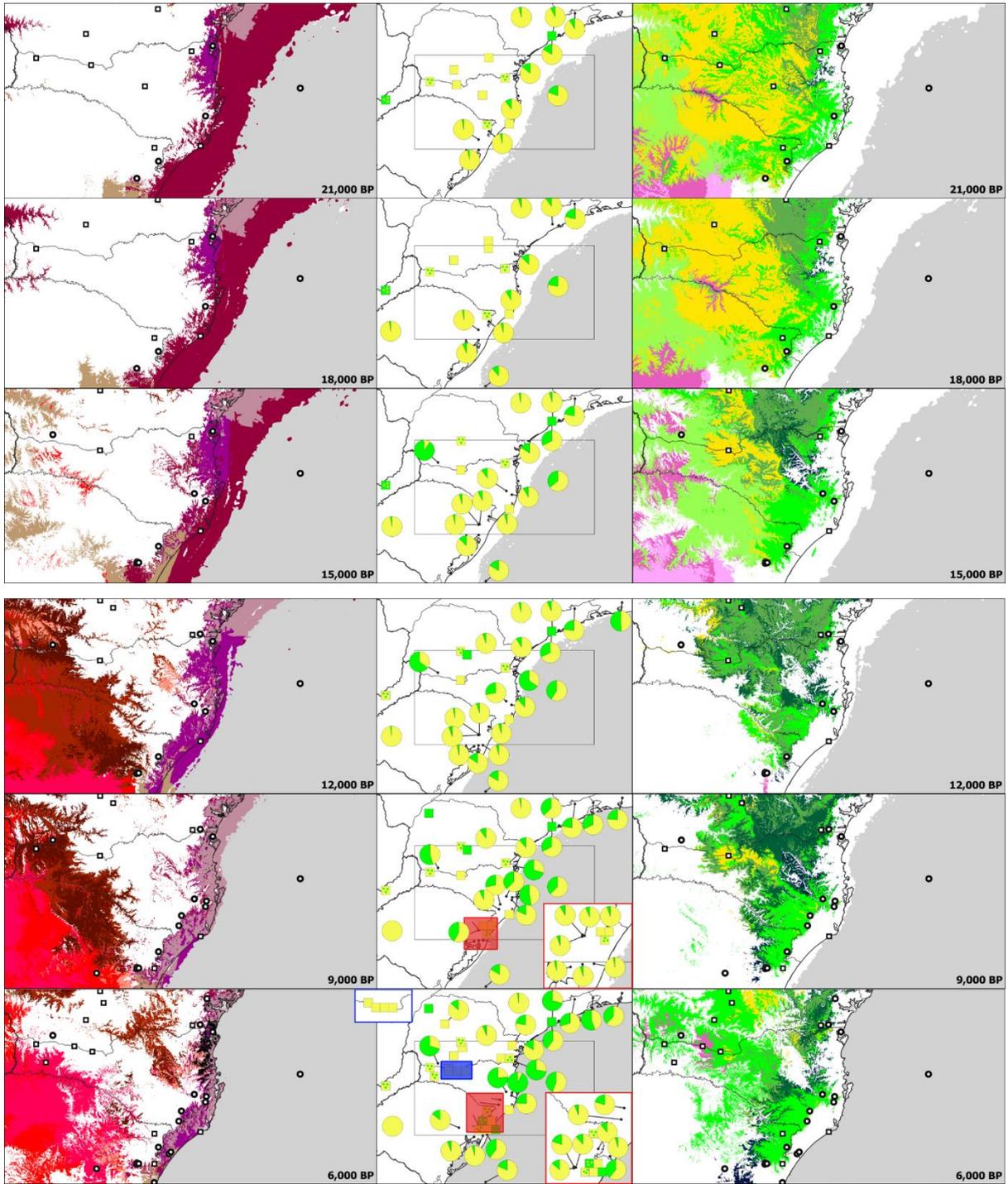
649 Fewer species characterise assemblage 17, found along parts of the Uruguay and Iguazu river valleys,  
650 and, still further to the north-west, other parts of the Iguazu valley are predicted to be unsuitable for  
651 all our modelled species by the 2070s. These assemblages are interspersed with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

655 Across the northern part of our study area, the only species of AMF, Campos and Cloud forest which  
656 largely maintains its range is *M. elaeagnoides*; most others are predominantly or completely lost  
657 from this region, but much less change is predicted for the area's shared SDF/AMF species.

658 Combined with northward expansions of *Myrocarpus frondosus* (SDF), *Euterpe edulis*, *Cecropia*  
659 *glaziovii* and (to a lesser extent) *Alchornea triplinervia* (all ARF), our study region's north becomes  
660 classified as assemblage 6, presently a relatively rare grouping found around AMF's ecotones with  
661 SDF and ARF.

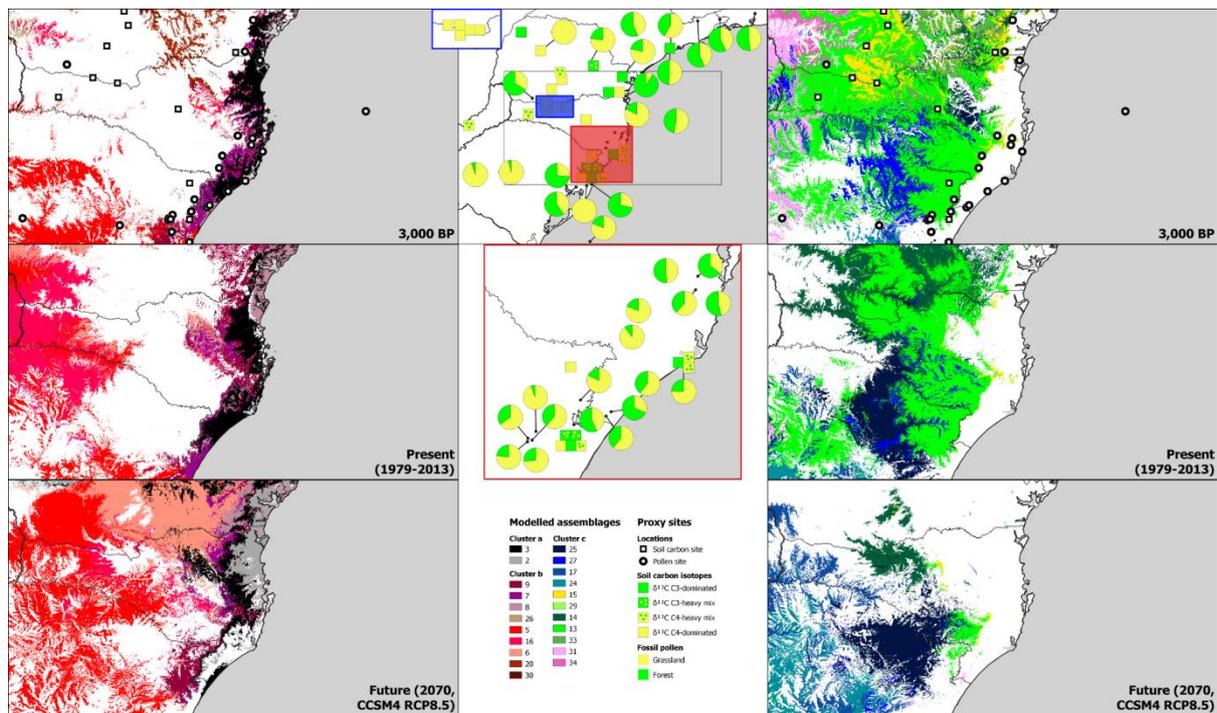
662 The loss of climatically suitable habitat for AMF, Campos and Cloud forest species across our study  
663 area's northern region leads to a dramatic retraction in the area covered by their associated  
664 assemblages. Assemblage 13 covers a smaller area in the 2070s than in any other modelled time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

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



682

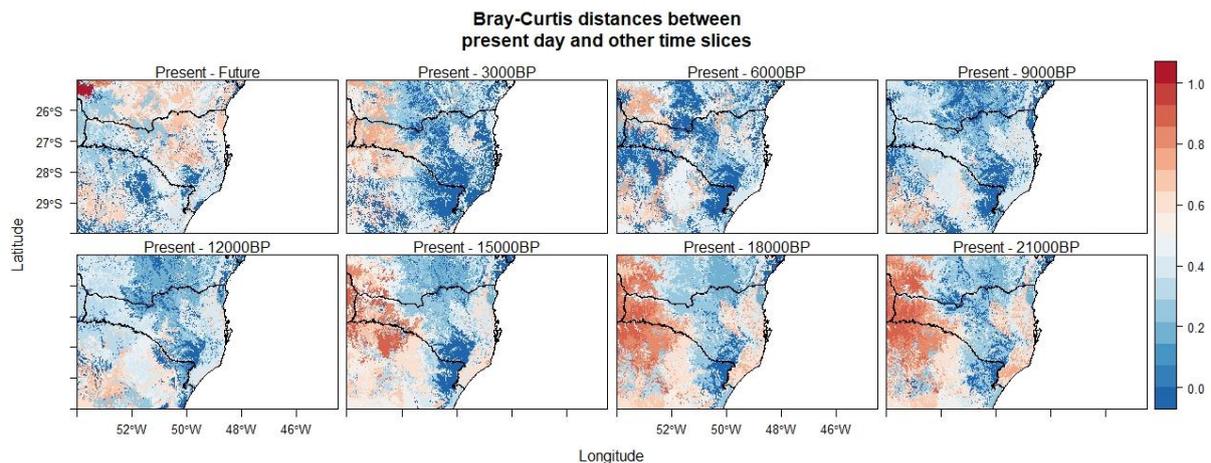
683



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

### 688 3.4. Long-term context for present and future floristic assemblages

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

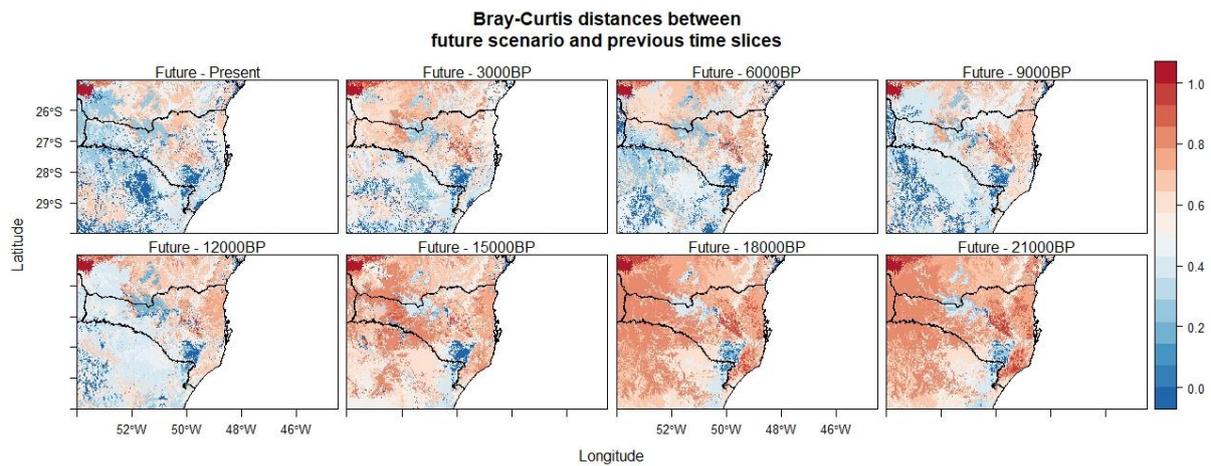


701

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

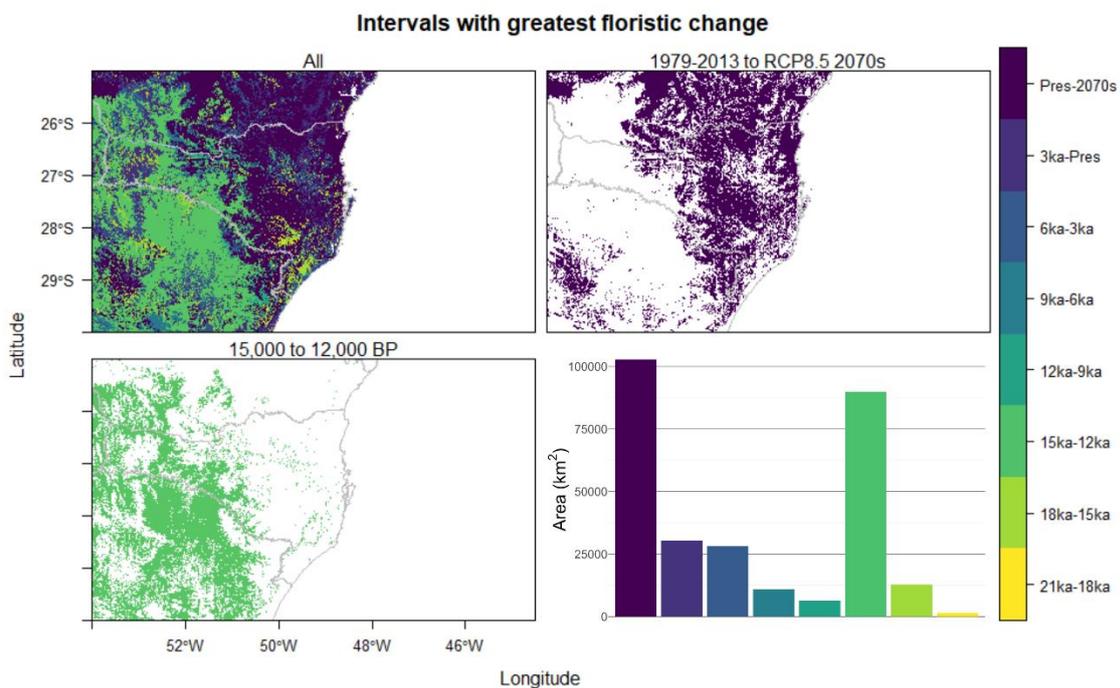
704 Our results also show that, without reductions in greenhouse gas emissions, by the 2070s much of  
 705 the southern Atlantic Forest will have – or at least will be on track to have – very different floristic  
 706 composition to any experienced since at least the LGM (Fig. 8). Close local analogues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

712 More than 102,000 km<sup>2</sup> of our study area is predicted to experience greater floristic change between  
 713 the present day and the high-emissions future scenario than in any other 3,000-year interval  
 714 modelled here (Fig. 9, Table S3). By comparison, deglacial warming during the last glacial-Holocene  
 715 transition (15,000 – 12,000 BP) brought the greatest vegetation change to over 105,000 km<sup>2</sup>; around  
 716 15% of that area would experience even greater floristic change over the coming decades in a high-  
 717 emissions 21<sup>st</sup> Century (Table S3). Notably, the spatial distribution of vegetation changes during the  
 718 21<sup>st</sup>-Century and glacial-Holocene transition differ: climate change associated with the onset of the  
 719 Holocene affected vegetation in the south and western parts of our study area significantly, whereas  
 720 future climate changes are predicted to have their greatest impact on vegetation in northern and  
 721 eastern regions which have otherwise experienced relatively little change since the LGM (Figs. 9,  
 722 S13-14).



723

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



726

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

## 730 4. Discussion

731 Our study demonstrates the value of combining species-level distribution modelling with a granular  
 732 synthesis of palaeovegetation-proxy evidence to better understand how plant species in Brazil's

733 southern Atlantic Forest have responded to climate changes since the LGM. The results generated  
734 show that our downscaled climate data and predicted species distributions are broadly aligned with  
735 independent proxy evidence, and provide a number of important novel insights into the past and  
736 future of southern Brazil's Atlantic Forest.

#### 737 4.1. Plant community change since the LGM

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

755 Our species-level modelling approach provides important new insights into Holocene plant  
756 communities that were unlike any currently known from the region. Although no-analogue  
757 Quaternary floristic assemblages have been inferred from previously published fossil pollen studies  
758 elsewhere in the neotropics, including Brazil's Cerrado biome and the central sector of the Atlantic  
759 Forest biome to the north (De Oliveira, 1992; De Oliveira et al., 2020; Francisquini et al., 2020;  
760 Horák-Terra et al., 2020; Raczka et al., 2013), the taxonomic limitations of pollen analysis, combined  
761 with the paucity of sites, mean their full nature, extent, and presence in southern Brazil have not  
762 previously been ascertained. Our palaeo SDM results provide the first evidence that significant  
763 species turnover in Brazil's southern Atlantic Forest in the early Holocene (12,000-9,000 BP) – most  
764 notably across the plateau's (south-)west sector – created novel plant communities without modern  
765 analogue. However, the absence of existing palaeovegetation data sites from much of our study area  
766 makes these predictions hard to verify. Buriti (Bertoldo et al., 2014), at the modelled assemblages'



767 northern edge, does provide some support for this early Holocene no-analogue plant community  
768 hypothesis, recording high levels of Asteraceae pollen and an unusual mixture of cold- and warm-  
769 adapted trees (*Araucaria*, *Ilex*, *Hieronyma*, *Luehea*) at this period. Other sites (Jeske-Pieruschka and  
770 Behling, 2012; Leal and Lorscheitter, 2007; Leonhardt and Lorscheitter, 2010; Scherer and  
771 Lorscheitter, 2014) at the opposite ends of this putative non-analogue community differ from Buriti  
772 and one another, suggesting that floristic composition was not homogeneous across this region.  
773 More fossil pollen records are therefore needed to more rigorously test the accuracy of these  
774 findings and confirm, clarify or refute the model predictions.

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

#### 796 4.2. Grassland-forest mosaics across space and time

797 The palaeoecological value of model-data comparisons for understanding the biogeographic history  
798 of the Atlantic Forest can be effectively illustrated with Araucaria Mixed Forest and Campos.  
799 Millennial-scale interplay between these ecosystems is generally attributed to rainfall and/or  
800 temperature changes (Behling, 2002; Behling et al., 2004), but our analysis shows that SDMs of their

801 constituent species cannot distinguish the two ecosystems in the present, suggesting significant  
802 overlap between their climatic niches and therefore that non-climatic factors dictate their  
803 boundaries. This corroborates other published modelling studies (Barros et al., 2015; Bergamin et  
804 al., 2019; Costa et al., 2017; Maksic et al., 2019; Wilson et al., 2019), as well as contemporary and  
805 palaeoecological observations of AMF expanding over Campos in the absence of fire and/or grazing  
806 (Behling, 2002; Behling and Pillar, 2007; Dümig et al., 2008; Müller et al., 2012; Oliveira and Pillar,  
807 2005; Silva and Anand, 2011; Sühs et al., 2020). One consequence of this difficulty in differentiating  
808 forest and grassland in our SDMs is that, where predicted past assemblages include both herb and  
809 tree species, their actual physiognomy is unclear. Our LGM (21,000-18,000 BP) data are a case in  
810 point: at this time, most palaeo-data sites in our study area record pollen, soil stable-carbon isotope  
811 and phytolith evidence for dominant grasslands, barely differing between modelled assemblages 9  
812 (modern escarpment forests), 15 (Campos/Cloud Forest) and 13 (which encompasses both Campos  
813 and AMF; Fig. 6). Which non-climatic factors might explain why these LGM plant assemblages were  
814 grasslands rather than forests (as large parts are today)?

815 There is little evidence that fire restricted forest species' distributions at the (cold, generally wet)  
816 LGM; although only three microcharcoal records cover the period (Behling, 1997b; Behling et al.,  
817 2004; Jeske-Pieruschka et al., 2013), fire does not appear to have been common across the  
818 highlands. As yet, there is also no evidence that herbivory played a role, despite their importance in  
819 controlling modern AMF-Campos ecotones: although southern Brazil's herbivorous megafauna  
820 persisted into the early Holocene (Asevedo et al., 2020; Lopes and Buchmann, 2011; Raczka et al.,  
821 2018), proxies indicative of megafauna, such as *Sporormiella* spores, have not yet been examined in  
822 the region. It is likely, however, that the LGM's reduced atmospheric CO<sub>2</sub> concentrations (ca. 190  
823 ppm) would have disproportionately stressed C3-photosynthesising plants, conferring a competitive  
824 advantage to C4-photosynthesisers and potentially confining woody vegetation to moister  
825 microclimates such as river valleys (Gerhart and Ward, 2010; Montade et al., 2019; Pivel et al., 2010;  
826 Svenning et al., 2011). Our evidence suggests that these non-climatic factors may explain southern  
827 Brazil's extensive LGM grasslands better than climatic determinants (e.g. extremely cold  
828 temperatures or long dry seasons, cf. Behling, 2002; Behling et al., 2004), and so require greater  
829 consideration and direct investigation.

830 One consequence of non-climatic influences on vegetation physiognomy is that modelled  
831 assemblages may have manifested quite differently in the past than in the present (e.g. assemblages  
832 9, 15 and 13, detailed above). At the LGM and subsequently, many plant communities predicted to  
833 have co-occurring herbaceous and tree taxa may have been grassland landscapes with embedded  
834 forest (micro)refugia. Such formations have previously been inferred in southern Brazil from

835 modelling (Barros et al., 2015; Costa et al., 2017; Stefenon et al., 2019), palynology (Behling et al.,  
836 2004; de Oliveira et al., 2008; Ledru et al., 2016, 2007) and phylogeography (Auler et al., 2002; de  
837 Sousa et al., 2020; Lauterjung et al., 2018; Ledru et al., 2007; Stefenon et al., 2019, 2008, 2007).  
838 Direct evidence can also be observed in our synthesised palaeo-proxy sites: a valley's base sheltering  
839 more woody vegetation than its head during the Last Glacial (Paisani et al., 2019); 7,500 years of  
840 forest and grassland respectively occupying opposing sheltered and exposed aspects of valley slopes  
841 (Robinson et al., 2018); and 15,000 years of continuous forest pollen in Buriti's topographic  
842 depression, while surrounding soil profiles show grasslands (Bertoldo et al., 2014). The buffering  
843 effect of small-scale topography (beyond our climate data's spatial resolution) may also have  
844 permitted species to persist in apparently unsuitable areas – Buriti records *Araucaria angustifolia*  
845 pollen 15,000 years ago, for instance, when our SDMs suggest it should have been absent (though  
846 this could also be because each sediment subsample covers a longer period than our palaeoclimate  
847 time slices). Refugia such as these will have played important roles in AMF's late-Holocene  
848 expansion across the plateau, and explain the development of *A. angustifolia*'s western populations  
849 more parsimoniously than long-distance human-mediated dispersal in the late Holocene (cf.  
850 Lauterjung et al., 2018).

851 Compared to the plateau, inferring past vegetation physiognomies from meso-scale SDM predictions  
852 and finer-scale topographic data is much more difficult for the coastal lowlands, where detailed  
853 palaeo-topography is poorly known, due to submerged LGM coastlines. The prevalence of grassland  
854 pollen (and the near-absence of tropical forest pollen) in coastal proxy sites between the LGM and  
855 early Holocene has led some to suggest that grasslands replaced Atlantic Rainforest wholesale, with  
856 tropical tree species' southern limits found several hundred kilometres further north than at present  
857 (Bauermann, 2003; Behling, 2002; Behling and Negrelle, 2001) – a Pleistocene 'Forest Refuge  
858 Hypothesis' supported by early palaeo-distribution modelling (Carnaval and Moritz, 2008). However,  
859 a subsequent 'Atlantis Forest Hypothesis' argues that continental shelf exposed by lower LGM sea-  
860 levels could have supported large areas of forest (Leite et al., 2016). Our modelling and palaeo-data  
861 synthesis support an intermediate scenario of subtropical forest patches in a matrix of cold-adapted  
862 grassland/Campos (Bauermann, 2003; Behling and Negrelle, 2001; Gu et al., 2017). Our results  
863 suggest that the coastal lowlands and continental shelf had temperatures and rainfall suitable for  
864 both tropical trees (cf. Leite et al., 2016) and highland Campos species (cf. Behling and Negrelle,  
865 2001), but available palaeoecological records show much more herb than forest pollen (Bauermann,  
866 2003; Behling and Negrelle, 2001; Carvalho do Amaral et al., 2012; Gu et al., 2017), indicating that  
867 non-climatic factors likely dictated the distribution of these patches as they did with AMF and  
868 Campos on the highlands. However, without detailed topographic data for the presently submerged

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

#### 871 4.3. Context for a high-emissions future

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

886 We also find some indication that these climate change-induced alterations are already underway. In  
887 the present day, our models place the lower boundaries of more cold-adapted floristic assemblages  
888 at higher elevations than suggested by Brazil's official vegetation classification, and more warm-  
889 adapted groups extend higher up (Fig. 5; IBGE, 2012). This could be an artifact of the data used to  
890 construct our models, as extensive deforestation in the west of our study area (Fig. 1) has eradicated  
891 many climatically suitable localities for some species, which may have led the SDM algorithms to  
892 assume conditions are unsuitable for them. The IFFSC's systematic sampling (Vibrans et al., 2020,  
893 2010) should mitigate against this, though, and AMF and SDF species are not similarly affected,  
894 being respectively under- and over-predicted. It could also reflect the fact that ecosystems' current  
895 potential distributions were likely dictated by pre-industrial climates somewhat different to those of  
896 the CHELSA data's present period (1979-2013), which includes recent decades' anthropogenic  
897 warming (de Barros Soares et al., 2017; Karger et al., 2017b). This mismatch between 'present day'  
898 climate data and when climate conditions were last physiologically relevant may be non-trivial for  
899 ecosystems or long-lived tree species, and its impact on SDMs warrants both consideration and  
900 research. Taken together, the apparent over-/under-prediction of warm-/cold-adapted species could  
901 therefore be a genuine pattern resulting from the inclusion of recent anthropogenic warming in

902 'present' climate data, which is likely to become exacerbated through the 21<sup>st</sup> century as the  
903 magnitude of climate change increases.

#### 904 4.4. Implications for Conservation

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

927 Our palaeoecological insights provide invaluable baselines which can help inform restoration or  
928 conservation strategies, but they must be explicitly (and rationally) chosen and many historical  
929 baseline landscapes may become unviable under future conditions (Barnosky et al., 2017; Dietl et al.,  
930 2015; Loughlin et al., 2018; Rick and Lockwood, 2013; Willis et al., 2010). Under a high-emissions  
931 scenario, future floristic assemblages in the southern Atlantic Forest will have few close analogues  
932 from the last 21 millennia, possibly favouring 'taxon-free' conservation measures – prioritising  
933 biodiversity *per se* or ecosystem function, structure or services, rather than the protection or  
934 restoration of specific, historically known landscapes (Barnosky et al., 2017). Drastic increases in  
935 atmospheric CO<sub>2</sub> concentrations will make structure-preserving measures particularly difficult in

936 Araucaria Mixed Forest-Campos mosaics – which, in contrast to our LGM reconstruction, will  
937 increasingly favour forest over grassland (Fair et al., 2020; McElwain, 2018) – and will also impact the  
938 structure, function and biodiversity of the biome’s other forests (Esquivel-Muelbert et al., 2019). But  
939 regardless of the conservation approaches taken, a key task will be facilitating species’ individualistic  
940 movements in response to climate changes, including through forest restoration (Rezende et al.,  
941 2018; Zwiener et al., 2017). This too will come with challenges, however: increasing landscape  
942 connectivity amid anthropogenic climate change may erode endemic-rich marginal habitats and aid  
943 biotic homogenisation across the Atlantic Forest (Neves et al., 2017; Zwiener et al., 2018), and risks  
944 introducing competitor and antagonist species to populations sheltering in microrefugia (Ashcroft et  
945 al., 2012).

#### 946 4.5. Conclusions

947 Our findings show the value in combining species-level palaeo-distribution modelling with detailed  
948 synthesis of palaeoecological proxy data. The results highlight that 21,000 years of continual species  
949 reassortment in response to natural climate changes likely resulted in important (occasionally  
950 palynologically silent) compositional changes within southern Atlantic Forest ecosystems, as well as  
951 changes to their overall distributions. We demonstrate that different plant communities of this  
952 globally-important biodiversity hotspot vary in the degree of species reassortment they underwent  
953 in response to climate change since the LGM. Our analyses point to highly novel species assemblages  
954 in both the past (in particular, the early Holocene, a period rarely covered in other modelling  
955 studies) and future (late 21<sup>st</sup> century). Our close linkage of palaeo-SDMs and proxy data provides  
956 important insights into the biome’s vegetation history even at periods that have been well studied,  
957 revealing that, at the LGM, low atmospheric CO<sub>2</sub> concentrations (rather than climate) confined  
958 (sub)tropical forest to microrefugia among expansive open grasslands across highland plateaus, and  
959 that Araucaria forest taxa persisted throughout the Holocene in the west of our study area. Our  
960 models highlight a number of promising avenues for future research in southern Brazil, including  
961 times and places where significant dynamics might be recorded in as-yet unstudied sedimentary  
962 archives. Finally, this study puts into long-term context the magnitude of disruption that  
963 unrestrained anthropogenic climate change could bring to parts of the Atlantic Forest over the  
964 coming decades. Our findings suggest that the magnitude of plant species’ range shifts, and  
965 associated floristic turnover, predicted to occur by 2070 due to anthropogenic global warming is  
966 likely to have been unparalleled since at least the LGM, 21,000 years ago. We suggest that  
967 conservation efforts in the southern Atlantic Forest take account of species reassortment in the face  
968 of climate change, enhancing features which enable these distribution changes and protecting areas  
969 likely to shelter (micro)refugia, to support species’ resilience.

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## 975 Author contributions

976 Conceptualisation: OJW, FEM. Methodology: OJW, RJW. Resources and data curation: OJW, DVL,  
977 ACV. Software: OJW. Formal analysis: OJW. Investigation: OJW. Interpretation: OJW, FEM.  
978 Supervision: FEM, RJW. Writing: original draft OJW; review and editing OJW, FEM, RJW, DVL, ACV;  
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## 985 Conflicts of interest

986 The authors have no conflicts of interest to declare.

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