University of Reading

Assessing the resilience of Brazil's iconic Araucaria Forests to past and future climate change

PhD in Environmental Science

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Contents

Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Oliver Wilson

Acknowledgements

A lot of life has happened over the course of my PhD: five years*, four papers, three house moves, two children, and one pandemic… I'm enormously grateful to many people for their help and support in this time; in what follows I won't even attempt to name them all for fear of leaving out someone important. *Part-time (about 39-45 months FTE), not that I'm sensitive about it…

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Abstract

Southern Brazil's Araucaria Forests are unique, iconic, and vanishing. Part of a globally important biodiversity hotspot, they are threatened by 20th-Century deforestation and 21st-Century anthropogenic climate changes. Natural climate variability and Indigenous people also affected Araucaria Forests over many millennia, but considerable uncertainty remains over the type and scale of their impacts. Interweaving ecological models and data on past, present and future human, climate and vegetation dynamics, this thesis seeks to better understand the roles of climatic and non-climatic factors – including topography, human land use, and fire – in shaping Araucaria Forests over the last 21,000 years and into the late 21st Century.

Results show that 21st-Century anthropogenic climate change will likely bring greater disruption to Araucaria Forests than the last 21 millennia of natural variability. Key species will experience major range contractions and novel warm-adapted forests will replace long-established floristic associations, echoing and exceeding changes from the Holocene onset 12,000 years ago. Araucaria populations will likely find shelter in small-scale microrefugia, but more than a third of these have already lost their natural vegetation cover and few remnants are well protected.

But results also show that climate only partially controls Araucaria Forest dynamics. 21,000 years ago, low atmospheric CO_2 concentrations helped grasslands dominate woody vegetation, a dynamic which continued until recent millennia. Araucaria Forests then flourished late in the Holocene, as climate changes tipped landscapes over fire-suppression thresholds, triggering runaway forest expansion. Although subtle human impacts can be difficult to see in fossil pollen data, pre-colonial Indigenous communities did significantly shape Araucaria Forest structure and composition with fire, crop cultivation, and enriched Araucaria populations.

This understanding of how past climatic and non-climatic factors combined to shape contemporary Araucaria Forests provides vital information for their future – from non-linear responses to climate shifts to conservation strategies and pathways for sustainable resource use.

Introduction

Brazil's Araucaria Forests are among the most interesting ecosystems in the world. Found in the highest and coldest region of one of Earth's richest and most threatened biodiversity hotspots, South America's Atlantic Forest, they are ancient, iconic, and vanishing (Bellard *et al.*, 2014; Neves *et al.*, 2017). 20th-Century deforestation, along with rampant exploitation of Araucaria trees (*Araucaria angustifolia*) for timber, devastated the landscapes on southern Brazil's highlands – some 80-90% of their natural vegetation was destroyed (de Carvalho and Nodari, 2010). Now, a warming world with disrupted rainfall patterns further threatens this ecosystem and the relatively cool, constantly moist climatic conditions it requires (Beck *et al.*, 2018).

Predicting what the future holds is always riven with uncertainties. One way of narrowing the range of predictions surrounding Araucaria Forests' future dynamics is to look to their past, taking advantage of the highlands' responses to climate changes and human land use over the long term. This is the aim of the work in this thesis, which examines how Araucaria Forests (and the rest of the southern Atlantic Forest) responded to the slow natural climate changes which unfolded over the last 21,000 years, and to the human impacts which played a significant role in driving vegetation change in recent millennia. These provide the context for the even greater climate and vegetation changes predicted to occur over the coming decades of the 21st Century, and suggest ways future disruptions could be mitigated.

This thesis is structured around four main chapters: each is a scientific paper which stands alone, but all build on one another to form a cohesive whole. Three of the four chapters have already been published at time of submission (Cárdenas *et al.*, 2019; Wilson *et al.*, 2019, 2021), and the fourth has been submitted to a journal. The first chapter predicts responses of Araucaria trees to 21st-Century climate change, considering topographic microrefugia and historic habitat loss. The second chapter examines how contemporary Araucaria Forest vegetation is represented in modern pollen spectra, to guide interpretations of past floristic change. (This chapter was led by another member of the research group, and is included here as the results are relevant and I made a substantial contribution to the study; the other three chapters are more central to this thesis.) Chapter 3 investigates floristic changes to Araucaria Forests and their neighbouring ecosystems over the last 21,000 years and into the late 21st Century. Chapter 4 untangles the contributions of natural climate changes and Indigenous land use to shaping Araucaria Forests in the Late Holocene.

Bookending the main chapters are a literature review and a concluding discussion. The literature review seeks to situate the main chapters in a wider context, examining the crucial concept of resilience and providing an overview of research into ancient human impacts in tropical forests, before introducing the specific ecological context for this thesis and the knowledge gaps its research aims to fill. The concluding discussion summarises the main chapters' findings, synthesises them in relation to the wider literature, and then sets out potential future directions for this work and the studies' wider relevance.

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Literature review

This literature review is divided into four sections, each covering a key component of the background to my PhD research. The first section, 'Palaeoecology, resilience and conservation', examines the concept of ecological resilience and how understanding ecosystems' centennial or millennial-scale pasts can play a critical role in predicting and safeguarding their futures. The second section, 'Domesticated/wilderness: tropical forests' past plants and people, and present polarisation' explores one of (palaeo-)ecology's most contentious issues: the extent to which modern tropical forest biodiversity was and remains shaped by past climate changes and Indigenous people.[1] Section three, 'The present, recent past, and near future of Brazil's Araucaria Forests', introduces the contemporary ecological context within which I examine these broader concepts. Finally, the fourth section, 'Plants and people in southern Brazil's past', places the former section's 'long present' period into a wider temporal context, reviewing our understanding of the palaeoclimates, palaeoecology and archaeology of southern Brazil's highlands.

Each of these sections is, to some extent, interdependent, and together they help to set the scene for the research in this thesis. Where necessary, I clarify differences between the state of knowledge at present and when my PhD research was conceived. Throughout, I endeavour to highlight how the chapters which follow provide important advances in our understanding of Brazil's Araucaria Forests and their resilience to past and future climate changes.

1 Palaeoecology, resilience and conservation

This section introduces some of the key underpinning concepts in this thesis, highlighting the value of palaeoecology for future-focused conservation. It explores concepts of resilience and vulnerability, and how palaeoecological insights improve our understandings of biodiversity responses to disturbance, using past periods with different climates to examine community- and species-level responses at different spatial and temporal scales. In doing so, it demonstrates the value of connecting observations of the past with planning for the future – a key aim for this research.

> *How do you study an ecosystem no ecologist has ever seen?*
>
> Jack Williams & Stephen Jackson (2007, p. 475)

Life on Earth is in the grip of intersecting, existential climate and biodiversity crises, with around a million species threatened with extinction, including one or two in every five plants (Brummitt *et al.*, 2015; IPBES, 2019; Nic Lughadha *et al.*, 2020). Drastic action in the present is urgently needed to avoid significantly damaging potential futures – for nature and for human societies (IPBES, 2019). In this context, researching ecosystems in the distant past might appear esoteric – but palaeoecology has a vital role to play in understanding how populations, species, communities and ecosystems may respond to our planet's rapidly changing conditions (Dietl *et al.*, 2015; Barnosky *et al.*, 2017; McElwain, 2018; Fordham *et al.*, 2020; Tierney *et al.*, 2020). Understanding the past, therefore, is essential for understanding the present and gaining insight into the future.

A key concept which spans the temporal divide is that of resilience (along with its counterpoint, vulnerability), which can generally be considered as the ability of a system to respond to

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[1] I capitalise 'Indigenous' in this thesis in recognition that it refers more accurately to a community identity than to a descriptor of geographic origins. This decision was inspired, and is explained, by this editorial on the style guide for the anthropology magazine Sapiens: https://www.sapiens.org/language/capitalize-indigenous/. For further discussion, see Supplementary Information 1 of Garnett et al. (2018).

perturbations. Ecosystems can display at least two types of resilience: resistance to, and/or recovery from, change (Davies *et al.*, 2018; Willis, Jeffers and Tovar, 2018). More resilient ecosystems may resist more significant pressures for longer without undergoing structural, compositional and/or functional reorganisation, or they may more readily rebound to their previous state after their capacity to resist has been exceeded, or both (Davies *et al.*, 2018; Willis, Jeffers and Tovar, 2018).

Palaeoecological research provides invaluable insights into ecosystems' resilience to disturbances (both human and climatic) – as the only available source of concrete, empirical data on how biodiversity responds to disturbances over longer-than-observational timescales, past-focused research is irreplaceable (Willis *et al.*, 2010; Wilmshurst *et al.*, 2014). This section examines several of the contributions palaeoecology can make to conservation, and how plans to maintain ecosystems' resilience to future climate changes can draw on vegetation histories.

Biogeographers have potentially powerful tools for predicting potential ecological responses to future climatic conditions (e.g. ecological niche models), but their outputs are subject to uncertainties and their accuracy for future time periods is difficult to verify. In this context, it can be informative to examine how ecosystems have responded to past climates which are analogous to potential future conditions; although our planet's average temperatures are rapidly warming to levels unprecedented in human evolutionary history, such analogues can still be found (Tierney *et al.*, 2020). For instance, mid-Holocene (ca. 6,000 years ago) conditions in Amazonia were significantly drier and potentially somewhat warmer than the present, yet the region's rainforests persisted apparently intact throughout (Smith and Mayle, 2017; Smith, Singarayer and Mayle, 2021). This finding suggests that the coming decades' climatic changes alone should not be sufficient to cause biome-level savannisation or dieback – avoiding potentially catastrophic consequences for the global climate (Smith, Singarayer and Mayle, 2021). Indeed, for tens of millions of years, Earth's tropical rainforests have persisted through conditions even more extreme than the mid-Holocene, demonstrating more resilience to elevated temperature and CO_2 levels than contemporary observations alone would suggest (McElwain, 2018; Carvalho *et al.*, 2021).

This is one of the most significant challenges with using past climates as analogues for the future: "research into long-term ecological dynamics, past or future, is heavily conditioned by our current observations … [yet] the further we move from the present, the more it becomes an inadequate model for past and future system behaviour" (Williams and Jackson, 2007, p. 475). Species' distributions in the present may cover only a portion of their wider fundamental niches, meaning they could respond in unexpected ways to changed conditions. Past climates extend the range of conditions over which species' responses can be observed, allowing palaeoecology to clarify the limits of their climatic resilience and indicating where, when and how future climates may challenge these boundaries (Williams and Jackson, 2007). Using palaeoecological data to account for this contemporary 'niche truncation' can change predictions of species' vulnerability and resilience to future climate changes in significant and complex ways (Nogués-Bravo *et al.*, 2016).

Palaeoecological research has demonstrated that ecological responses to climate changes occur at the species level – ecosystems do not react *en masse* (Williams *et al.*, 2004; Williams and Jackson, 2007; Jackson and Blois, 2015). Combined with species' unexpected climate tolerances, this can produce 'ecological surprises' (Williams and Jackson, 2007). Some of the most significant such surprises are species assemblages with no present analogue, some of which have had extensive distributions in North and South America (including Amazonia) at points in the past (Colinvaux, De Oliveira and Bush, 2000; Bush *et al.*, 2004; Williams *et al.*, 2004; Lima *et al.*, 2018). These demonstrate that ecological communities are neither inevitable nor robust through time, but rather each "comprises a single place that happens to be occupied by an assemblage of species with overlapping distributions and environmental tolerances" – "one small, ephemeral point in a roiling, dynamic unfolding of environmental change, distribution dynamics, and spatially aggregated ecological processes" (Jackson and Blois, 2015, p. 4917). Consequently, land managers must choose between 'classical' and 'emerging' conservation paradigms: whether protected landscapes should be preserved in or restored to historically known states (Willis *et al.*, 2010; in which case palaeoecology can provide crucial information on ecological baselines; Rick and Lockwood, 2013; Wilmshurst *et al.*, 2014); or whether to implement taxon-agnostic measures which maximise ecosystem services or biodiversity per se, or which mimic the ecosystem's historical structure and functions (Barnosky *et al.*, 2017).

Even at species level, however, responses to past and future climate changes can be variable. Under unfavourable past conditions, some species in some landscapes underwent apparently wholesale range contractions, retreating to refugia in areas with more suitable climates (Magri, 2008; Gavin *et al.*, 2014). Areas with moderate, stable climates are more likely to act as refugia for species in both past and future, so can be treated as conservation priorities – especially as past refugia may conserve important genetic diversity as well as the conditions needed for it to evolve (Gavin *et al.*, 2014; Tang *et al.*, 2018). However, palaeoecological research has also demonstrated that small-scale refugia can also play an important role in allowing populations to survive in areas experiencing generally unfavourable conditions (Rull, 2009; Montade *et al.*, 2014; Valencia *et al.*, 2016; Bemmels, Knowles and Dick, 2019). These microrefugia occur in locations whose topography or hydrology uncouple their microclimates and/or fire regimes from broad-scale climatic conditions and trends, such as river valleys which collect relatively cool, moist air (Rull, 2009; Ashcroft, 2010; Dobrowski, 2011; Wilkin, Ackerly and Stephens, 2016; McLaughlin *et al.*, 2017). Depending on their capacity, the extent to which they can retain favourable conditions, and how quickly the macroclimate improves again, these locations can act in various ways: as stepping stones, facilitating migration to new suitable areas; as temporary microrefugia (sensu Hannah *et al.*, 2014), providing relief in transient periods of unsuitable climate conditions; or as final holdouts, in which dwindling populations are confined under progressive climatic change (Hannah *et al.*, 2014; Keppel and Wardell-Johnson, 2015). Microrefugia, and the topographic features that often give rise to them, are important targets for conservation – not just because of the species they can be predicted to protect, but because their climate-decoupling features will make them valuable components of the landscape for species not yet threatened (Mosblech, Bush and van Woesik, 2011; Valencia *et al.*, 2016; Suggitt *et al.*, 2018).

Each of these lessons or concepts from palaeoecology is relevant for future-focused conservation, and each plays a part in this thesis. Previous studies modelling ecological responses to southern Brazil's palaeoclimates have generally focused on the Last Glacial Maximum and mid-Holocene, but these are relatively poor analogues for southern Brazil's future (Cruz *et al.*, 2007, 2009; Chou *et al.*, 2014). The early Holocene, for example, was the region's driest period for tens of millennia (Figure 4-3), so could provide more valuable information on the limits of ecosystems' resilience to more extreme climates (Cruz *et al.*, 2007, 2009); this was a key motivation for examining a wide range of past time slices in Chapter 3 (see also Sections 4.1 and 4.2). The modelling in Chapters 3 and 4 also allows for compositional change and the development of no-analogue assemblages, rather than examining only contemporary (so potentially ephemeral) communities – in recognition that this is likely to have been a key part of how ecosystem responses to unusual past and future climates. Chapter 1 incorporates fine-scale topography in its predictions of ecosystem dynamics under climate change because these sites are likely to provide conservation-critical holdout microrefugia for Araucaria trees in the future. In Chapter 4, similar techniques are included because more favourable micro-environments could significantly enhance Araucaria Forests' persistence and recolonisation in the landscape under past fluctuations between challenging and favourable conditions – a crucial step for increasing the realism of model predictions and marrying them effectively to palaeoecological vegetation proxy data.

2 Domesticated/Wilderness: tropical forests' past plants and people, and present polarisation

This section outlines one of the key conceptual areas to which this thesis relates – the extent to which Indigenous people affected (sub-)tropical ecosystems in the past, and the extent to which these ecological legacies can still be seen. It provides a high-level overview of the debates which dominate this controversial topic, the lines of evidence which inform the discussion, and how the methods in this thesis can advance our understanding in this area.

> *[W]as the landscape encountered in the sixteenth century primarily pristine, virgin, a wilderness, nearly empty of people, or was it a humanized landscape, with the imprint of native Americans being dramatic and persistent?*
>
> William Denevan (1992, p. 369)

Tropical and subtropical forests are some of the most important ecosystems on the planet, holding disproportionate shares of global biodiversity and sequestered carbon, and playing an outsized role in global climate regulation (Lewis, Edwards and Galbraith, 2015; IPBES, 2019; Raven *et al.*, 2020; Roberts, Hamilton and Piperno, 2021). They are also significantly threatened, suffering from often precipitous rates of habitat loss – almost a third of Neotropical forest has been lost, for example, and less than 12% of remnant Indo-Malay forests have high landscape integrity (IPBES, 2019; Grantham *et al.*, 2020). In addition to their ecological value, tropical forests have nurtured disproportionate shares of human cultural and linguistic diversity, with unique attendant knowledge of the natural world, and they have been home to tens of millions of Indigenous people for tens of thousands of years (Roberts *et al.*, 2017; Cámara-Leret and Bascompte, 2021; Ellis *et al.*, 2021; Roberts, Hamilton and Piperno, 2021).

In the course of forging and sustaining cultures and communities, Indigenous people altered the landscapes around them in many different ways, some impacts of which can still be seen in the makeup of the forests (Roberts *et al.*, 2017; Levis *et al.*, 2018; McMichael, 2021; Roberts, Hamilton and Piperno, 2021). Understanding the extent to which Indigenous people changed tropical forests in pre-colonial times [2] – the changes' spatial coverage, magnitude, and durability through time – is crucially important for conservation and management decisions, Indigenous land claims, assessments of resource use sustainability, and our understanding of the forests' resilience to disturbance (Mayle and Iriarte, 2014; McMichael, 2021). Most importantly for this thesis, being able to separate out human causes for observed past vegetation changes clarifies the extent to which tropical forests' long-term dynamics have been driven by climatic conditions – and therefore how resilient these ecosystems are to climate changes (Mayle and Iriarte, 2014; Roberts *et al.*, 2017; McMichael, 2021; Roberts, Hamilton and Piperno, 2021).

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[2] I use 'pre-colonial' in preference to alternatives like 'pre-Columbian' because it is a more general term. It is the more intuitive and descriptive phrase, and applies beyond the Americas. It also implicitly recognises that the changes to Indigenous ways of life came more from spatially and temporally heterogeneous changes in local/regional governance than from the fact that Europeans had discovered the Americas (which came centuries before direct European impacts on southern Brazil's highlands).

The extent to which Indigenous people affected tropical landscapes before European arrival has been researched and debated in many parts of the world, but possibly the fiercest and most consequential debate surrounds legacies of past human impacts in Amazonia, as befits the world's largest tropical rainforest (Mayle and Iriarte, 2014; S Yoshi Maezumi *et al.*, 2018; McMichael, 2021). Since associated research, debates and controversies are better developed here than elsewhere, Amazonia's plants, people and past represent a useful vehicle for studying the broader issue. This section does not therefore seek to comprehensively review the literature on past human impacts on Amazonia, but rather to examine how the scientific consensus has evolved and the types of evidence which have helped to inform the debate, with a view, ultimately, to their application to similar questions in southern Brazil's highlands.

The first Europeans to arrive in Amazonia reported finding dense, well-developed settlements along major waterways, but more dedicated exploration in later centuries generally found tracts of forest apparently untouched by the now-sparse Indigenous populations – a consequence of catastrophic depopulation in the intervening period (Denevan, 1992; Loughlin *et al.*, 2018). As recently as the late 20th Century, the prevailing wisdom from available research was that tropical forests could not sustain large populations or complex societies – but more recent archaeological research has revealed widespread evidence for significant human occupation across much of the region, and ecological and palaeoecological research has demonstrated that associated environmental changes could be significant (McMichael *et al.*, 2014; Roberts *et al.*, 2017; de Souza *et al.*, 2018, 2019; Fletcher *et al.*, 2021; Roberts, Hamilton and Piperno, 2021). This has led to the revaluation of the so-called 'pristine myth', and the rise of the countervailing idea that Amazonia was instead 'domesticated' at European arrival (Denevan, 1992; Heckenberger *et al.*, 2003; Clement *et al.*, 2015; Levis *et al.*, 2018). Each paradigm is immensely consequential for Amazon ecosystems and the people who live in, think about, or manage them at local, regional and global scales (Bush and Silman, 2007).

For rhetorical convenience (as in the title of this section), the two competing views of Amazonia's past plants and people are often presented as polar opposites (which they are) with researchers split between the two camps (which, for the most part, they are not). In the contemporary scientific literature, the pristine myth is mostly vanquished, whereas the idea of Amazonia as 'cultural parkland' (Heckenberger *et al.*, 2003) is the more dominant extreme. For the most part, however, the debate chiefly concerns where Amazonia sits on the continuum between these two views. It is widely accepted that contemporary Indigenous people intentionally and incidentally affect the forests they live among in various ways (reviewed in depth by Levis *et al.*, 2018), and that these activities and their impacts also occurred in the past. Still at issue is the spatial extent of those impacts (were they near-universal or largely confined to seasonal and fluvial areas?) and their magnitude (how much of a difference did they make, and can their effects still be seen?). To help resolve these questions, researchers have used various lines of evidence from a range of techniques and disciplines.

The Brazil nut tree (*Bertholletia excelsa*) has exceptional cultural and economic importance to Indigenous people across Amazonia; it may in turn owe much of its ecological importance to those people. It has a distribution far wider than closely related species without having any inherent dispersal advantages, yet its genetic diversity suggests recent and rapid expansions – human influence in these could be reflected in the connections among the species' names in different languages (Shepard and Ramirez, 2011). Comparing ecological models with forest surveys shows that Brazil nut trees are more likely to be encountered around archaeological sites, as well as growing larger and in denser stands there – though a climatic contribution to this pattern cannot be ruled out (Thomas *et al.*, 2015). Contemporary observations show that Kayapó Brazil nut harvesters plant and unintentionally disperse Brazil nuts in groves, villages, and along the trails between them, providing a potential mechanism for these patterns (Ribeiro *et al.*, 2014); dendroecological research shows that Brazil nut trees experienced reduced growth rates in the post-colonial period, suggesting that Indigenous management had been favourable for them (Caetano Andrade *et al.*, 2019).

The Brazil nut is one of the 220 or so hyperdominant tree species in Amazonia, which together make up half of the region's roughly 390 billion trees (ter Steege *et al.*, 2013, 2020). These hyperdominant trees are more likely to show signs of potential incipient domestication than would be expected by chance alone, and individuals of potentially-domesticated hyperdominants are more regionally widespread than their non-domesticated counterparts (Levis *et al.*, 2017). Across much of Amazonia, forests close to known archaeological sites have larger and richer populations of potentially-domesticated hyperdominant trees than those further away (Levis *et al.*, 2017). Yet inferences from this basin-wide analysis are complicated: it is challenging to demonstrate that a species has undergone incipient or advanced domestication, rather than simply having naturally attractive traits; the 1,100 or so locations in the Amazon-wide network of forest plots oversample areas with higher pre- and post-colonial human impact (McMichael *et al.*, 2017); and the causal link between human occupation and useful species locations is not certain – while people may have promoted key plants, they might also have preferentially settled more resource-rich areas (Levis *et al.*, 2017).

Effectively disentangling the causal relationships between Indigenous occupations and useful plant populations requires research that looks to the past – palaeoecology, archaeology, and studies which integrate them both (Mayle and Iriarte, 2014). Archaeological research in south-western Amazonia has shown, for example, that Brazil nuts were harvested, selected for size, and used alongside palm fruits and other useful species – strongly suggesting 'domestication in motion' (Pärssinen *et al.*, 2021). Palaeoecological records close to archaeological sites have recorded a plethora of pre-colonial human-environment interactions – from using fire to hold off expanding forests (Carson *et al.*, 2014) to maintaining high canopy cover (Kelly *et al.*, 2018), and from crop cultivation (Bush *et al.*, 2016) to enriching forests with useful tree species (Iriarte *et al.*, 2020). On the other hand, other palaeoecological studies have also found that some currently hyperdominant species have had long histories of high abundance, irrespective of human occupation, and some Amazon forest records show little sign of pre-colonial human impact on the vegetation (McMichael *et al.*, 2015; Bush and McMichael, 2016; Piperno, McMichael and Bush, 2019; Piperno *et al.*, 2021). All these findings are built on foundations which relate palaeo-proxies (fossil pollen, phytoliths, soil stable carbon isotopes ($\delta^{13}C$), etc.) to the distribution, structure and composition of modern vegetation (Gosling *et al.*, 2009; Jones *et al.*, 2011) – something that can be challenging, especially for landscapes with intermediate canopy cover (Whitney *et al.*, 2019).

Almost all of the above techniques have been brought to bear in studying forest changes associated with one of Amazonia's most important indicators of Indigenous occupation – Amazonian (or Anthropogenic) Dark Earths (ADEs). Found predominantly (but not exclusively) along watercourses, these were (and are still) formed by Indigenous people enriching soils with charcoal and refuse over long periods of occupation, conferring on ADEs far higher fertility than surrounding natural soils (McMichael *et al.*, 2014; Levis *et al.*, 2020). In palaeoecological records, the onset of human occupations and development of ADEs is associated with changes to fire regimes, soil chemistry, and forest composition (including increasing abundance of useful species, such as palm trees) – changes which cannot be explained by climate alone (S Yoshi Maezumi *et al.*, 2018; S. Yoshi

Maezumi *et al.*, 2018; Iriarte *et al.*, 2020). These changes are not confined to the past: forest inventories across different parts of Amazonia have found that ADE forests remain compositionally and structurally different to those on non-ADE substrates, with some structural differences visible in satellite imagery (Palace *et al.*, 2017; S Yoshi Maezumi *et al.*, 2018; S. Yoshi Maezumi *et al.*, 2018; Ferreira *et al.*, 2019; Oliveira *et al.*, 2020). The presence of ADEs helps to describe the basin-wide abundance patterns of potentially-domesticated hyperdominant trees – including, it seems, the Brazil nut (Thomas *et al.*, 2015; Levis *et al.*, 2017). And these legacies of past human-environment relationships are important for the future, too: the persistent structural and compositional changes in ADE forests appear to influence the vegetation's contemporary susceptibility to fire – and, by extension, to climate change (S. Yoshi Maezumi *et al.*, 2018).

In recent decades, the consensus view of Amazonia's human history has shifted considerably, largely putting to rest the myth of virgin Amazon wilderness and small-scale, low-impact human occupation (at least in the most relevant sectors of academia), and turning to test the assumptions of widespread, significant and persistent human changes to the forest. It may not be wise – or even possible – to characterise the entire, vast Amazon region as simply 'pristine' or 'domesticated', or even somewhere in between. But what various investigations across multiple disciplines have certainly shown is that humans have had significant impacts on the forest across wide expanses of both space and time. Improving our understanding of these is crucial for clarifying these critical ecosystems' resilience to contemporary human impacts, including anthropogenic climate change.

Such questions are, of course, relevant further afield than Amazonia. Brazil's Atlantic Forest biome (the focus of this thesis), for example, has an equivalent claim to attention on grounds of biodiversity and human history (see Sections 3.1 and 4.3), and in parts has excellent palaeoecological, archaeological, palaeoclimatological and ethnographic data. Yet the debate between 'pristine' and 'domesticated' here has barely begun, and significant human impacts are rarely discussed – chiefly because extremely few studies have brought together the various disciplines' strands of evidence to investigate how human history shaped the Atlantic Forest's contemporary biogeographic patterns (Section 4.3). My thesis attempts to do just this.

Chapter 2 (Cárdenas *et al.*, 2019) lays important groundwork for using fossil pollen data to understand past human impacts on Araucaria Forests, clarifying the extent to which floristic and structural changes in the vegetation can be detected. Chapter 3 (Wilson *et al.*, 2021) develops and evaluates modelling and palaeo-data synthesis techniques that help to interpret predicted and observed past changes in southern Brazil's vegetation. And Chapter 4 brings these techniques together: using different modelling approaches, advanced palaeoclimate analysis, syntheses of archaeological and palaeoecological data, and new multiproxy records of fire and vegetation history in archaeological contexts, it examines the extent to which climate changes, fire dynamics and human interventions affected Araucaria Forests through the Late Holocene. In so doing, it complements the future-focused research in Chapters 1 and 3 (Wilson *et al.*, 2019, 2021), together demonstrating the potential vulnerabilities of southern Brazil's highland vegetation to perturbations by people and climatic changes.

Finally, just as the central issues in the question of anthropogenic Amazonia are relevant in the Atlantic Forest and elsewhere, so are the techniques in this thesis (especially Chapter 4) more widely relevant. By combining spatiotemporally explicit predictions of vegetation change with observations, examining multiple potential drivers of vegetation change (humans, climate, fire), incorporating chronological uncertainty, and comparing palaeoecological records across archaeological gradients, Chapter 4 provides a comprehensive view of the complexities of past human impacts on (sub-)tropical ecosystems. These methods should help shed light on similar, critical questions elsewhere too – in Amazonia and beyond.

3 The present, recent past, and near future of Brazil's Araucaria Forests

This section introduces the contemporary ecological context for my PhD research: the Atlantic Forest biome; its Atlantic Rainforests and Seasonally (semi-)Deciduous Forests; and the highland ecosystems that sit between them at the biome's southern extreme, on which my research has most closely focused. I provide key ecological background on Araucaria Forests, Campos grasslands, the mosaic they form and the Araucaria trees which characterise it, as well as the highland ecosystems' recent history, present state, and the future threats my PhD research addresses.

3.1 The Atlantic Forest biome

The Atlantic Forest biome (Mata Atlântica), which covers more than 3,000 km of Brazil's coast and stretches inland into Argentina and Paraguay, is a global biodiversity hotspot (Myers *et al.*, 2000; Oliveira-Filho and Fontes, 2000). It contains 26% more seed plant species than the Brazilian Amazon (15,004 vs. 11,902), half of which are endemic (a proportion three times higher than that of Amazonia; 49.5% vs. 16.0%) – indeed, 2% of all the world's species of seed plants (as well as about 3% of its non-fish vertebrates) are found in the Atlantic Forest and nowhere else (Oliveira-Filho and Fontes, 2000; Oliveira-Filho *et al.*, 2014; Brazil Flora Group, 2015; Lughadha *et al.*, 2016; Scheffers *et al.*, 2019; Figueiredo *et al.*, 2021).[3]

The Atlantic Forest's immense biodiversity is gravely threatened. Precise estimates vary depending on the data and methods used [4], but the great majority – perhaps 63% (MapBiomas Trinational Atlantic Forest Project), 72% (Rezende *et al.*, 2018), 85% (Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais, 2020) or 88% (Ribeiro *et al.*, 2009) – of the biome has lost its natural vegetation, replaced by pasture, croplands, exotic forestry plantations, and some of South America's largest urban areas (Souza *et al.*, 2020; fig. 3-1; Rosa *et al.*, 2021). Almost a fifth of the natural forest areas still found in the Atlantic Forest are less than 30 years old (Rosa *et al.*, 2021). 83% of Brazil's Atlantic Forest fragments are less than 50 ha in size; three quarters of the remaining forest is within 250 m of a non-forested area; and despite the biome covering ca. 1.5 million km^2 in Brazil, none of its forest area is further than 12 km from a fragment edge (Ribeiro *et al.*, 2009). Those forest fragments cover 40% less climate space than the biome as a whole (Brown *et al.*, 2020), and have lost between a quarter and a third of their biomass, stored forest carbon, and tree species (de Lima, Oliveira, *et al.*, 2020). Across the tree of life, contemporary species assemblages are only about 45-50% similar to their historic or non-deforested composition (Bogoni *et al.*, 2018; Brown *et al.*, 2020). The erosion of these facets of diversity, and their disproportionate impact on

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[3] The designation of the Atlantic Forest as a global biodiversity hotspot was originally made by Myers *et al.* (2000) using a limited – and now outdated – circumscription of the ecosystem (Oliveira-Filho and Fontes, 2000); their estimates of biome-level and global species richness have also been superseded. However, updated estimates for species richness for seed plants in the Atlantic Forest *sensu lato* (Brazil Flora Group, 2015) and world (Lughadha *et al.*, 2016) – as also for non-fish vertebrate species (Scheffers *et al.*, 2019; Figueiredo *et al.*, 2021) – support the figures quoted here (see also supplementary material for Chapter 4).

[4] Satellite image resolution, tolerance of secondary vegetation, spatial extent (Brazil alone or including Argentina and Paraguay), and evaluation period all affect the estimate. Importantly, the estimate of Ribeiro *et al.* (2009) assumes the entire biome would naturally be covered in forest, which is untrue. References to 'original' cover are usually erroneous – rather, losses are normally assessed against a counterfactual present.

endemic species, is increasingly homogenising the Atlantic Forest's remarkable variety of life (de Lima, Oliveira, *et al.*, 2020).

My research focuses on superlative ecosystems in the Atlantic Forest's southern region: its most intact and biodiverse; its most fragmented and threatened; its highest, coldest and most unique. Floristically, these ecosystems are not generally separated by clear distinctions, but rather exist along a compositional continuum with high species turnover between (and often within) the region's forest formations (Oliveira-Filho and Fontes, 2000; Duarte *et al.*, 2014; Oliveira-Filho *et al.*, 2014; Bergamin *et al.*, 2017; Esser, Neves and Jarenkow, 2019). They are introduced in the following sections.

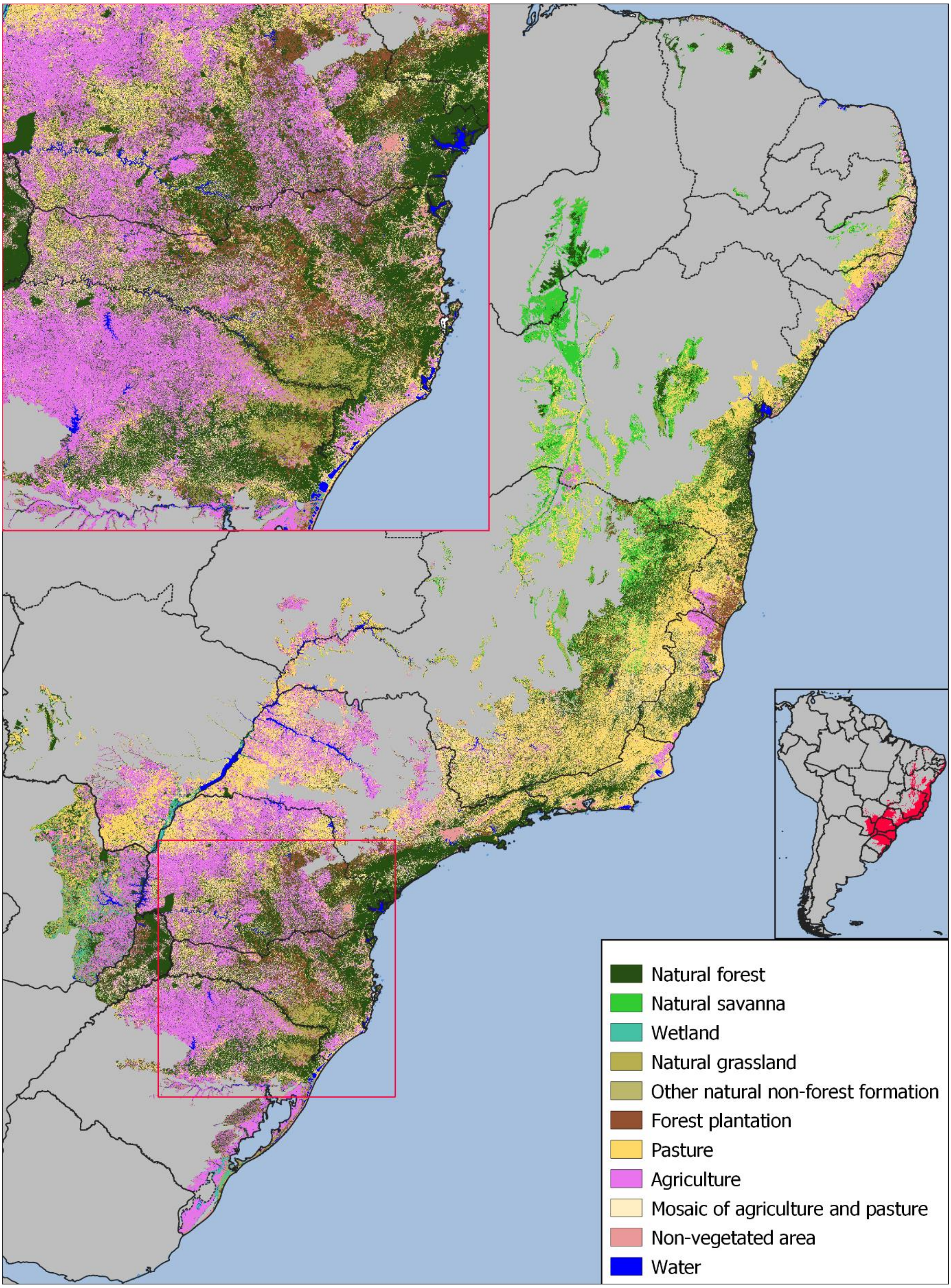

Figure 3-1: Current (2019) land cover and land use in the Atlantic Forest biome (*MapBiomas Trinational Atlantic Forest Project - Collection 1 of annual land use and land cover maps, accessed on 26/10/2021 via https://bosqueatlantico.mapbiomas.org*, no date). *Inset maps show a more detailed view of my main study area (top left) and the coverage of the Atlantic Forest (under its broadest definition) in the context of South America.*

3.2 Atlantic Rainforests and Seasonally (semi-)Deciduous Forests

> *The beauty of the forests is breathtaking and, in its majesty, almost suffocating. […] The variety of trees is so numerous that one life is too short to be able to know them all.*
>
> Hermann Blumenau, 1850, quoted in Nodari (2013).

The Atlantic Forest biome's currently accepted definition is broad, but originally it was conceived as covering only the evergreen tropical and subtropical rainforests that occurred in a relatively narrow band (generally <100 km) between highlands and coast (Oliveira-Filho and Fontes, 2000). This Atlantic Rainforest (also called Dense Ombrophilous Forest or Serra do Mar forests) was the ecosystem originally designated as a global biodiversity hotspot (Myers *et al.*, 2000), and it remains the biome's most biodiverse (up to twice the species richness and endemicity of other forest types), intact (37% natural cover), and protected formation (11% of its forest remnants, and 53% of all Atlantic Forest protected area) (Ribeiro *et al.*, 2009; Schorn *et al.*, 2012; Neves *et al.*, 2017; de Lima, Souza, *et al.*, 2020). Nonetheless, despite being the least threatened of the ecosystems in my PhD research, the Atlantic Rainforest is still an Endangered ecosystem – a result of contemporary and (especially) historical human-driven changes in its distribution (Ferrer-Paris *et al.*, 2019). Climatically, the Atlantic Rainforest is associated with high average annual temperatures and humidity, with no dry season and rare frosts, though significant variations in these conditions across the forests' broad elevational range (Figure 3-2) alter their composition; lowland, submontane and montane formations can be distinguished (Klein, 1975; Uhlmann *et al.*, 2012; Lingner *et al.*, 2013).

The Atlantic Forest ecosystem which most contrasts with the Atlantic Rainforest is the biome's Seasonally (semi-)Deciduous Forest (SDF, sometimes called Alto Paraná forests), found in the biome's western reaches, at the southern border of the highland plateau, and along the Uruguay river valley (Figure 3-2). The most extensive formation in the Atlantic Forest, SDF has been among the most damaged by human habitat conversion (Figure 3-2) – it has lost 93% of its natural vegetation and has been assessed as Critically Endangered (Ribeiro *et al.*, 2009; Ferrer-Paris *et al.*, 2019). This devastating deforestation mainly occurred in the mid-20th Century in Brazilian territory (Nodari, 2012), but its later onset in Paraguay has made it visible in satellite observations: natural vegetation coverage in Paraguay's SDF fell from 73.4% in 1973 to 24.9% in 2000, with about 30% of those 2000 remnants lost in the two decades since, mostly for farming (Da Ponte, Mack, *et al*., 2017; Da Ponte, Roch, *et al*., 2017; Huang *et al*., 2007; MapBiomas Trinational Atlantic Forest Project). Although Atlantic Forest SDF is often grouped into the Neotropical seasonally dry forest biome, the semi-deciduous SDF in southern Brazil, Argentina and eastern Paraguay does not actually experience dry periods (Dryflor, 2016) – in fact, its range sees comparably high average temperatures and rainfall to the Atlantic Rainforest, but greater temperature seasonality and more frequent frosts (Gasper *et al.*, 2012). Many canopy trees shed their leaves in winter as a response to these low temperatures and the shorter photoperiod, exposing an evergreen sub-canopy layer (Klein, 1975; Gasper *et al*., 2012).

Although the Atlantic Rainforest and SDF are both relevant to this thesis (especially Chapter 3), my PhD research focuses primarily on the landscapes found in between them on southern Brazil's highland plateau: the unique Araucaria Forests, the ancient Campos grasslands, the complex mosaic they form, and the iconic Araucaria trees which characterise them all.

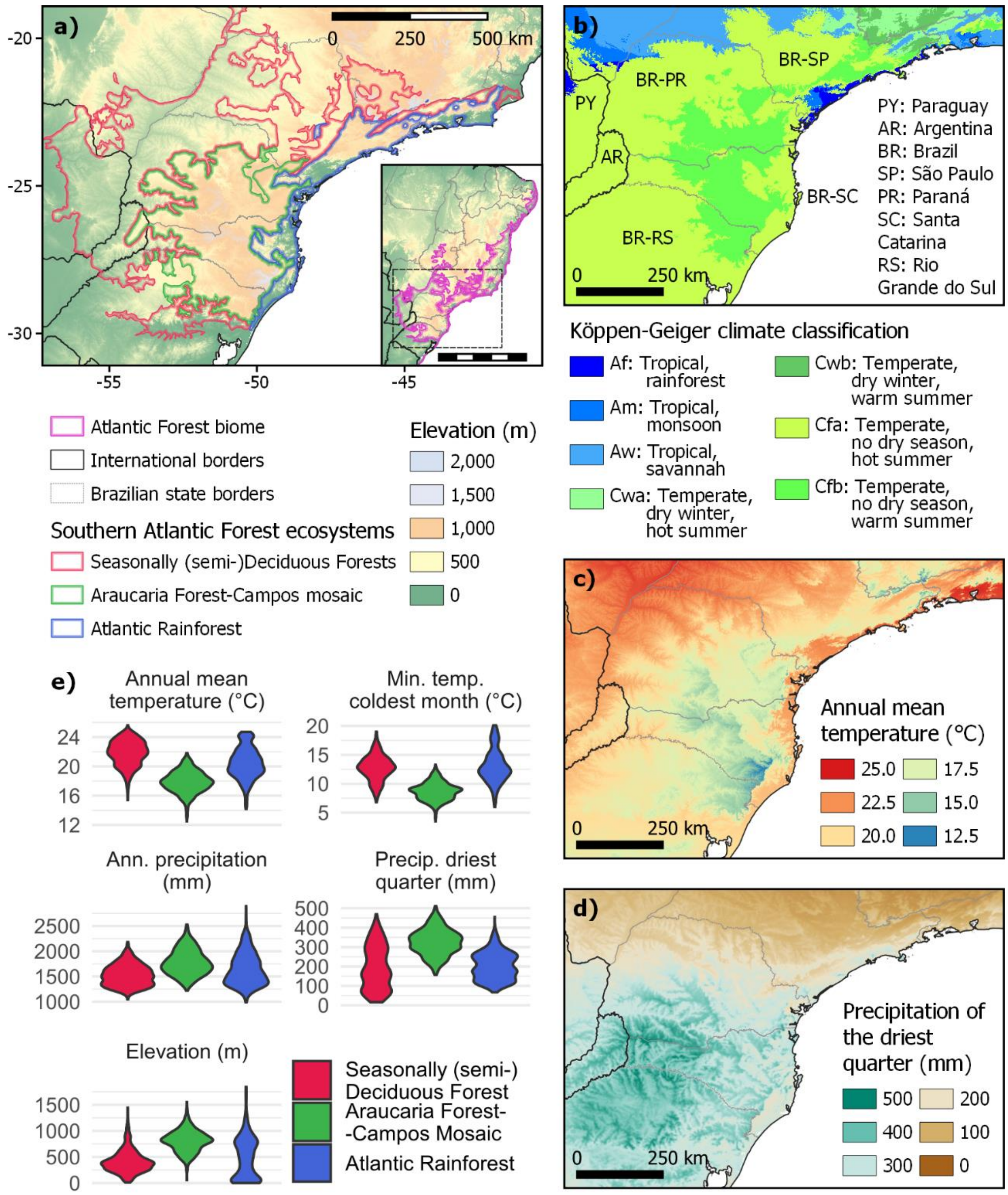

Figure 3-2: Climatic overview of the southern Atlantic Forest [5] *(clockwise from top left): a) elevation and the potential natural extent of Seasonally (semi-)Deciduous Forests, Araucaria Forest-Campos mosaic, and Atlantic Rainforest* (Olson *et al.*, 2001)*; b) Köppen-Geiger climate classifications* (Beck *et al.*, 2018) *and regions mentioned in the text; c) and d) the region's annual mean temperature and dry-quarter precipitation* (Karger *et al.*, 2017)*; e) the ecosystems' relationships to key climatic variables and elevation (based on a random sample of 1,000 points within each).*

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[5] Seasonally deciduous forests and Atlantic coastal rainforests extend further north than depicted here, but under increasingly different (and therefore less relevant) conditions to the more southerly ecosystems in this thesis. Even the more limited extent of seasonally (semi-)deciduous forest shown in Figure 3-2a covers a wider range of climatic conditions than the parts of it most relevant to this research (see Figure 3-2b-e). There is also more nuance to ecosystems' distributions than shown (see e.g. Figure 3-6 for the Araucaria Forest-Campos mosaic), which skews some of the relationships illustrated in Figure 3-2e.

3.3 Araucaria Forests

> *Araucarias in hundreds and thousands. Wondrous sight. [… The] Most interesting forest I have seen in my whole life. Formal, yet variable, and always impressive*
>
> John Muir, (1911a, 1911b).

Figure 3-3: Araucaria Forest in Campos de Jordão, São Paulo state (Ana Taemi via Wikimedia Commons, CC-BY-SA 3.0).

Araucaria Forests (also called Mixed Ombrophilous Forest or Araucaria Moist Forest) are, with Campos, among the most extreme formations in the Atlantic Forest, occupying the biome's coldest and highest-elevation niches and requiring high year-round rainfall (Figure 3-2; Higuchi *et al.*, 2012; Uhlmann *et al.*, 2012; Neves *et al.*, 2017). Araucaria Forests are generally found above 500 m elevation (Figure 3-2), though European records documented them close to sea level in the early 18th Century (Noelli, 2000b) and scattered apparently-natural patches still persist at low elevations south of the highlands (Behling *et al.*, 2016). At the highest elevations in their range (>1,800 m), along the escarpment at the plateau's eastern edge, elements of Araucaria Forests meld with high-altitude Atlantic Rainforest taxa to form cloud forests (Falkenberg and Voltolini, 1993; Bertoncello *et al.*, 2011; Scheer, Mocochinski and Roderjan, 2011; Higuchi *et al.*, 2013; Oliveira-Filho *et al.*, 2014). However, Araucaria Forests are generally more floristically similar to SDF – the two blend together at intermediate elevations and can be considered different expressions of a similar seasonal forest flora (Oliveira-Filho and Fontes, 2000; Oliveira-Filho *et al.*, 2014).

Araucaria Forests are distinguished from other Atlantic Forest formations by their composition. The forest's defining feature is an emergent layer of the characteristic conifer *Araucaria angustifolia* (Bertol.) Kuntze (Araucariaceae; Brazil's Araucaria tree, Paraná or Brazilian pine, or pinheiro) above a lower, angiosperm-dominated sub-canopy and understorey (Klein, 1975; Oliveira-Filho *et al.*, 2014; Souza, 2021). Araucaria Forest composition is heterogeneous throughout its range and varies with a number of factors – longitude, altitude, temperature, river basin, and distance to other forest types (Klein, 1975; Higuchi *et al.*, 2012; Duarte *et al.*, 2014; Gonçalves and Souza, 2014; Oliveira-Filho *et al.*, 2014; Sevegnani *et al.*, 2016) – but is characterised throughout by a mixture of typical tropical trees (e.g. Myrtaceae) and more cold-adapted relicts from the Gondwanan and Andean floras (e.g. Araucariaceae, Podocarpaceae, Winteraceae) (Klein, 1975; Duarte *et al.*, 2014; Oliveira-Filho *et al.*, 2014; Bergamin *et al.*, 2017). The resulting phylogenetic signature is unique, and sets Araucaria Forests apart from the Atlantic Forest's other formations (Duarte *et al.*, 2014). This characteristic compositional balance is maintained by climatic conditions: low-temperature extremes and frequent frosts limit the expansion of warmer-adapted tropical taxa, keeping the Araucaria Forests' more cold-adapted relictual components competitive (Oliveira-Filho *et al.*, 2014; Neves *et al.*, 2017; Souza, 2021).

3.4 Campos grasslands

These fields undoubtedly constitute one of the most beautiful landscapes I have ever travelled since I arrived in America.

Auguste de Saint-Hilaire, 1820, quoted in Nodari (2013).

Figure 3-4: Campos in Parque Nacional de São Joaquim, Santa Catarina state (Mathieu Bertrand Struck via Flickr, CC-BY-NC-ND 2.0).

At the plateau's higher elevations, Araucaria Forests form mosaics with, and eventually give way to, natural Campos grasslands, one of the very few non-woody ecosystems in the Atlantic Forest biome (

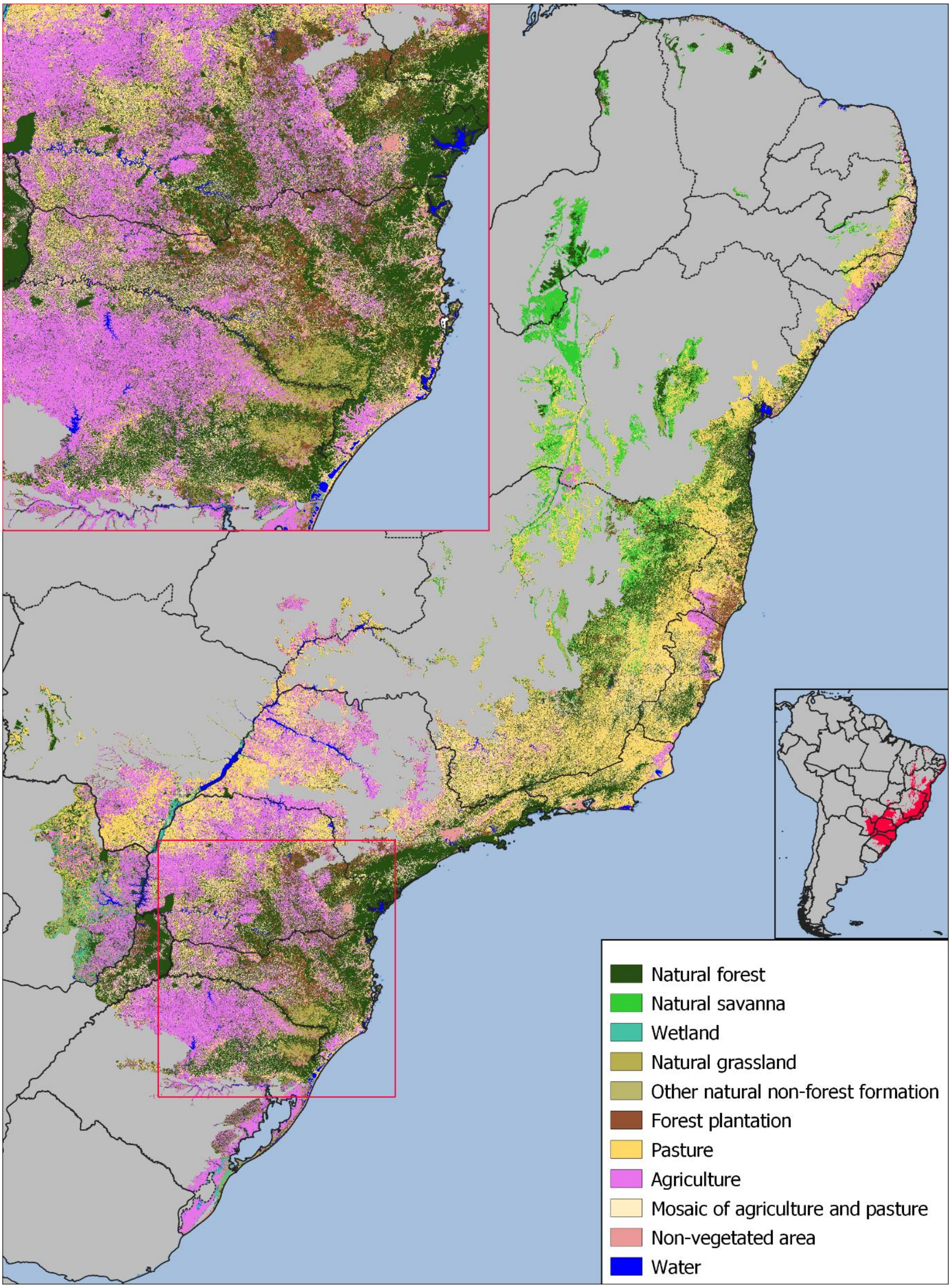

Figure 3-1). Frequently misclassified as savanna or steppe, or considered together with the more southerly lowland Pampas biome, Campos are instead floristically distinct 'old-growth grasslands' (Andrade *et al.*, 2019; IBGE, 2012; Müller *et al.*, 2012; Overbeck *et al.*, 2007, 2015; Veldman *et al.*, 2015). Compositionally, Campos are dominated by grass (Poaceae) species, a significant majority of which employ the C4 photosynthesis pathway; structurally, changes between different grass life forms (e.g. tussock, stoloniferous, prostrate) and between grasses, forbs and shrubs are mediated

by natural or anthropogenic fire and grazing (Overbeck *et al.*, 2018; Andrade *et al.*, 2019). Although they are ancient (some Campos areas have been in place for over 40,000 years) and highly biodiverse (about a quarter of their flora is endemic), Campos are among Brazil's most neglected ecosystems – less studied, protected or appreciated than the forests which surround them (Behling *et al.*, 2004; Iganci *et al.*, 2011; Overbeck *et al.*, 2015; Plá *et al.*, 2020). Despite this, however, it is important to consider Campos and Araucaria Forests together, since the two formations are ecologically intertwined.

3.5 The Araucaria Forest-Campos mosaic

> *The beauty of the landscape and the graceful forms of the surfaces essentially consist of a single motif: the contrast between bright field and dark Araucaria forest. […] the field and the woods in their dynamic game of change.*
>
> Balduíno Rambo, 1948, quoted in Nodari (2013).

Figure 3-5: The Araucaria Forest-Campos mosaic in Parque Nacional de São Joaquim, Santa Catarina state (Mathieu Bertrand Struck via Flickr, CC-BY-NC-ND 2.0).

The Araucaria Forest-Campos mosaic has arisen because, across much of their ranges, the two formations are alternative ecosystem stable states (Beisner, Haydon and Cuddington, 2003; Innes, Anand and Bauch, 2013; Henderson, Bauch and Anand, 2016): contemporary climate conditions favour the encroachment of woody species, but this can be stymied by fire or grazing, to which Campos species are more resilient than tree seedlings (Oliveira and Pillar, 2005; Jeske-Pieruschka *et al.*, 2010; Müller *et al.*, 2012; Blanco *et al.*, 2014; Overbeck *et al.*, 2018; Sühs, Giehl and Peroni, 2020; Sühs *et al.*, 2021). In balance, the result is a landscape with riverine gallery forests and small- to medium-sized forest patches embedded within a grassland matrix, with the two exhibiting sharp ecotonal boundaries (Müller *et al.*, 2012; Matte, Müller and Becker, 2015). Although both Araucaria

Forest and Campos can reach almost complete coverage in parts of the landscape (Figure 3-6), where the two are found together Araucaria Forests often occupy sheltered hillsides and valley slopes or follow river banks, and Campos are generally found in more exposed areas – particularly on plateau tops (Hueck, 1953; Matte, Müller and Becker, 2015; Robinson *et al.*, 2018).

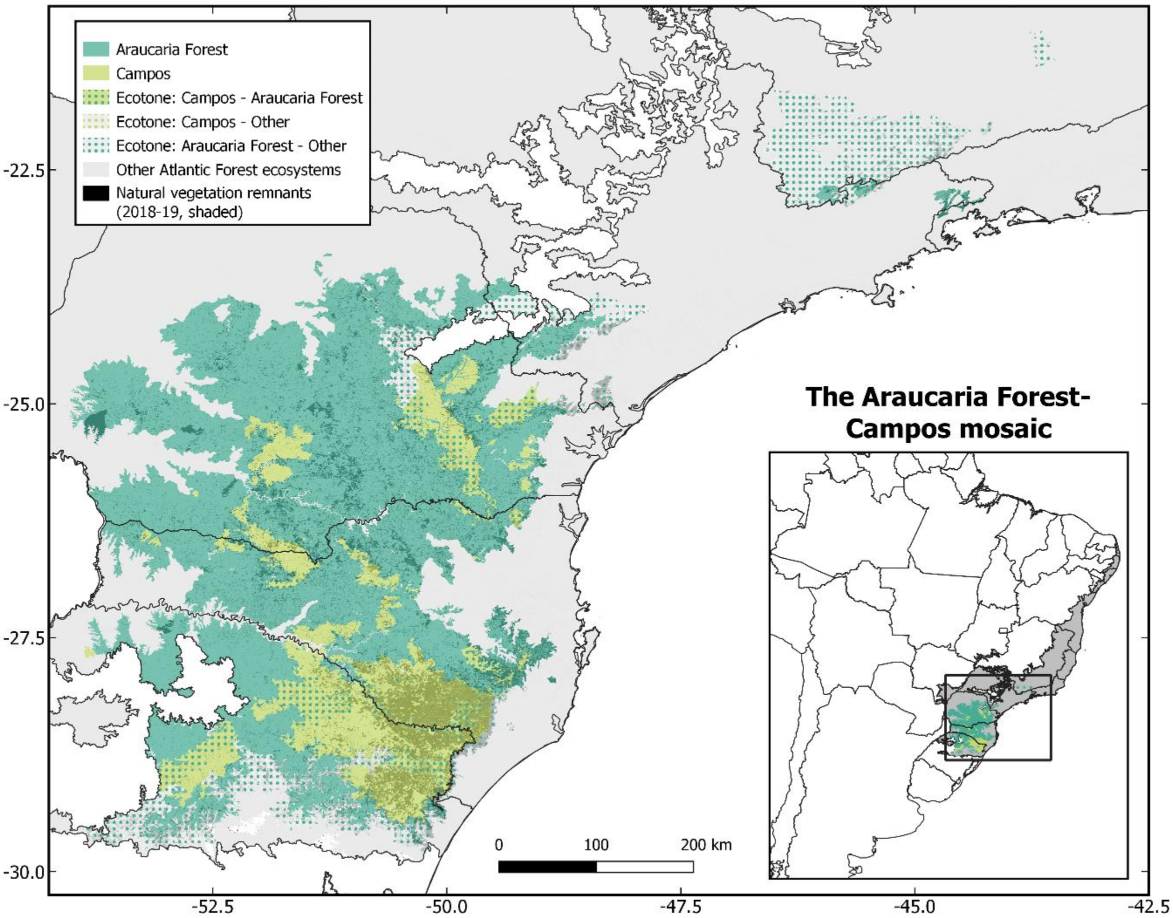

Figure 3-6: The potential and remnant extent of the Araucaria Forest-Campos mosaic in Brazil. Potential natural ecosystem limits are from IBGE (2019), and remnant natural vegetation from SOS Mata Atlântica/INPE (2020). Ecosystems outside Brazil's portion of the Atlantic Forest biome (Pampas, Cerrado, Argentine Araucaria Forest) are not included.

Forest expansion takes place in the absence of disturbances or management, generally by expansion from the edges of existing forest patches, by the gradual increase of shrub coverage in the grassland, or by nucleation, where tree seeds are dispersed into grasslands and eventually form new, increasingly large and structurally complex patches of woody vegetation (Duarte, Dos-Santos, *et al.*, 2006; Duarte, Machado, *et al.*, 2006; Silva and Anand, 2011; Müller *et al.*, 2012; Matte, Müller and Becker, 2015). Nucleation often happens on rocky outcrops (which are less affected by fires) and/or under nurse plants (e.g. isolated trees) which provide perches for seed-dispersing birds and can ameliorate their local microenvironment (Zanini and Ganade, 2005; Duarte, Dos-Santos, *et al.*, 2006; Müller *et al.*, 2012; Korndörfer, Dillenburg and Duarte, 2015; Matte, Müller and Becker, 2015; Sühs, Hettwer Giehl and Peroni, 2018).

When these processes of forest expansion are largely offset by fire and/or grazing, the mosaic remains stable and Araucaria Forest patches grow extremely slowly – perhaps as little as 100 m in 4,000 years (Silva and Anand, 2011). However, when these disturbances are excluded, woody vegetation can encroach onto Campos very rapidly. The first decade without fire or grazing can see exponential increases in woody vegetation cover and modelling suggests that shrubs could completely overtake grassland within 30 years (Sühs, Giehl and Peroni, 2020) – though a 25-year observational study of unmanaged Campos recorded greater stability than this (Oliveira and Pillar, 2005).

3.6 Araucaria trees

> *There were but few other trees that grew to any size besides the pine [Araucaria] itself. Many of these latter were of gigantic dimensions, [...] rising perfectly straight and branchless to within a few feet of their summits, when they spread out into a broad flat head, about 35 or 40 feet in diameter. Seen from a distance the general effect was very curious, the trees looking like a forest of enormous toad stools. They were the lords of the soil in this part.*
>
> Thomas Bigg-Wither, 1878, quoted in Nodari (2013).

Figure 3-7: Araucaria tree in Campos de Jordão, São Paulo state (Adrian Michael via Wikimedia Commons, CC-BY-SA 3.0)

Brazil's iconic Araucaria trees (*A. angustifolia*) characterise the mosaic landscape on southern Brazil's highlands. They are the definitive unifying feature of the variable Araucaria Forests (Oliveira-Filho *et al.*, 2014), and their biological characteristics (adults' thick bark, largely branchless trunks and high crowns) suggest they may have been part of fire-prone Campos grasslands for many millennia (Overbeck *et al.*, 2018). They have significant, multifaceted importance in ecological dynamics, evolutionary history, and human societies.

Araucaria trees play an important role in mediating the interplay between Araucaria Forest and Campos. They are excellent nurse plants – perhaps the best in the mosaic – and facilitate the colonisation of a disproportionate abundance of woody seedlings in their vicinity (Duarte, Dos-Santos, *et al.*, 2006). In part this is because isolated Araucaria trees provide perching spaces for seed-dispersing birds, which leads to elevated seed rain under their crowns, but the trees also significantly reduce vapour pressure deficit and summer air temperatures, increase air circulation, and improve soil fertility (Duarte, Dos-Santos, *et al.*, 2006; Korndörfer, Dillenburg and Duarte, 2015; Souza, 2021). Notably, young Araucaria trees themselves appear to benefit less from these effects than do other taxa: Araucaria saplings occur far more often in open areas than under crowns of conspecific adults, though fire and grazing prevent most from growing to maturity (Sühs, Hettwer Giehl and Peroni, 2018; Sühs *et al.*, 2021). Although they can survive and grow in shaded conditions, Araucaria trees regenerate best in sites with greater light availability following disturbances of the dense angiosperm sub-canopy (Duarte, Dillenburg and Rosa, 2002; Souza *et al.*, 2008; Orellana and Vanclay, 2018; Souza, 2021; Sühs *et al.*, 2021). Even without regeneration, though, established Araucaria populations can remain in place for centuries (large mature trees are probably 300-600 years old at 1.5m trunk diameter), with a handful of giant living individuals demonstrating that the species can reach girths of 2-3 m and heights above 40 m (Paludo *et al.*, 2016; Orellana and Vanclay, 2018; Scipioni *et al.*, 2019).

As well as structuring the plant communities of southern Brazil's highlands and helping dictate their dynamics, Araucaria trees are vitally important to the region's fauna. The principal reason is their seeds, called pinhão, which are consumed by 70 species of mammals and birds (Dénes *et al.*, 2018; Tella *et al.*, 2019; Bogoni, Batista, *et al.*, 2020). These animals act as important secondary dispersal agents for the predominantly barochoric seeds; while scatter-hoarding rodents and other mammals move seeds moderate distances (91% of Araucaria seeds disperse under 250 m), birds facilitate dispersal over the larger distances important for nucleation into Campos (Sant'Anna *et al.*, 2013; Streit, Carlucci and Bergamin, 2014; Tella *et al.*, 2019). Female Araucaria cones can each produce several dozen large (5-7 g) and nutritious pinhão, resulting in an abundant (10s to 100s of kg/ha) seed resource (Souza *et al.*, 2010; Bogoni, Batista, *et al.*, 2020; Bogoni, Muniz-Tagliari, *et al.*, 2020; Souza, 2021). Importantly, pinhão are produced consistently through time, including during periods where other resources are relatively scarce – although variation does occur within and between years, influencing animal populations, its magnitude is relatively slight, and different Araucaria varieties fruit throughout the year (Souza *et al.*, 2010; Corteletti *et al.*, 2015; Adan *et al.*, 2016; Bogoni, Batista, *et al.*, 2020; Bogoni, Muniz-Tagliari, *et al.*, 2020; Souza, 2021). Pinhão are such a reliable, irreplaceable and high-quality food source for so wide a range of southern Brazil's vertebrates that they can be considered a keystone plant resource, with disproportionate importance for animal communities (Bogoni, Muniz-Tagliari, *et al.*, 2020).

Figure 3-8: Pinhão and Araucaria seed cones, Rio Grande do Sul (public domain image)

The ecological importance of Araucaria trees has an exceptionally long history. The Araucariaceae family first emerged in the Jurassic or Triassic (Kershaw and Wagstaff, 2001; Kunzmann, 2007; Panti *et al.*, 2012; Setoguchi *et al.*, 2013; Forest *et al.*, 2018); its species' foliage was probably among the most important food sources for large sauropod dinosaurs (Hummel *et al.*, 2008), whose rise coincided with the evolution of large Araucariaceae seed cones – possibly as protection against seed predation or to exploit these newly available megafaunal seed dispersers (Leslie, 2011; Souza, 2021). Araucariaceae trees were some of the most floristically important constituents of the archaic, dinosaur-structured tropical forests that flourished in South America before the end-Cretaceous mass extinction event (Carvalho *et al.*, 2021). This cataclysm caused the extinction of three quarters of all species on Earth (including all the non-bird dinosaurs), the reduction by 45% of observed Neotropical plant diversity (which, after 6 million years of recovery, reconstituted as modern tropical forests), and the beginning of the decline of Araucariaceae globally (Kunzmann, 2007; Carvalho *et al.*, 2021). With its long evolutionary history and close connection to taxa and environments from deep in geological time, therefore, *A. angustifolia* can be justifiably considered a 'living fossil' (Bennett, Sutton and Turvey, 2018) [6] – it is one of the most evolutionarily distinct gymnosperm, and therefore seed plant, species in the world (Forest *et al.*, 2018).

Its uniqueness and utility have long conferred iconic status upon Brazil's Araucaria tree. As with their ecological role, Araucaria trees' cultural importance has extremely deep roots – they have probably been important to people for as long as their surroundings have been inhabited (Noelli, 2000a). The highest level in Kaingang shamanic territory – the domain of glory, where God lives – is

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[6] As discussed by Bennett *et al*. (2018), 'living fossil' is a somewhat contentious label – even Charles Darwin, who coined it, called it 'fanciful'. (Among more technical objections, if traced back far enough the evolutionary history of all extant taxa spans the same 4.3-billion-year period.) The term is generally used to imply that a taxon has a long evolutionary history with apparently slow/limited changes, and can provide insights into much more ancient, potentially extinct, life forms (Bennett, Sutton and Turvey, 2018). Although Bennett *et al*. (2018) did not quantify the 'living fossil-ness' of the Araucariaceae specifically, this label is warranted for *A. angustifolia*: on the authors' metric, gymnosperms as a whole rank in the top 2-3% of studied seed plant taxa, and *A. angustifolia* is the 16th most evolutionarily distinct extant gymnosperm species (Forest *et al.*, 2018).

characterised and named after Araucaria trees (Réus Gonçalves Da Rosa, 2005); living Kaingang might reach it by climbing Araucaria trees (Réus Gonçalves Da Rosa, 2005). Araucaria trees "could be considered the ritual object par excellence" in Kaingang tradition (Fernandes and Piovezana, 2015, p. 120), having a central role in the Kiki/Kikikoi funerary ritual – itself "the centre of Kaingang religious life" (Fernandes and Piovezana, 2015, p. 117): an Araucaria trunk forms the trough (konkéi) for the crucial kiki drink, Araucaria knots are essential for keeping alight the ritual bonfires, and their ashes are used to paint the faces of individuals from the Kamé moiety (Fernandes and Piovezana, 2015). Traditionally, the Xokleng definition of a year was "one period of no pine nuts [pinhão]" (Henry, 1964, p. 68); Araucaria trees structured Xokleng territories and fruiting drove their seasonal movements on pinhão-collecting expeditions (Moura, 2021). Prior to 'pacification' [7], pinhão formed a crucial part of Indigenous peoples' diets, and were apparently traded from the highlands to the coast, hundreds of kilometres away (Wesolowski *et al.*, 2010; Corteletti *et al.*, 2015; Scheel-Ybert and Boyadjian, 2020).

Figure 3-9: In 2018, a Kaingang and Guarani community action planted 4,000 Araucaria seedlings on re-occupied Indigenous land whose official demarcation had been stalled for 14 years, to protest government inaction, restore the landscape, and symbolically mark their claim to the land (Conselho Indigenista Missionário/Kaingang Community)

In contemporary non-Indigenous society, Araucaria trees continue to be highly valued. Araucaria trees are the most used native plant species in Paraná and Santa Catarina states, primarily for food, and pinhão collectors recognise several sub-specific varieties (Adan *et al.*, 2016; Serviço Florestal Brasileiro, 2018a, 2018b; Quinteiro, Alexandre and Magalhães, 2019). Annual pinhão extraction in Brazil averaged 4,782 tonnes between 1986 and 2010, rising to 9,031 tonnes per year in 2011-2020 (IBGE, 1986-2021). In parts of the highlands, pinhão harvesting is connected to traditionally managed landscapes, which, though variable, generally involve extensive livestock grazing under Araucaria Forest canopies (Mello and Peroni, 2015; dos Reis *et al.*, 2018; Zechini *et al.*, 2018).

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[7] 'Pacification' is a misleading term. Southern Brazil's non-Indigenous society secured for itself peace from aggressive Indigenous resistance to their presence by inflicting violence – mass murder, abduction, devastating disease epidemics, and the coercive removal of Indigenous groups from their traditional territories (Urban, 1985; Hoffmann, 2011; Fernandes and Piovezana, 2015; Fernandes and Góes, 2018).

Notably, however, while Araucaria trees define these landscapes and the pinhão they produce are appreciated, these areas' principal commercial value is derived from cattle rearing and erva-mate (*Ilex paraguariensis* leaves) for chimarrão tea, whose production is ten times more valuable than pinhão (Mello and Peroni, 2015; dos Reis *et al.*, 2018). Instead, for most of the last two centuries, the most valuable commercial exploitation of Araucaria trees has been for timber and other wood products – and this, more than almost any other factor, has defined the highlands' recent history.

3.7 The highlands' colonial history

Frighteningly, the Araucaria forests are being reduced. Loggers throw themselves on them from all sides. The environment is transformed, the living conditions for the pine tree disappear. "ARAUCARILANDIA" is losing its last children. [...] Within a few decades, perhaps, only the memory of these forests will remain.

Frederico Hoehne (1930).

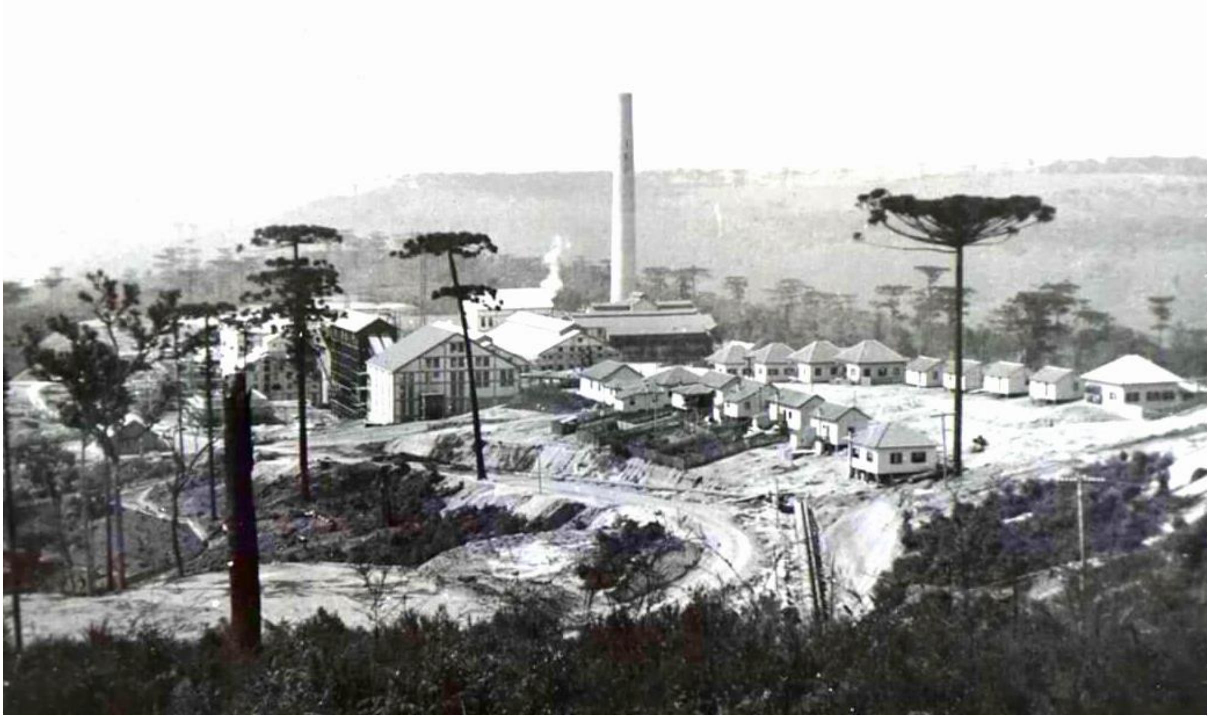

Figure 3-10: Klabin paper and cellulose mill, Telêmaco Borba, Paraná, 1946 (public domain image)

The intense, direct impacts of European colonisation were felt considerably later in southern Brazil's highlands than in many other parts of South America. During the late 17th and early 18th Centuries, drovers grazed cattle in Campos areas and travelled between São Paulo and the Jesuit missions south-west of the highlands, but military expeditions in Paraná in the 1770s encountered and noted widespread evidence of Indigenous occupation in landscapes that they nevertheless characterised as 'abandoned' or 'empty' (Fortkamp, 2009; de Carvalho, 2010; Fernandes and Góes, 2018; Moura, 2021) [8]. In the government's eyes, Santa Catarina's plateau region was officially unpopulated until the settlement of Lages was founded in 1766, and still had fewer than 2,500 inhabitants by 1833 (Peres, 2009). By 1852, there were no Indigenous settlements around Lages – the area's Kaingang

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[8] As well as witnessing frequent fires (many possibly funerary) and smoke, soldiers regularly encountered large settlements, some of which housed over four hundred people, saw fields planted with corn, and travelled along already-established routes between villages (Mota, 2008; Moura, 2021).

communities had withdrawn to the forests as a result of settlers "hunting them like animals, with the aim of catching them and captivating their children", according to the Lages police chief, though their numbers were still thought to be "considerable, for traces of them appear[ed] everywhere" (Peres, 2009, pp. 124, 126). Even as late as 1872, the European population in southern Brazil's Araucaria region was only about 182,000 people, fewer than 13,000 of whom lived in Santa Catarina (de Carvalho, 2010). This point, however, marked the onset of increasingly intense and unsustainable land use change on the highlands (Peres, 2009; de Carvalho and Nodari, 2010).

One of the principal drivers of the habitat conversion which followed was an influx of European migrants, predominantly from Germany and Italy, sparking more extensive agriculture and forest clearance (de Carvalho and Nodari, 2010; Nodari, 2016). Until about 1910, most Araucaria felling was small-scale and for primarily local uses, and the forests were considered to be practically infinite (de Carvalho and Nodari, 2010; Nodari, 2016). In the late 19th and early 20th Centuries, the Brazilian government began concerted efforts to concentrate Indigenous people in designated territories, with the effect that – exacerbated by attacks on [9], and disease outbreaks among [10], unconfined groups – more land became more readily available for colonisation (Peres, 2009; Fernandes and Piovezana, 2015; Fernandes and Góes, 2018).

After about 1910, a range of connected factors conspired to drastically increase the pressure on Araucaria forests. Railway lines linking Rio Grande do Sul and São Paulo opened up for exploitation previously inaccessible forests, facilitated the wider trade of their timber, and encouraged further European migration and population growth; the First World War also restricted Brazil's ability to import timber from abroad and focused attention on the country's own forest resources (de Carvalho, 2010; de Carvalho and Nodari, 2010). The Araucaria Forests no longer seemed infinite – Frederico Hoehne, travelling through in 1930, described the 'frightening' pace of destruction he witnessed and predicted an impoverished future for the highlands' natural landscape (Hoehne, 1930; quoted above). Yet within a decade the situation would become even worse.

From 1940, still greater population and economic growth in Brazil – and demand for resources to rebuild Europe following the Second World War – fuelled further increases in Araucaria timber extraction, supported by technological advances (de Carvalho and Nodari, 2010). In the 1950s, Kaingang lands held some of the last intact Araucaria Forests, but even these became extensively exploited in the following decade or two (Fernandes and Piovezana, 2015). Mounting official concern about the forests' future led to increasing efforts to monitor, regulate and mitigate their

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[9] Zoologist Hermann von Ihering, director of the São Paulo state museum, wrote, in 1906, "The present Indians of S. Paulo do not represent an element of labour and progress. As in the other parts of Brazil no serious and continuous labour can be expected of the civilized Indians and as the savage Caingangs are obstructing the colonisation of the forest regions inhabited by them, no other final result seems possible than that of their extermination." (Ihering, 1906, p. 42).

[10] Wãñpõ Payà was probably 16 or 17 in 1915, when efforts were underway to 'pacify' Xokleng groups like his: "It was at this point that the Indians began to get sick. First Zeca died. Everyone began to get grippe. They decided to divide up because of the sickness. This was the first time disease had come and many died. [...] Nobody in our group was really sick, except for Mõgñã, my [other] father, who later died. Zàgpope, son of Gakrã, died, Nil Paci, Wãnẽglõ, and Wãñpõ (another son of Gakrã) died. Uglõ (Gakrã's wife), Wãñẽki, and Zeca died. Zàgcò, Yacag, another Zàgcò, and Yagnan Ãgrè all died. Mõgñã, my father, died too. Cãtag, Wãñluñ, and Mu all died. Wày died too. And Kaga, Wãñkuklõ, Kowi, Kagnan, and Pankle died. The wife of Mõkònã died, and then Mõkònã died. Zeñkug died as well. And this was only among the adults. Many, many more children died." (Urban, 1985, p. 230). The horrific toll of these outbreaks fractured the groups' ritual practices: "At this point, no one was holding the [period of] seclusion [for the spouse of the deceased], because the spouse, in general, was sick as well, and we were afraid to leave her in seclusion, for fear she would die." (Urban, 1985, p. 230).

exploitation, but from the mid-1960s a pivot to exotic *Pinus* plantations and drastic declines in Araucaria exploitation marked "the end of the Araucaria era for the logging industry" (de Carvalho and Nodari, 2010, p. 723). Wood products from *A. angustifolia* are still traded in greater volumes than almost any other Brazilian species, but Araucaria Forests are now an Endangered ecosystem, at very high risk of collapse, and experiencing some of the Atlantic Forest's worst trends for forest cover loss and increasing isolation (Ferrer-Paris *et al.*, 2019; Brandes *et al.*, 2020; Rosa *et al.*, 2021) *A. angustifolia* itself is Critically Endangered – one of the most evolutionarily distinct and globally endangered tree species on the planet (Thomas, 2013; Forest *et al.*, 2018).

Quantifying the losses from Araucaria's century of destruction is difficult. Surveys of southern Brazil in 1949/50 found the region's Araucaria 'resource' was 298 million trees (Nodari, 2016), untold millions of which were felled in the following three decades, which saw Brazil export at least 24.3 million m^3 of sawn conifer (overwhelmingly Araucaria) timber (Figure 3-11; de Carvalho and Nodari, 2010).[11] Of 'original' Araucaria Forest areas which survived the 20th Century minimally impacted, as little as 1-4% remain (see de Carvalho, 2010; de Carvalho and Nodari, 2010, and citations therein). Most studies using satellite imagery have produced higher estimates of natural vegetation cover than this (Figure 3-12), though Araucaria Forests have been the focus of surprisingly few such forest cover estimates. Synthesising data from various sources (de Carvalho, 2010; de Carvalho and Nodari, 2010; IBGE - Instituto Brasileiro de Geografia e Estatística, 2018; Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais, 2020; Souza *et al.*, 2020) natural forests of various quality cover around 19-36% of the Araucaria Forest region, but high-quality areas cover no more than about 5%, and exceedingly few patches – if any at all – have survived relatively unscathed from the 19th Century (Figure 3-12).

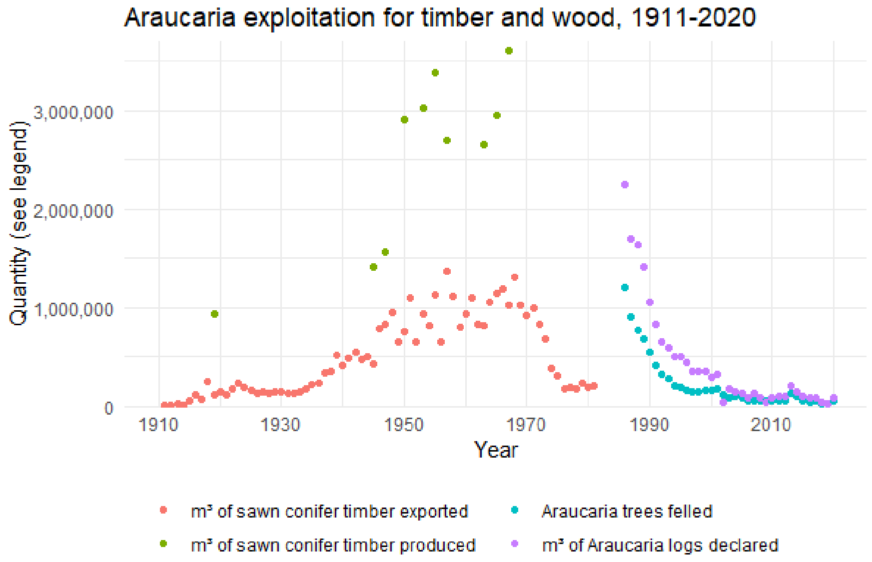

Figure 3-11: Data on the exploitation of Araucaria trees for timber and wood, 1911-2020. Data from de Carvalho & Nodari (2010; sawn timber production and exports 1911-1981) and IBGE (1987-2021; Araucaria trees and logs

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[11] Estimates using the data in Figure 3-11 could plausibly cover an order of magnitude. If each Araucaria tree produced an average of 1.5 m^3 of sawn timber (between 1986-2020 a felled Araucaria tree produced 1.96 m^3 of log wood on average), 1950-1981's potential 72.9 million m^3 sawn conifer timber production (24.3 million m^3 exports x 3 to scale up to production) would equate to 48.6 million trees (16.3% of the 1949/50 population). If 1.5-2 million Araucaria trees were felled in 1981 (extrapolating the 1986-2020 trends) when sawn conifer timber exports were ca. 200,000 m^3, then scaling up to cover the timber extracted after 1950 would equate to 182-243 million trees (61.1%-81.5% of the 1949/50 population).

1986-2020). Much of the more historic data is patchy, especially for timber production; export data will be incomplete; and from the 1970s conifer timber includes increasing contributions from Pinus plantations (for more caveats, see de Carvalho and Nodari, 2010).

Many of the same 20th-Century trends which conspired to decimate southern Brazil's Araucaria Forests also played roles in the reduction of Campos. Increasing, and increasingly prosperous, settler populations required expanding agricultural and grazing production; the World Wars opened opportunities for Brazilian producers to enter valuable markets for timber and crops that had previously been dominated by Europe; and technological innovations helped southern Brazil's produce reach those markets (Overbeck *et al.*, 2007; Rossi and Nodari, 2012). Importantly, too, the economic demise of Araucaria logging left landholders in need of new ways of ways to earn money – with stocks of Araucaria trees and other valuable timber species depleted, working with or maintaining native forest ceased to be financially worthwhile, so many pivoted to extensive crop monocultures (e.g. soya) or used government incentives to afforest grasslands with exotic tree (*Pinus, Eucalyptus*) plantations (Overbeck *et al.*, 2007; Rossi and Nodari, 2012; Nodari, 2016). The large and comparatively recent land use changes in Campos are reflected in Figure 3-12 – between 1985 and 2018, grassland areas declined far faster than Araucaria Forest (Souza *et al.*, 2020). In the 33 years covered by these MapBiomas data, 34% of natural grassland in Campos areas – as well as 60% of ecotonal areas' natural grassland – was lost.

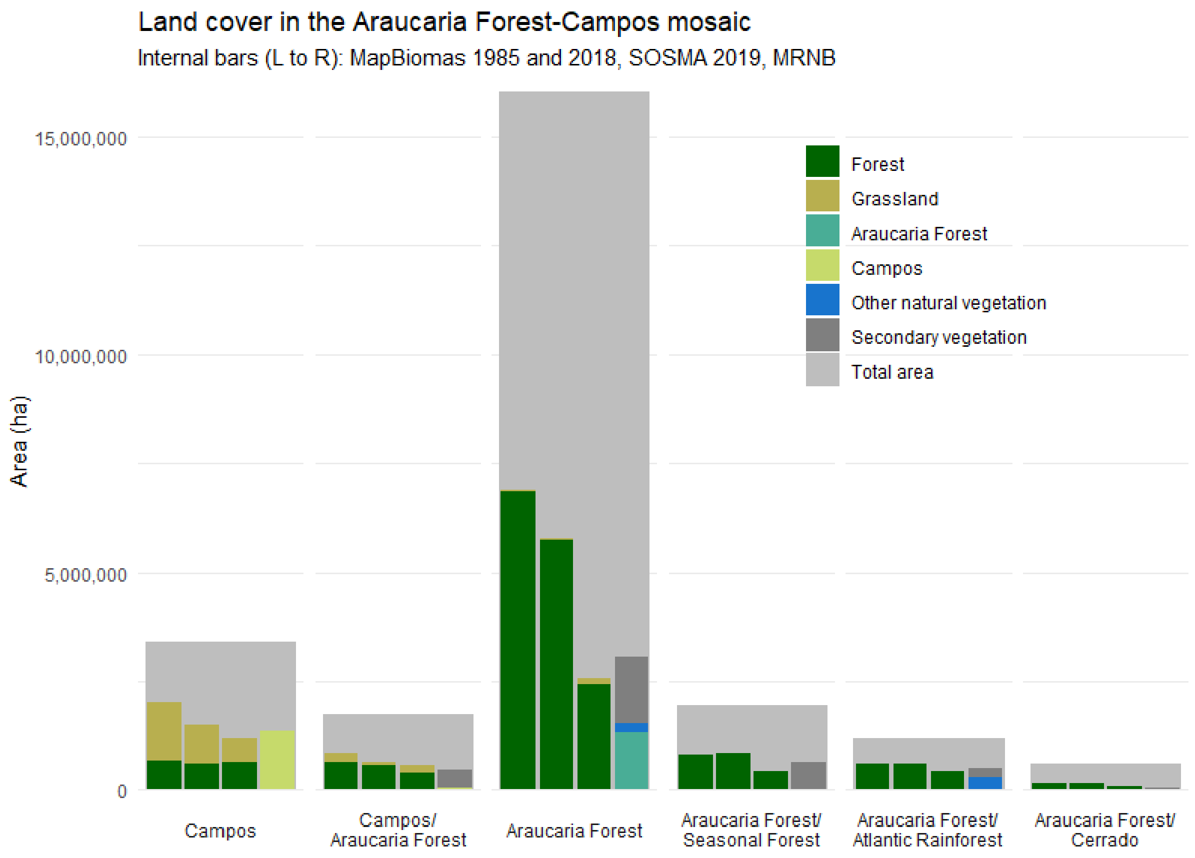

Figure 3-12: Potential and actual natural vegetation coverage in southern Brazil's highlands. MapBiomas (collection 4.1; Souza et al., 2020; 1985 at far left, 2018 at second left) includes more human-altered forest areas than SOS Mata Atlântica/INPE (2020; right of centre); this in turn combines vegetation of different successional

stages/maturity, which are somewhat separated out in Mapeamento de Recurso Naturais do Brasil (IBGE - Instituto Brasileiro de Geografia e Estatística, 2018; far right).

Reductions in natural vegetation cover represent only part of the harm caused to the Araucaria Forest-Campos mosaic in the last 150 years, however: they suffer diminished structural diversity and homogenised species composition, large trees have been disproportionately removed, and the forest's considerable carbon storage capacity is significantly eroded (Souza, 2007; Scipioni *et al.*, 2019; Sevegnani *et al.*, 2019; de Lima, Oliveira, *et al.*, 2020; Oliveira and Vibrans, 2020). Non-logging disturbances, which include overgrazing and trampling from cattle, excessive fire use, and mowing of the forest understorey, all suppress regeneration (Oliveira and Vibrans, 2020; Souza, 2021). This problem is particularly acute for Araucaria trees: because mature trees are legally protected and therefore difficult to fell within the law, many landowners kill Araucaria seedlings to avoid restrictions on how they use their land (Vibrans *et al.*, 2011; Mello and Peroni, 2015; Adan *et al.*, 2016). Overgrazing and excessive fire use, along with exotic species invasions, are also impacting Campos vegetation: in Rio Grande do Sul, 45-69% of natural highland grasslands have been converted to other land uses, and an additional 5-8% are degraded, with impacts on plant species composition, soil properties, and ecosystem functioning (Andrade *et al.*, 2015). The management balance is precarious, though, because, conversely, the exclusion of grazing and fire also leads to grassland degradation and loss to woody encroachment (Overbeck *et al.*, 2007, 2015; Andrade *et al.*, 2015, 2016; de Oliveira Portes, Safford and Behling, 2018; Sühs, Giehl and Peroni, 2020).

The negative effects of human disturbance and degradation on Araucaria Forests and Campos are predominantly combatted through the use of legally protected areas, though these cover a proportionally smaller area of the mosaic (0.65%) than any other major ecosystem in the Atlantic Forest biome (Ribeiro *et al.*, 2009; Tagliari, Levis, *et al.*, 2021). Strictly protected areas effectively conserve Araucaria Forest cover, biodiversity and biomass, and shelter forest remnants which are closer to their fully natural state than unprotected ones (de Lima, Oliveira, *et al.*, 2020; Oliveira and Vibrans, 2020; Tagliari, Levis, *et al.*, 2021). However, they can often be detrimental to Campos conservation, since their management – formulated with forests as the focus – generally excludes the anthropogenic fire and grazing the grasslands require (Overbeck *et al.*, 2007, 2015; Andrade *et al.*, 2015, 2016; de Oliveira Portes, Safford and Behling, 2018; Sühs, Giehl and Peroni, 2020). An alternative paradigm to such top-down conservation measures views the ecosystems as socio-ecological systems with human populations integrated within them (Overbeck *et al.*, 2015; Tagliari, Levis, *et al.*, 2021). Such collaborative management, and the positive feedbacks it could engender, might increase the resilience of Araucaria Forests to future disturbances and improve the management of Campos grasslands (Overbeck *et al.*, 2015; Tagliari, Levis, *et al.*, 2021). There is evidence that traditionally managed Campos and Araucaria Forest landscapes can conserve Araucaria genetic diversity about as effectively as legally protected areas, and they also provide economic incentives for maintaining natural vegetation cover, so increasing the integration of people into conservation measures for these ecosystems could have merit (Medina-Macedo *et al.*, 2016; dos Reis *et al.*, 2018; Zechini *et al.*, 2018).

People also have a critical role in conserving the Araucaria Forest-Campos mosaic itself – even over and above its component ecosystems – because the mosaic results from a management-mediated equilibrium between forest and grassland. Its continuation into the future, therefore, is vulnerable to changes in human management and the feedbacks which can result (Beisner, Haydon and Cuddington, 2003; Blanco *et al.*, 2014; Henderson, Bauch and Anand, 2016). Strong human influence makes it more difficult for the two ecosystems to co-exist, and people's perceptions of the value of Araucaria Forest, Campos, and the anthropogenic land cover types which replace them, have significant impacts on the mosaic's stability and expression (forest, grassland, mixed, transformed) (Innes, Anand and Bauch, 2013; Henderson *et al.*, 2016). Retaining the contemporary and historically known Araucaria Forest-Campos mosaic into the future is very far from guaranteed (Henderson, Bauch and Anand, 2016).

Figure 3-13: Araucaria tree in cultivated field, Ponta Grossa, Paraná (Luiz Maffei via Wikimedia Commons, CC-BY-SA 4.0)

3.8 Looking to the future

The ecosystems of the southern Atlantic Forest have suffered significantly in recent history, but the future – at almost all timescales – seems unlikely to offer any significant relief. A major imminent and mounting threat is anthropogenic climate change, which has been driven by many of the same short-sighted and unsustainably exploitative processes which catalysed the destruction of the Araucaria Forest-Campos mosaic. The magnitude and pace of these climate changes exceed anything that has happened since millions of years before *Homo sapiens* evolved and there is a good chance their effects will continue to be felt for millennia to come (Tierney *et al.*, 2020).

Brazil's climate has warmed significantly even since the late 20th Century as a result of anthropogenic greenhouse gas emissions, with southern Brazil experiencing temperature rises of about 0.25°C per decade and seasonally variable disruptions to previously stable rainfall regimes (de Barros Soares *et al.*, 2017). These changes are predicted to continue – and even accelerate – in the decades to come, across a range of emissions scenarios (Chou *et al.*, 2014). A worst-case emissions scenario would see large-scale reassortment of southern Brazil's climate types by the end of the 21st Century, including the near-total transformation or loss of the temperate, relatively cool and constantly moist conditions to which southern Brazil's highland species and ecosystems are adapted (Figure 3-14; Beck *et al.*, 2018).

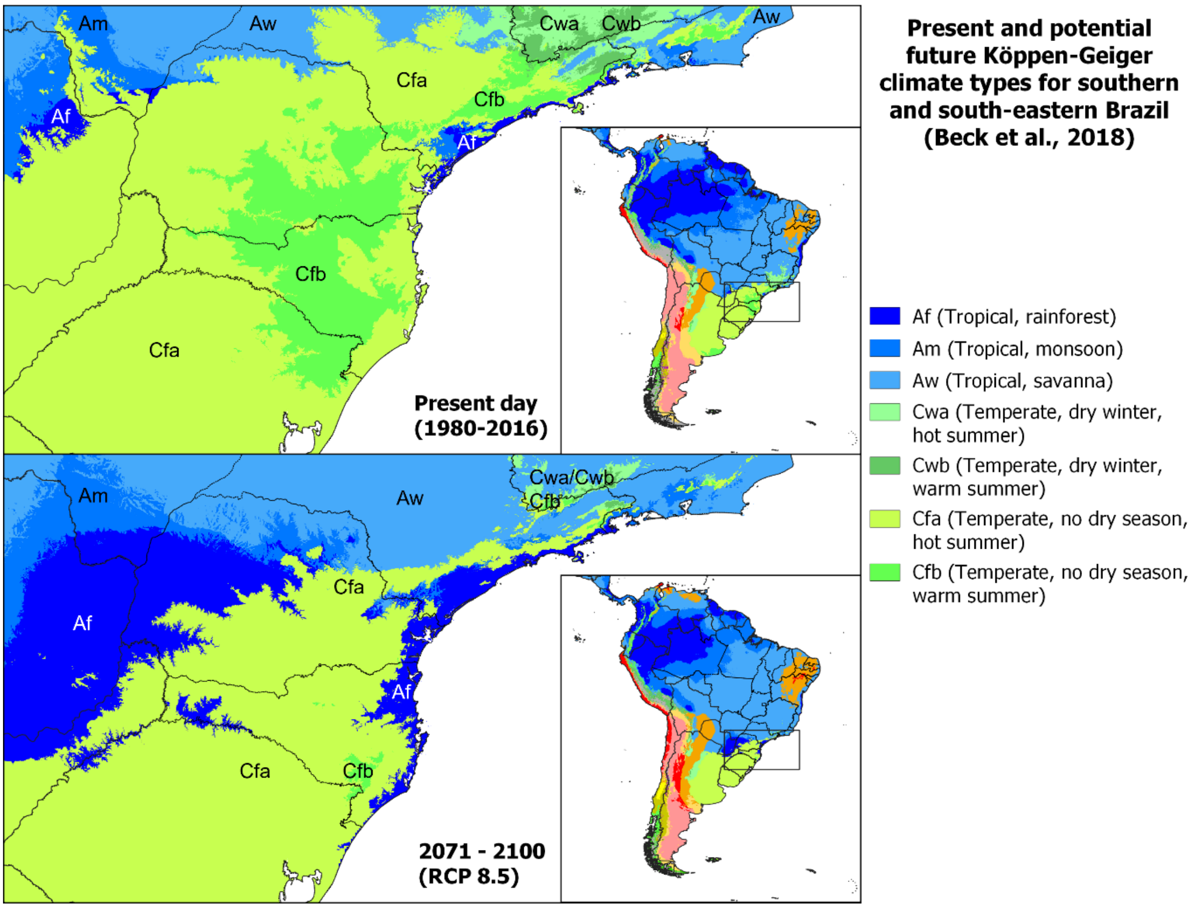

Figure 3-14: Köppen-Geiger climate types in southern and south-eastern Brazil in the present day and late 21st Century, under a pessimistic climate change scenario (RCP8.5). Data from Beck et al. (2018).

Logically, these changes are likely to have major effects on Araucaria trees and the ecosystems they form. But perhaps surprisingly, given that climate change is one of the most significant challenges facing the biosphere, that well-established tools and data exist to explore its impacts, and that Araucaria trees are an iconic, culturally valuable and obviously vulnerable species, the impacts of climate change on *A. angustifolia* had barely been examined when I started my PhD. Only two studies had then been published – one (Wrege *et al.*, 2009) was very brief (only three pages of text) and not peer-reviewed [12], and the other (Wrege *et al.*, 2016) was published in a potentially predatory journal [13]. Both studies used now-outdated ecological niche model (ENM) techniques and, among other quality issues (especially for Wrege *et al.*, 2016), lacked important information that would have allowed their approach and results to be properly evaluated. An additional, significantly better, study had been conducted, but was then unpublished (Bergamin, 2017 - unpublished PhD thesis; Bergamin *et al.*, 2019 - published paper).

However, despite representing a marked improvement over the previous work in this area, the latter study did not consider the potential intersection of future climate changes and historical habitat loss, nor the potential mitigating effects of small-scale topographic features on broader-

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[12] Unasylva's guide to authors makes no mention of any peer review processes, and submissions appear to require invitation: https://www.fao.org/forestry/unasylva/8579/en/.

[13] Horizon Research Publishing (http://www.hrpub.org/) features in Beall's list of potential predatory journals and publishers (https://beallslist.net/); Environment and Ecology Research is not indexed in the Directory of Open Access Journals (https://bit.ly/3l7Yh6d) and was only indexed by Scopus in 2020 (https://www.scopus.com/sourceid/21101037318).

scale climate trends. As discussed above, land use change is among the most important factors dictating Araucaria's contemporary distribution – spatially non-random (Figure 3-6) and a clear real-world constraint on the species' ability to respond as predicted to climate changes, its inclusion should add significant value to such modelling studies. Similarly, fine-scale topography is an important factor to consider, both because it is widely acknowledged that species do not actually experience climatic conditions at the relatively coarse scales represented in gridded climate data (Ackerly *et al.*, 2010; Ashcroft, 2010; Dobrowski, 2011; Keppel *et al.*, 2012; Hannah *et al.*, 2014; Lenoir, Hattab and Pierre, 2017; see Section 1 above), and because Araucaria trees also appear to preferentially occur in certain, generally more sheltered, microenvironments in parts of their range (Hueck, 1953; Robinson *et al.*, 2018). Neither land use change nor potentially microrefugial topography are commonly included in studies forecasting the ecological impacts of climate change.

This was the context for the research in Chapter 1 (Wilson *et al.*, 2019), which became the first published, peer-reviewed study to examine the effects of 21st-Century climate changes on *A. angustifolia*, while also evaluating the exacerbating and mitigating effects of historic land use change and fine-scale topography. Several other studies have since been published on this general question (Bergamin *et al.*, 2019; Castro *et al.*, 2020; Marchioro, Santos and Siminski, 2020; Trindade, Santos and Artoni, 2020; Saraiva *et al.*, 2021; Tagliari, Vieilledent, *et al.*, 2021; Lima *et al.*, 2022), corroborating our broad-scale findings and, in some cases, also acknowledging the importance of past habitat loss in the context of a changing climate (Marchioro, Santos and Siminski, 2020; Tagliari, Vieilledent, *et al.*, 2021). To my knowledge, though, ours remains the only study to have examined the potential effects of microrefugia on Araucaria trees or any component of the Atlantic Forest.

In general, how the Atlantic Forest's flora is likely to be affected by climate change has been relatively little investigated, with few studies available early in my PhD – though research on these questions is continuing (Colombo and Joly, 2010; Zwiener *et al.*, 2018; Bergamin *et al.*, 2019; Esser, Neves and Jarenkow, 2019; Trindade, Santos and Artoni, 2020; Gasper *et al.*, 2021; Leão *et al.*, 2021). An early study (Colombo and Joly, 2010) found 'alarming' reductions and southward shifts in species' potential occurrences, but southern Brazil's ecosystems (especially those on the highlands) were omitted. Additionally, the climate data used (particularly future projections) were extremely coarse and, although the study examined individual species, the different communities they form and their potential reassortment was not considered. Bergamin *et al*. (2019) did study the responses of several Araucaria Forest taxa, but considered them together and did not evaluate how their changing ranges may interact with each other or with those of species from other Atlantic Forest ecosystems. Zweiner *et al*. (2018) modelled species from across the biome, but considered compositional change in the abstract, dealing primarily with questions of alpha and beta diversity rather than ecosystems' floristic identity. Esser *et al*. (2019), by contrast, did examine how future climate change might affect the gradients of floristic composition along which the Atlantic Forest's different ecosystems are arrayed. Surprisingly, they found that high elevation/latitude forest (their category encompassing Araucaria Forest, Campos and Pampas) was the ecosystem least affected by predictions of future climate change, barely changing between timepoints or emissions scenarios – a finding which ran contrary to the authors' own expectations as well as those from other data (e.g. Figure 3-14), and which is not clearly explained in the paper. It could feasibly be because increasing rainfall in the future offsets rising temperatures, or it might have been a processing artefact (L. F. Esser, pers. comm.).

The effects of future climate change on the composition of southern Brazil's ecosystems remained an open question, therefore, when I undertook the research in Chapter 3 (Wilson *et al.*, 2021). As noted by Esser *et al*. (2019) and discussed above, the floristic gradients within and between the southern Atlantic Forest's vegetation are important but complex, and are likely to become more so in the future. Understanding how and where they are likely to change, and whether they are likely to generate new plant communities, is a crucial prerequisite for their conservation in the future. But understanding how these future changes sit in a long-term context is also valuable (Bergamin *et al.*, 2019; Trindade, Santos and Artoni, 2020) – after all, episodes in their past might provide helpful insights into their potential futures.

4 Plants and people in southern Brazil's past

This section provides a longer temporal context for the (relatively) recent histories, present and potential futures of southern Brazil's ecosystems discussed above. Considering events primarily from the late Pleistocene (earlier data are extremely sparse), what follows is divided broadly into three sections: palaeoclimates (introducing the region's main climatic features and our understanding of their variation over past millennia), palaeoecology (how the distributions and compositions of southern Brazil's contemporary ecosystems have developed through time), and archaeology (focusing on characteristics and developments in the southern Jê cultures, and their potential involvement with the region's vegetation history). Inevitably, however, these sections overlap – to effectively understand southern Brazil's natural history (with emphasis on the 'history'), all three are essential.

4.1 Climates and palaeoclimates

Most of southern Brazil currently experiences humid subtropical climates without dry seasons, with the principal distinctions across space coming from maxima and minima of summer and winter temperatures, respectively (Alvares *et al.*, 2013; Beck *et al.*, 2018). Genuinely tropical conditions are generally rare in my study area (Figure 3-14). Temperatures are predominantly linked to latitude and elevation (Figure 3-2), but the region's rainfall patterns are more complex, depending on a number of interacting climatic features which affect much of South America (Garreaud *et al.*, 2009; Prado *et al.*, 2013; Smith and Mayle, 2017). Two key features are the Inter-Tropical Convergence Zone (ITCZ) and the South Atlantic Convergence Zone (SACZ; Figure 4-1). The ITCZ is an east-west oriented band of high rainfall and minimum pressure where trade winds converge over the tropical oceans (Garreaud *et al.*, 2009). The SACZ, which lies further south, is South America's main convective system – a diagonally (north-west to south-east) oriented region of year-round rainfall that extends from southern and south-eastern Brazil into the South Atlantic (Garreaud *et al.*, 2009; Prado *et al.*, 2013).

Seasonal variations in the ITCZ and SACZ combine to drive the rainfall of much of Brazil. During austral summer (December, January and February), solar heating of the Amazon basin increases its temperature and leads to the development of an area of low pressure. At the southernmost point in its seasonal migration the ITCZ feeds moisture into the system and strong, low-level winds turned southward by the Andes form the South American low level jet (SALLJ) carry it south from the Amazon to the intensified SACZ (Cruz *et al.*, 2005; Garreaud *et al.*, 2009; Prado *et al.*, 2013; Flantua *et al.*, 2015). This greater summertime rainfall over continental South America is known as the South American Summer Monsoon (SASM), and is the principal source of precipitation for southern Brazil during late spring and summer. At other times of the year, when the ITCZ is further north, the SACZ less intense and the SASM absent or still developing, southern Brazil receives rainfall from moisture blown in with storms from the southern Atlantic and overland incursions of polar air (Cruz *et al.*, 2005; Wang *et al.*, 2006; Ledru, Mourguiart and Riccomini, 2009; Gu *et al.*, 2017). Unlike other parts of Brazil, the SASM therefore contributes only around 60% of annual precipitation to most of the southern region, hence there are not distinct, observable wet and dry seasons (Cruz *et al.*, 2005, 2007; Wang *et al.*, 2006).

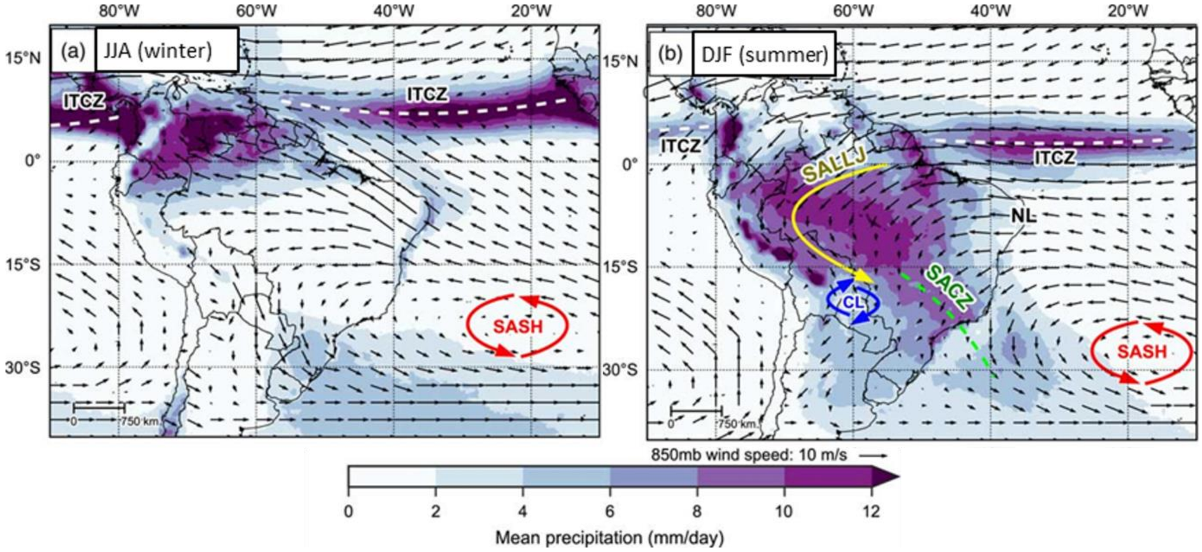


Figure 4-1: Observed long-term mean precipitation (mm/day, 1998-2014), 850 mb wind speed and wind direction (1979-2010) for (a) June, July, and August (JJA, austral winter), and (b) December, January, and February (DJF, austral summer). Labels indicate key climate features: Intertropical Convergence Zone, ITCZ; South American Low Level Jet, SALLJ; Chaco Low, CL; South Atlantic Convergence Zone, SACZ; South Atlantic Subtropical High, SASH; and Nordeste Low, NL. Figure and caption adapted from Smith & Mayle (2017).

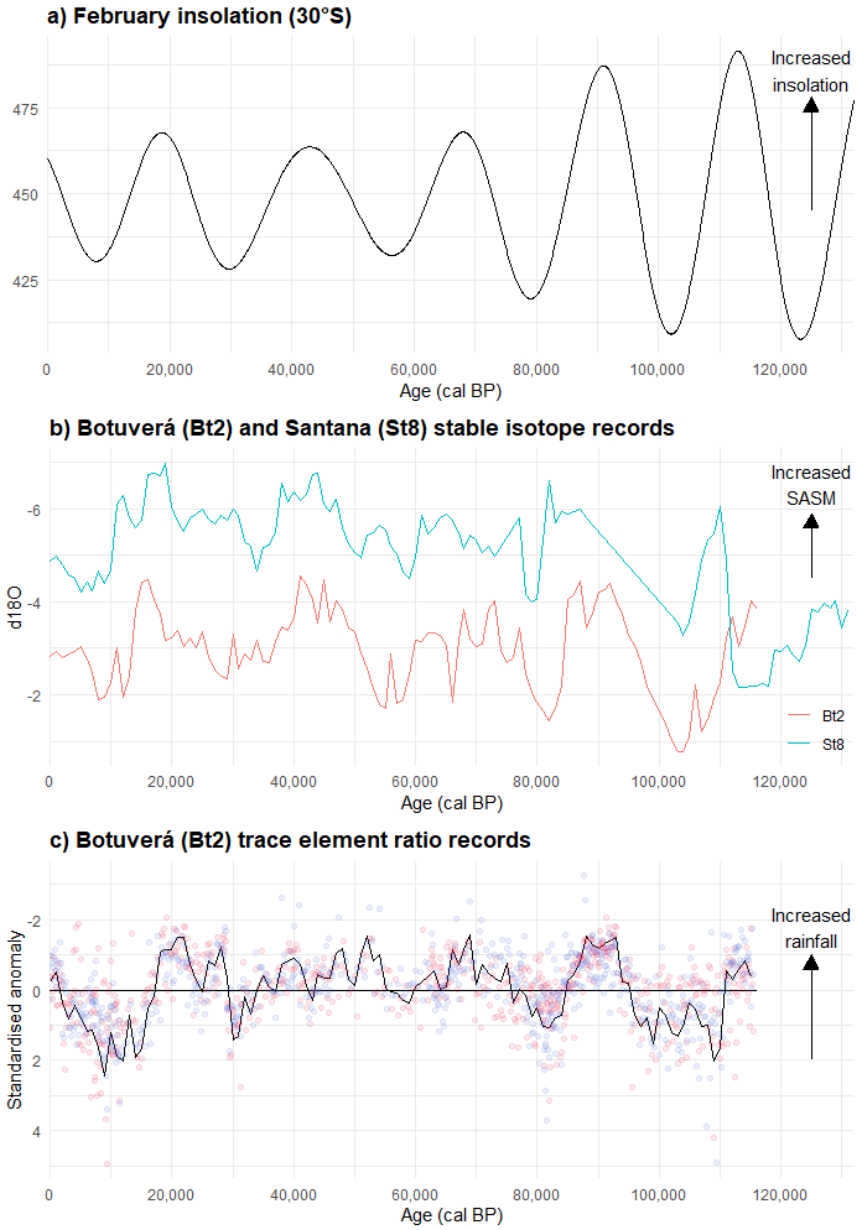
The first reconstructions of southern Brazil's past climates depended on inferences from fossil pollen assemblages (Behling, 1993, 1995, 1998). *Araucaria* pollen might suggest that conditions were cool and constantly moist, for example, and increases in forest pollen might indicate increasing temperatures and/or precipitation (Behling, 1995; Behling *et al.*, 2004). On this basis, Behling et al. (2004), finding Campos-dominated and near-treeless pollen assemblages at the Last Glacial Maximum (LGM, approximately 21,000 years ago), interpreted southern Brazil's climate at the time to have been seasonal, with long annual dry periods, mean annual temperatures 5-7°C colder than at present, and minimum winter temperatures below -10°C. Similarly, the early and mid-Holocene was considered to have been warm and dry, owing to the continued rarity of Araucaria Forest taxa and frequent and abundant spores from *Phaeoceros laevis*, a moss apparently indicating soil dryness and low vegetation cover (Behling *et al.*, 2004) – though Leonhardt and Lorscheitter (2010) instead suggested the authors' palynological assemblages were characteristic of warmer and more humid conditions.

Synthesising pollen records to infer climatic conditions – especially at scale – is challenging. This is not just related to differences in opinion about how individual taxa should be interpreted, or to the difficulties of integrating and generalising heterogeneous signals. Rather, using pollen data to construe climatic conditions rests on an imperfect central assumption: that past plant communities were structured and changed largely or solely by climate, in approximately the same ways as in the present. In reality, however, non-climatic factors can be extremely important for community assembly, and the present becomes an ever more imperfect guide to the past the further back we look (Williams and Jackson, 2007; Jackson and Blois, 2015). Crucially, inferring climate from vegetation records introduces a logical circularity to the interpretation: 'the pollen did x because the climate did y, and the evidence the climate did y is that the pollen did x.' This circular reasoning *a priori* excludes other potential explanations for observed vegetation change, such as grazing, low atmospheric CO_2, or human land management, unless they are specifically targeted by other proxies.

Southern Brazil is fortunate that excellent vegetation-independent palaeoclimate reconstructions are available from within the region, allowing climate and vegetation dynamics to be disentangled. Reconstructions of temperatures from foraminiferal $\delta^{18}O$ or from lipid biomarkers remain somewhat rare (especially for terrestrial sites; Figure 4-2), but several speleothems from Botuverá cave (and one from Santana cave) provide millennia-long, high-resolution records of rainfall source and amount (Cruz *et al.*, 2005, 2006, 2007, 2009; Wang *et al.*, 2006, 2007; Bernal *et al.*, 2016). Southern Brazil's two different sources of precipitation have different isotopic signatures: the SASM rainfall, having travelled long distances, arrives in southern Brazil depleted of heavy oxygen isotopes, whereas the more local oceanic moisture is comparatively enriched with ^{18}O (Cruz *et al.*, 2005, 2009). Thus, records of more depleted oxygen isotope ratios (more negative $\delta^{18}O$ values) suggest more convective activity, a more intense hydrological cycle, and a stronger SASM (Cruz *et al.*, 2005, 2009; Wang *et al.*, 2006, 2007). When reduced rainfall leads to lower water levels in the aquifers above speleothems, air circulation increases, encouraging calcite to precipitate and allowing trace elements like strontium, barium and magnesium to be incorporated into the speleothem layers instead of calcium; thus, elevated Sr/Ca, Ba/Ca and Mg/Ca ratios signify emptier aquifers and less rainfall (Cruz *et al.*, 2007).

Figure 4-2: The last 21,000 years of air and sea surface temperatures from six proxy sites, of which Colônia is the only terrestrial record (see Figure 4-5 for site locations, and the text for source publications). Points show all available data, and lines plot the average for each 1,000-year bin.

Over the last 120,000 years, southern Brazil's rainfall amount, recorded by speleothem proxies from Botuverá and Santana, has generally tracked summer insolation and been driven by changes in the SASM (Figure 4-4; Cruz *et al.*, 2005, 2006, 2007). Also visible in Figure 4-3 is the generally greater contribution of SASM rainfall (depleted $\delta^{18}O$ ratios) in Santana cave, thanks to its location in south-eastern Brazil within the SACZ, further north than Botuverá (Cruz *et al.*, 2006). Botuverá's trace element ratios (Figure 4-3c) suggest that the period around the LGM had considerably more rainfall than almost any point in the Holocene (last 11,600-12,000 years), and that the time around the Holocene onset was the driest southern Brazil had experienced for many tens of thousands of years. Southern Brazil's rainfall through much of the Holocene can be seen in higher resolution from another Botuverá speleothem in Figure 4-4 (Bernal *et al.*, 2016); despite the slightly different trajectories across the different trace element ratios, the driest period in the last nine millennia appears to have been around 7,000 years ago, followed by a general increase in rainfall before the last millennium or so was punctuated by some sharp changes in precipitation amount. Similarly fine-scale trends are not visible in the region's proxy records of palaeo-temperatures (Figure 4-2), but the most recent millennia are generally the warmest since the LGM, when sea surface temperatures appear to have been 2-4°C lower than present (Toledo *et al.*, 2007; Carlson *et al.*, 2008; Pivel *et al.*, 2013; Chiessi *et al.*, 2014, 2015; Dauner *et al.*, 2019; Rodríguez-Zorro *et al.*, 2020). Colônia's terrestrial air temperature record has only coarse temporal resolution (it covers 180,000 years) and each point is accompanied by significant uncertainty (root mean squared error of ca. 4.7°C), but it shows constant lower annual average temperatures (21-22°C) from the LGM until about 3,600 years ago, after which temperatures dropped to about 20°C then rose to approximately 26°C at present (Rodríguez-Zorro *et al.*, 2020).



a) February insolation (30°S)

b) Botuverá (Bt2) and Santana (St8) stable isotope records

c) Botuverá (Bt2) trace element ratio records

Figure 4-3: ca. 120,000 years of past insolation and rainfall variability recorded by Botuverá and Santana speleothems. A) Insolation, calculated for February at 30°S (as in Cruz et al., 2007) using the R package 'palinsol'. B) Stable oxygen isotope ($\delta^{18}O$) proxies recorded at Santana (St8, blue, Cruz et al., 2006) and Botuverá (Bt2, red, Ctuz et al., 2005). C) Trace element ratio anomalies (Mg/Ca, red, and Sr/Ca, blue; values standardised to plot on a shared axis) and their mean (black line, 1,000-year bins) from Botuverá (Bt2). Speleothem data kindly provided by F.W. Cruz.

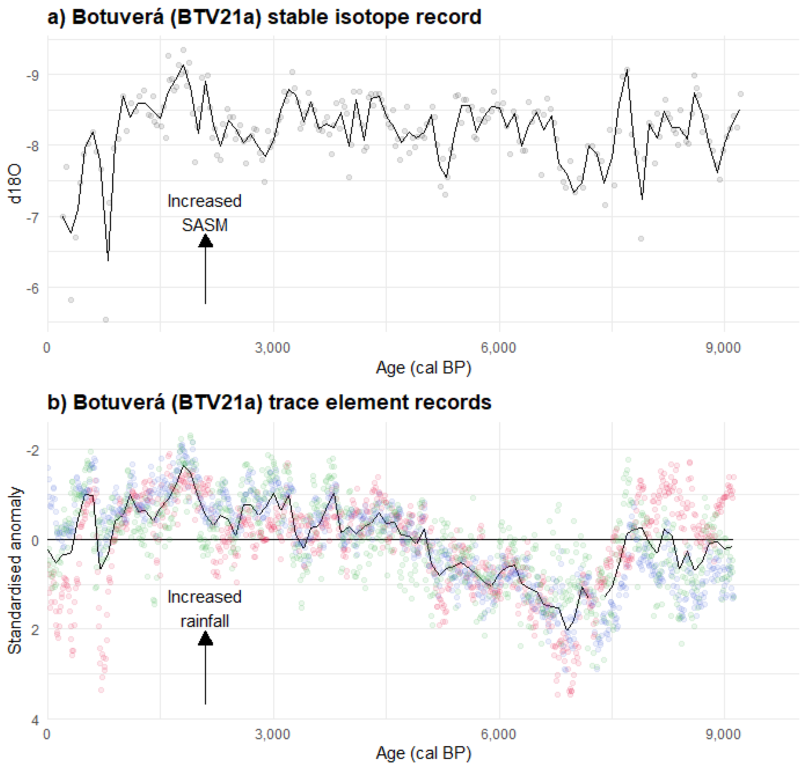


Figure 4-4: The last 9,000 years of rainfall in southern Brazil, recorded in high (sub-annual) resolution the BTV21a speleothem (Bernal et al., 2016). Lines plot the proxy values averaged to 100-year bins and points show all available measurements. A) Stable oxygen isotopes ($\delta^{18}O$). B) Trace element ratio anomalies (Mg/Ca, red, Sr/Ca, blue, and Ba/Ca, green; values standardised to plot on a shared axis).

Independent palaeoclimate proxy records are not very well aligned with the main results from pollen-derived inferences – the LGM, for instance, appears to have been wetter than previously conceived, with less extremely cold annual average temperatures. Several factors likely contribute to the discrepancy. Plants may be more sensitive to temperature or precipitation seasonality or extremes than the averages which are captured by the proxy records; additionally, planktonic foraminiferal $\delta^{18}O$ proxies (e.g. SAN-76, LaPAS KF02, KNR159-5-36GGC) generally reflect summer temperatures, whereas colder winter temperatures may have exerted a stronger physiological limit on the region's plants at the LGM (Toledo *et al.*, 2007; Carlson *et al.*, 2008; Pivel, Toledo and Costa, 2010; Pivel *et al.*, 2013). Grazing by now-extinct herbivorous megafauna may have played a role in promoting Campos at the expense of forest, but this has not been studied in southern Brazil. Fire would have had a similar effect but was probably depressed under cooler, wetter conditions, and charcoal is not notably high in the few sites which record it on the highlands at this time (Behling, 1997; Behling *et al.*, 2004; Jeske-Pieruschka *et al.*, 2013). A factor which likely did have a very significant impact, though, is the LGM's low atmospheric CO_2 concentrations (180-190 ppm [14]) (Gerhart and Ward, 2010). These conditions would have provided a competitive boost to the C4-photosynthesising plants which dominate Campos vegetation – outweighing the negative effects of cold temperatures on C4 photosynthesis – while inflicting disproportionate water stress on C3 photosynthesisers, including all southern Brazil's woody vegetation (Mayle *et al.*, 2004; Gerhart and Ward, 2010; Pivel, Toledo and Costa, 2010; Svenning *et al.*, 2011; Montade *et al.*, 2019). This important factor has generally been neglected in discussions of southern Brazil's past climate and

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[14] Compared to about 270 ppm before the Industrial Revolution, 354 ppm when I was born, and 417 ppm in late 2021.

vegetation, however, and is usually omitted in studies which have tried to reconstruct the region's climatic conditions from pollen data.

The comparative wealth of vegetation-independent palaeoclimate data for southern Brazil is vital for understanding the region's past vegetation dynamics. It breaks the circularity of pollen-derived climate reconstructions and opens up opportunities to examine and weigh alternative drivers of observed palaeoecological changes – not only climate, but CO_2, fire, grazing, biotic interactions, historic factors, and humans (Mayle and Iriarte, 2014; Jackson and Blois, 2015). Unpicking how these and other factors combined to shape southern Brazil's ecosystems in the past is of paramount importance for explaining their contemporary situations and understanding their likely responses to future changes.

4.2 Plants and the past in the southern Atlantic Forest

The palaeoecology of the southern Atlantic Forest is better known than almost any other region in the tropics, with the highlands especially well studied (Figure 4-5) (Smith and Mayle, 2017). Campos have been present for at least 40,000 years (Cambará do Sul record, Behling *et al.*, 2004), and dominated the highland landscape for the great majority of that time (Behling, 2002; Behling *et al.*, 2004; Behling, Pillar and Bauermann, 2005; Leonhardt and Lorscheitter, 2010; Jeske-Pieruschka and Behling, 2012; Jeske-Pieruschka *et al.*, 2013; Mareschi Bissa and de Toledo, 2015). At the LGM, grasslands also appear to have dominated the coastal lowlands – Atlantic Rainforest taxa are extremely rare in fossil pollen records at the time (Volta Velha record, Behling and Negrelle, 2001; GeoB2107-3 record, Gu *et al.*, 2017). Their distribution may have shrunk such that the ecosystem's southern limit was found hundreds of kilometres to the north (the Forest Refuge Hypothesis), or they may have persisted on land exposed by drastically lowered sea levels (the Atlantis Rainforest Hypothesis) – the evidence is equivocal (Behling and Negrelle, 2001; Behling, 2002; Bauermann, 2003; Carnaval and Moritz, 2008; Leite *et al.*, 2016; Gu *et al.*, 2017). Even less is known about the long-term dynamics of the region's

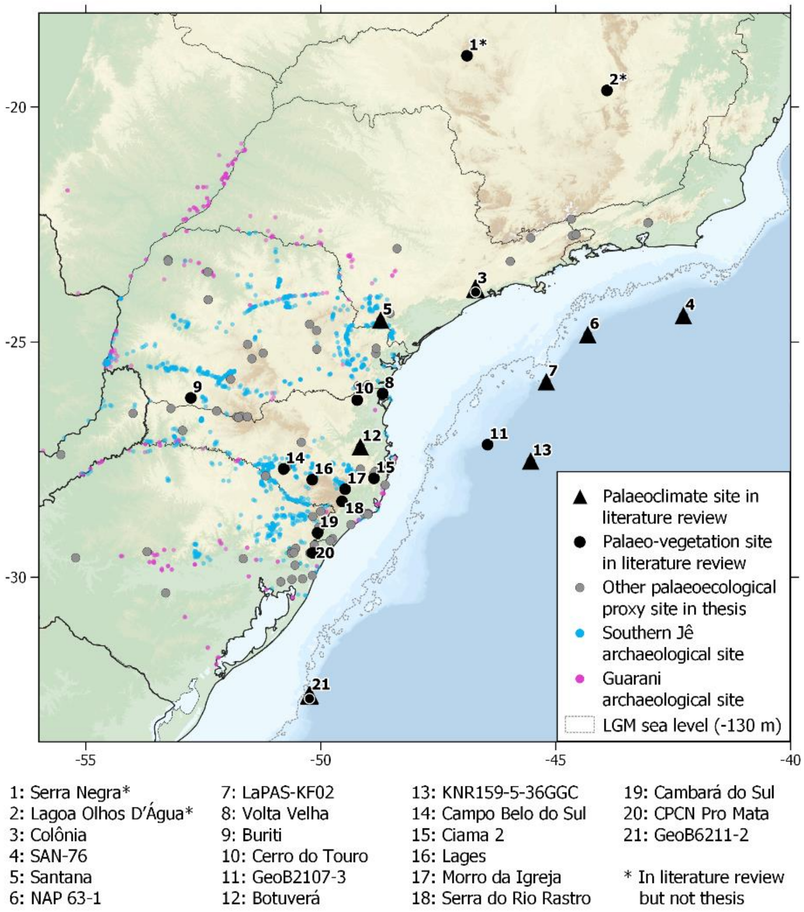

Figure 4-5: Map showing palaeoecological and palaeoclimate proxy records in this thesis, highlighting those mentioned in this literature review, with southern Jê and Guarani archaeological sites.

Seasonally (semi-)Deciduous Forests, in which exceedingly few palaeoecological studies have been conducted (Figure 4-5).

The millennial-scale history of Araucaria Forests, though, is more wide-ranging and complex. They have periodically been part of the landscape in southern Brazil for at least 73,500 years (GeoB2107-3 record, Gu *et al.*, 2017) and in south-eastern Brazil for at least 130,000 years (Colônia record, Ledru, Mourguiart and Riccomini, 2009), yet much of their contemporary distribution appears to have developed comparatively recently. At the LGM, sampled areas of the southern plateau appear to have been largely treeless and Campos dominated – even in the marine core GeoB2107-3's presumably regional catchment, pollen from Araucaria Forest taxa is then generally rare (Behling *et al.*, 2004; Jeske-Pieruschka *et al.*, 2013; Gu *et al.*, 2017). Indeed, it appears that no published fossil pollen sites in Brazil record *Araucaria* pollen during the LGM [15]. In the Late Glacial period (ca. 18,000-12,000 years ago), however, Araucaria Forest elements appear in a number of palaeoecological records over a far more extensive area than the ecosystem's current distribution – including, notably, in central Brazil, where today the dominant vegetation is Cerrado savanna (Pinaya *et al.*, 2019). The pollen spectra from some sites in this region, in the Late Glacial as well as in some millennia previously, lack modern equivalents, with Araucaria Forest taxa occasionally occurring alongside others from drier or warmer environments (e.g. *Caryocar*) (Salgado-Labouriau, 1997; Lagoa Olhos D'Água record - Raczka *et al.*, 2013; Serra Negra record - De Oliveira *et al.*, 2020).

The earliest terrestrial record of Araucaria Forests in southern Brazil is from about 50,000 years ago, in a buried peat bog at the Cerro do Touro valley head, but *Araucaria* pollen is absent or extremely rare throughout the abbreviated record (de Oliveira *et al.*, 2008). The oldest record documenting changes to the present is from Buriti in south-western Paraná (Bertoldo, Paisani and Oliveira, 2014), where *Araucaria* pollen is found almost continuously from the Late Glacial onwards, alongside more variable contributions from other tropical trees and Araucaria Forest taxa. Further south and east, smaller-than- blocks of highland forest are found in CPCN Pro Mata from about 10,000 years ago (Silva and Anand, 2011), and a brief buried peat record in the Cerro do Touro valley bottom cold-adapted forest (again without *Araucaria* pollen) developing over several centuries at the start of the Holocene (de Oliveira *et al.*, 2008).

Later in the Holocene, multiple records in the plateau's south-east (the highlands' best-sampled area – see Figure 4-5) attest to modest Araucaria Forest expansions over previously dominant Campos between about 3,000 and 4,000 years ago, a period with increased rainfall (Figure 4-4) (Behling, 2002; Behling *et al.*, 2004; Silva and Anand, 2011; Jeske-Pieruschka and Behling, 2012; Scherer and Lorscheitter, 2014; Spalding and Lorscheitter, 2015; Bernal *et al.*, 2016). Some sites (such as Ciama 2, Morro da Igreja, Serra do Rio Rastro, CPCN Pro Mata and, especially, Cambará do Sul) record subsequent forest expansions after about 1,500 years ago – some of them notably larger and faster than those which went before (Behling, 1995; Behling *et al.*, 2004; Silva and Anand, 2011; Jeske-Pieruschka *et al.*, 2013). Originally interpreted, in many cases, as evidence for transitions towards warmer and wetter conditions (see Section 4.1), these more recent changes appear to have weaker links to the rainfall changes independently recorded in the BTV21a speleothem (Figure 4-4) (Bernal *et al.*, 2016; but see Rodrigues, Behling and Giesecke, 2016; Robinson *et al.*, 2018). This disconnect has raised the possibility that the changes Araucaria Forests experienced during the Common Era (last 2,000 years) were instead driven, at least in part, by human actions (Bitencourt and Krauspenhar, 2006; Iriarte and Behling, 2007; dos Reis, Ladio and Peroni, 2014; Robinson *et al.*, 2018) – a suggestion explored and reviewed in Section 4.3, and tested in Chapter 4.

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[15] Admittedly, relatively few fossil pollen records in the region cover the LGM period.

However, well though we understand the palaeoecology of southern Brazil in general – and the region's highlands in particular – in the context of the world's (sub)tropics, many significant gaps remain. The great majority of the area's palaeoecological proxy sites are small, with local catchments that cannot pick up broader, more regional vegetation dynamics (Mayle and Iriarte, 2014; Smith and Mayle, 2017). Spatial skew in the distributions of these sites, with most coastal ones found in the lagoons of northern Rio Grande do Sul and most Araucaria Forest-Campos records clustered around the plateau's south-eastern edge (Figure 4-5), means that even local changes are unsampled in large parts of the region. For example, while the south-eastern plateau is well studied, yielding important insights into the dynamics of Araucaria Forest patches embedded in high-elevation Campos, Buriti has long been the only fossil pollen site in the continuous mid-elevation Araucaria Forests, and it is uncertain how well findings translate from the former context to the latter (Bertoldo, Paisani and Oliveira, 2014; Cárdenas *et al.*, 2019; Wilson *et al.*, 2021).

One solution to problems of proxy sites' spatial coverage is to use ecological niche models (ENMs). Contingent on data availability, these can predict species', communities' and/or ecosystems' responses to past climate changes at high spatial and temporal resolution, with continuous spatial coverage (Svenning *et al.*, 2011). Several studies have used ENMs to predict past changes in the southern Atlantic Forest's vegetation (Carnaval and Moritz, 2008; Porto, Carnaval and da Rocha, 2013; Carnaval *et al.*, 2014; Vitorino *et al.*, 2016; Arruda *et al.*, 2017; Costa *et al.*, 2017; Ledo and Colli, 2017; Bergamin *et al.*, 2019), but each shares one or more notable limitations (expanded on in Chapter 3, Wilson *et al.*, 2021). Many focus only on the two past time slices for which gridded palaeoclimate data are most readily available (the mid-Holocene, 6,000 years ago, and the LGM, 21,000 years ago), despite other periods (such as the start of the Holocene, around 12,000 years ago) having similar or greater palaeoecological relevance (Figure 4-3). Efforts to cross-reference predictions and palaeoecological data tend to be less extensive or detailed than they could be – important sites such as Buriti (Bertoldo, Paisani and Oliveira, 2014) are often omitted, perhaps because authors rely on incomplete databases such as Neotoma when searching for proxy records. Finally, ecosystems are frequently modelled as units, without consideration for changes in floristic composition, community reassortment, or the development of no-analogue assemblages – factors which could be considerable in the past (Williams and Jackson, 2007; Section 1) and to which the southern Atlantic Forest's complex floristic gradients (see Section 3) may have been especially sensitive.

These weaknesses in existing palaeo-ENM studies focusing on the southern Atlantic Forest were a key motivation for the research in Chapter 3 (Wilson *et al.*, 2021). Specifically, this study uses high-resolution climate data for seven past time slices (incorporating major fluctuations in sea levels) to track vegetation changes through time; models the distributions of 30 key forest and Campos species and aggregates them into assemblages to examine fine-scale floristic changes; and closely compares the predicted results against an extensive dataset of palaeoecological records. This research is informed and supported by the results from Chapter 2 (Cárdenas *et al.*, 2019, described further in Section 4.3), which shed light on how changes to Araucaria Forest structure and composition are reflected in fossil pollen records – important when evaluating connections between model-predicted and pollen-observed past vegetation changes.

4.3 Putting people in the picture

> *[F]or centuries the Kaingang groups and their ancestors led processes of cultural construction of the landscapes of Brazil's South. The araucária [...] is a living expression of this culturalized landscape.*

Southern Brazil has been inhabited by humans for 10,000 years or more (Noelli, 2000a). Along the region's coasts, fisher-gardener communities built shellmounds called sambaquis and altered sandy-substrate coastal restinga ecosystems, showing remarkable continuity over at least 8,500 years (Iriarte *et al.*, 2016; Scheel-Ybert and Boyadjian, 2020). Inland, archaeological sites from early in the region's human occupation are ascribed to the loosely defined Umbu and Humaitá hunter-gatherer traditions, though Umbu lithic sites at high elevations are yet undated (Moreno de Sousa and Okumura, 2018; Araujo and Okumura, 2021; Corteletti *et al.*, 2021). Most relevant to the research in this thesis, though, are the archaeological traditions which are first recorded in southern Brazil late in the Holocene – the southern Jê and, to a lesser extent, the Guarani.

The macro-Jê linguistic family has its origins in central Brazil, from where migration and cultural diffusion gave rise to the highlands' southern Jê groups about 2,000 years ago (Noelli, 2000a; de Souza, Mateos and Madella, 2020; Corteletti *et al.*, 2021). Although at least four southern Jê groups existed at the time of first contact with Europeans, the Kaingang and Xokleng are the only two remaining, the Ingain and Kimdá languages having been exterminated from the plateau's western edge (Jokelsky, 2010; Iriarte *et al.*, 2016; Noelli and De Souza, 2017). The preserved material cultures of these different groups and their ancestors cannot currently be distinguished, so archaeologists often refer to the 'southern proto-Jê' (cf. Robinson, Iriarte, De Souza, *et al.*, 2017); in this thesis I generally use the broader term 'southern Jê', since it also encompasses extant and historically known groups (cf. Noelli and De Souza, 2017).

The pre-colonial southern Jê were at least semi-sedentary and practised a mixed economy, hunting game, cultivating maize (*Zea mays*), manioc (*Manihot* spp.), squash (*Cucurbita* spp.) and beans (*Phaseolus* spp.), and exploiting forest resources such as fruit trees from the Myrtaceae family (Corteletti *et al.*, 2015). Pinhão from Araucaria trees were among the most important resources to communities, representing a food source that was nutritious, could be effectively preserved, and was available in large quantities over long periods – especially at times of year when other forest resources were scarce (Henry, 1964; Noelli, 2000a; Corteletti *et al.*, 2015; Loponte *et al.*, 2016; Bogoni, Muniz-Tagliari, *et al.*, 2020). Their cultural and economic importance was such that *Araucaria* starch has been found extensively in coastal sambaquis from pinhão carried and traded over hundreds of kilometres (Wesolowski *et al.*, 2010; Scheel-Ybert and Boyadjian, 2020). Cycles of Araucaria fruiting also appear to have driven seasonal movements among at least some southern Jê groups, including in the historically known Xokleng (Henry, 1964; Noelli, 2000a; Moura, 2021).

The two principal types of southern Jê archaeological sites are domestic and funerary. In the archaeological record, southern Jê settlements consist of semi-subterranean pit houses [16] (some of them extremely large, suggestive of social hierarchy and inequality) in settlements which, in some instances, were continuously occupied for many centuries (de Souza, Robinson, *et al.*, 2016; Noelli and De Souza, 2017; de Souza, 2018). These settlements appear to have proliferated and increased in complexity from around 1,000 years ago (Bitencourt and Krauspenhar, 2006; Iriarte and Behling, 2007; Robinson *et al.*, 2018); at about the same time, the southern Jê began to build monumental funerary structures known as mound and enclosure complexes (MECs), which have striking parallels with Kaingang cosmology, social organisation and ritual practices (Iriarte, Gillam and Marozzi, 2008; Iriarte *et al.*, 2013; Robinson, Iriarte, de Souza, *et al.*, 2017; Robinson, Iriarte, De Souza, *et al.*, 2017). Frequently constructed in prominent topographic positions, on hilltops with wide viewsheds, MECs and pit-house settlements combined to form highly structured 'sacred landscapes' on Brazil's

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[16] By the time of the earliest European records, southern Jê communities no longer used pit houses.

southern highlands (Iriarte *et al.*, 2013, 2016; Robinson, Iriarte, de Souza, *et al.*, 2017; Robinson, Iriarte, De Souza, *et al.*, 2017)

The timing of the southern Jê's archaeological expansion coincides with an increase in the number – and expansion in the distribution – of Guarani archaeological sites in southern Brazil. Originating in Amazonia, people speaking Tupi-Guarani languages expanded into new territory late in the Holocene – most likely in response to changing climates and increased areas of gallery forests which could support their communities and the agroforestry on which they depended (Bonomo *et al.*, 2015; Pereira *et al.*, 2016; Iriarte *et al.*, 2017; de Souza, Mateos and Madella, 2020; Noelli *et al.*, 2021; Souza, Noelli and Madella, 2021). The Guarani probably reached southern Brazil early in the Common Era (last 2,000 years), initially occupying lowland areas around the edges of the plateau (including the Atlantic coast) before advancing along major rivers into the highlands about 1,000 years ago (Figure 4-5) (Bonomo *et al.*, 2015; Iriarte *et al.*, 2017). These developments may have spurred the southern Jê to erect MECs as an 'impermeable frontier' against Guarani incursions into their territories (de Souza, Corteletti, *et al.*, 2016).

Notably, these significant archaeological changes occur at the same time as some of the largest recent expansions of Araucaria Forest. This, along with the ecosystem's spatial overlap with the southern Jê's territory and the importance of Araucaria Forest resources – particularly Araucaria trees – to the southern Jê, has led to suggestions that the two developments are causally linked (Noelli, 2000a; Bitencourt and Krauspenhar, 2006; Iriarte and Behling, 2007; dos Reis, Ladio and Peroni, 2014). It is quite likely that more abundant resources from expanded Araucaria Forests helped to sustain the southern Jê's expansion (Iriarte and Behling, 2007), but the question of whether the southern Jê caused the Araucaria Forest expansions – entirely or in part – has not been fully resolved.

The possibility that the development of modern Araucaria Forests required input from Indigenous people was suggested as early as the mid-20th Century (for a fuller review, see the supplementary material for Chapter 4). Aubreville (1948) hypothesised that disturbances from fire and other land uses had opened up the forests and allowed Araucaria trees to regenerate, with the forests' modern structure – well-established canopies of mature Araucaria trees, dense angiosperm sub-canopies and understoreys, little Araucaria regeneration – a consequence of Indigenous people having been removed from their land. Bitencourt and Krauspenhar (2006) were among the first to highlight the increasingly apparent temporal overlap between palaeoecological and archaeological evidence, with dos Reis *et al*. (2014) highlighting aspects of Araucaria's biology, ecology and cultural role which together lend credence to anthropogenic input into the Araucaria Forest expansions. For some time is has been assumed that parts of the Araucaria Forest have had anthropogenic origins (including, potentially, from the more distant Umbu and Humaitá traditions; Noelli, 2000a); until recently evidence for this had been lacking, but several recent studies have helped make this a more widely accepted view (as stated in, among others, Bogoni, Graipel and Peroni, 2018; Sühs, Hettwer Giehl and Peroni, 2018; Bogoni, Batista, *et al.*, 2020; Bogoni, Muniz-Tagliari, *et al.*, 2020; Pereira Cruz *et al.*, 2020; Clement *et al.*, 2021; Sühs *et al.*, 2021).

Pereira Cruz et al. (2020) attempted to identify ecological legacies of Guarani and southern Jê occupations on southern Brazil's forests, overlaying data from the Santa Catarina Forest Floristic Inventory (Vibrans *et al.*, 2010, 2020) with modelled distributions of each group's archaeological sites. This effectively highlighted the spatial (and associated floristic) differences between the two groups – the Guarani along the coast and major rivers, with Atlantic Rainforest and Seasonally Semi-deciduous Forests (SDF); the southern Jê at high elevation, with some consideration for major rivers, in Araucaria Forests (and, to a lesser extent, SDF; Figure 4-5) – but did not examine differences within them or account for climatic confounders of the floristic patterns observed. Lauterjung *et al*. (2018) found genetic evidence of rapid expansions from a single refugium in *A. angustifolia*'s chloroplast DNA; they assigned it a human cause, calculating that, without assistance, Araucaria populations could not have reached the western extremes of their contemporary range from their putative refugium in the 4,000 years since their first observed expansion in highland palaeoecological records. However, other, larger genetic studies have found more evidence for spatial structure and multiple refugia, and Buriti's fossil pollen record shows that western Araucaria populations were well established early in the Holocene (Bertoldo, Paisani and Oliveira, 2014; Stefenon *et al.*, 2019).

To date, the best evidence for anthropogenic expansions of Araucaria Forests comes from Robinson *et al.*'s (2018) close integration of palaeoecological, palaeoclimatological and archaeological research. The authors note that the current spatial distribution of Araucaria Forest differs between an area with intense pre-colonial southern Jê occupation (Campo Belo do Sul) and an archaeologically empty region (Lages), and that forests in the archaeological area expanded during a period of burgeoning human occupation and stable rainfall whereas vegetation in the unoccupied region barely changed for 7,500 years – together suggesting anthropogenic forest expansion. This finding rests on the key assumption that the two locations would exhibit the same spatial and temporal vegetation patterns in the absence of past southern Jê occupation, but several confounding factors may invalidate the comparison. The regions are 60 km distant from one another, differing by 100-300 m of elevation; partly because of the resulting climatic gradient, Lages is covered more by Campos than Araucaria Forest, with the opposite being true of Campo Belo do Sul; 20th-Century habitat loss impacted Campo Belo do Sul more than Lages, so only a subset of its non-forest areas are natural. All these potentially confounding factors mean that natural explanations cannot be ruled out for (some of) the observed differences between the areas' Araucaria Forest distributions and histories.

In light of the above weaknesses and caveats in existing studies examining southern Jê impacts on Araucaria Forests, the question of the extent to which the ecosystems were transformed before European arrival has remained open. The research in Chapter 4 of this thesis is intended to fill this significant knowledge gap. To maximise the chances of addressing the question successfully, this chapter presents the first fossil pollen studies in southern Brazil to use closely linked palaeoecological and archaeological sites (cf. Mayle and Iriarte, 2014). Importantly, though, these data do not stand alone, with the study design accounting for both natural and climatic drivers of vegetation change, examining changing patterns in both space and time, and producing modelled predictions to evaluate against the most extensive possible combinations of empirical palaeoecological, palaeoclimatological and archaeological evidence.

To combine these different sources of evidence to their full effect, however, it is important to understand how human impacts would appear in palaeoecological records. Linking modern vegetation cover with modern pollen data is an important step in resolving how catchments' land cover might be reconstructed using fossil pollen data. This can show which taxa are indicative of different ecosystems, which are sensitive to ecological changes, which are abundant or poor pollen producers, etc. Such knowledge is also the foundation of quantitative landscape reconstruction methods (e.g. Bunting *et al.*, 2018). However, at the beginning of my PhD, no quantitative data relating modern pollen and vegetation had been published: the existing studies on modern pollen-vegetation relationships in Araucaria Forests (Behling, Bauermann and Neves, 2001; Garcia *et al.*, 2004; Jeske-Pieruschka *et al.*, 2010) had used largely qualitative approaches, identifying key indicator taxa but not analysing connections between pollen records and vegetation changes. The then-unmet need to understand how past human impacts on forest structure or composition may have been reflected in fossil pollen records motivated the research in Chapter 2 (Cárdenas *et al.*, 2019). Subsequent studies have further advanced our understanding of Araucaria Forest modern pollen-vegetation relationships (Montade *et al.*, 2019; Guarinello de Oliveira Portes *et al.*, 2020; Piraquive Bermúdez, Theuerkauf and Giesecke, 2021).

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Preface to Chapter 1: Cold spot microrefugia hold the key to survival for Brazil's Critically Endangered Araucaria tree

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Overview

This opening chapter examines how the intersection of historic habitat loss and future climate changes will affect the distribution of *Araucaria angustifolia*, and the extent to which small-scale microrefugia can ameliorate broad-brush losses. *A. angustifolia* is the most important and iconic species on the highlands – it literally defines the eponymous Araucaria Forests – so its resilience to future climate change is an effective shorthand for the responses of the wider ecosystem.

Starting at the present and incorporating the effects of the last century, this chapter looks ahead to the coming decades, setting up the longer timescales of the papers which follow. This work also introduces ecological niche/species distribution models (ENMs/SDMs) – the technique which underpins much of the other research in this thesis, but which here stands more alone than in the subsequent chapters. The research in Chapters 3 and 4 builds, in differing ways, on the methods and results presented here.

Contribution to the research

I had the lead role in conceiving this study and designing its analysis. Most of the location data were provided by Débora Lingner and Alexander Vibrans (Federal University of Blumenau), which I used to build the ENMs; I assessed and analysed their results and led the writing-up process, including writing the first draft. My contribution to this paper is estimated at 90%. The published author contribution statement is below:

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

Chapter 1: Cold spot microrefugia hold the key to survival for Brazil's Critically Endangered Araucaria tree

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Abstract

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

1. Introduction

Araucaria angustifolia (Bertol.) Kuntze (hereafter 'Araucaria') is a member of an ancient genus that dates back to the Jurassic period (Forest *et al.*, 2018). Its iconic candelabra shape defines southern Brazil's Mixed Ombrophilous Forests (MOF) (Oliveira-Filho *et al.*, 2014), a unique formation of the Atlantic Forest biodiversity hotspot (Myers *et al.*, 2000; Oliveira-Filho and Fontes, 2000; Duarte *et al.*, 2014). Araucaria has also been a cultural keystone (Cristancho and Vining, 2004; Garibaldi and Turner, 2004) for millennia: it "could be considered the ritual object par excellence" for the Indigenous southern Jê people (Fernandes and Piovezana, 2015, p. 120), and it is the most frequently-used plant species among Santa Catarina state's rural population (Justen, Müller and Toresan, 2012). Presently, Araucaria's chief economic value comes from its seeds (pinhão), which were a critical component in the southern Jê's diets before European arrival (Corteletti *et al.*, 2015; Loponte *et al.*, 2016) and remain a popular food source in Brazil today (Souza *et al.*, 2010; Adan *et al.*, 2016; Zechini *et al.*, 2018) – 9,293 tonnes, worth more than US$5.5 million, were harvested in 2017 (IBGE, 2018). A National Pinhão Festival has been held in Santa Catarina for 30 years, and Araucaria is celebrated on Paraná state's coat of arms. But despite its long-standing cultural and economic value, 20th-Century deforestation left Araucaria Critically Endangered (Thomas, 2013).

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

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

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

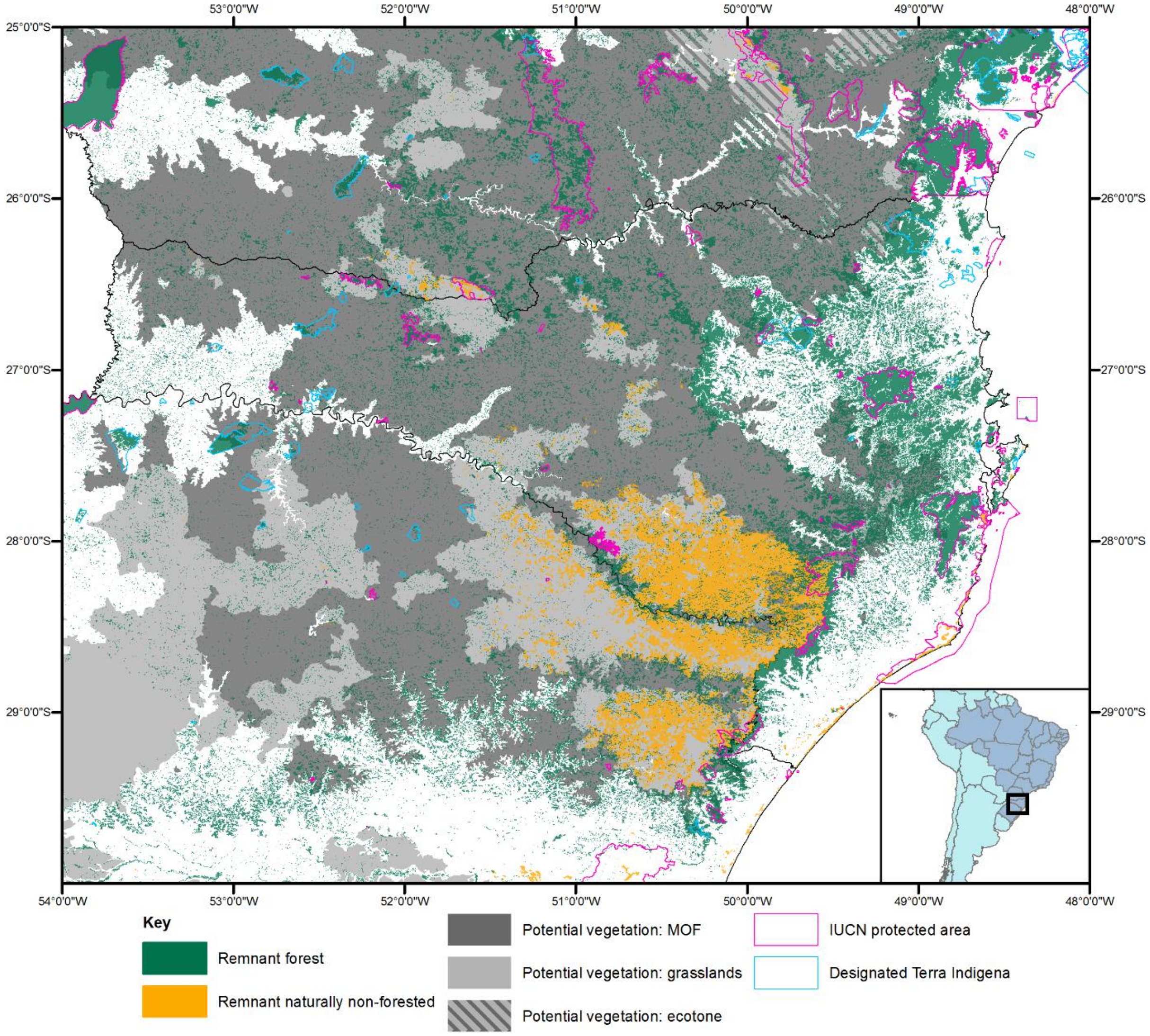

Figure 1: Map showing the study region's current potential vegetation (IBGE, 2004) and remnants >3 ha within the Atlantic Forest domain of Paraná, Santa Catarina and Rio Grande do Sul states (Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais - INPE, 2015)*. Pink outlines show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

2. Methods

To assess the role of microrefugia in promoting Araucaria's resilience to 21st-Century climate change, we first built ensemble species distribution models using established methodologies with climate data from Worldclim (Hijmans *et al.*, 2005) and CHELSA (Karger *et al.*, 2017a) (~800 m resolution). We then generated a further ensemble model ('CHELSA+') using CHELSA climate data and three topographic variables (relative elevation, exposure of surfaces to prevailing wind and to direct insolation) inferred from a 30m-resolution elevation model. These models estimated Araucaria's ecological niche at present and in 2070 under two emissions scenarios – RCP4.5 (relatively optimistic) and RCP8.5 (pessimistic, business-as-usual). We considered areas where Araucaria's predicted probability of occurrence (p_{occ}) was ≥75% in all three climate scenarios to be potential microrefugia. Using a map of remnant natural vegetation >3 ha in area (Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais - INPE, 2015), we identified potential microrefugia still within natural Campos (high-altitude grasslands) and forest fragments, as well as the larger vegetation patches these microrefugial populations may support. These locations were then cross-referenced with a database of Brazilian protected areas (UNEP-WCMC and IUCN, 2018) to assess their conservation status.

2.1. Occurrence, climate and topographic data

We modelled Araucaria's potential distribution between 25-30°S and 54-48°W. Presence and true absence records for Araucaria were taken from the Santa Catarina forest floristic inventory (IFFSC), a state-wide, systematic survey of natural forests using 4,000 m^2 sample plots spaced 5-10 km apart (Vibrans *et al.*, 2010). Overall, 1,670 individual Araucaria trees >10 cm diameter at breast height were identified in the survey, of which we used one presence record per plot. Additional occurrences from Misiones province (Argentina), Paraná and Rio Grande do Sul were obtained from the Global Biodiversity Information Facility (GBIF, 10th January 2018, https://doi.org/10.15468/dl.7b5jat). After cleaning coordinates from GBIF, this combined dataset yielded 106 presence records (83 from IFFSC plots, 23 from GBIF). Araucaria trees were not recorded in 334 IFFSC plots; these localities were treated as true absences, although Araucaria's absence from these plots may be influenced by dispersal limitations, biotic interactions or disturbance history as well as climatic conditions. A random 20% of the locality data was set aside for model evaluation, with the remainder used for building and cross-validating the models. A Mann-Whitney-Wilcoxon text showed no significant differences between these datasets in terms of latitude (p=0.48), longitude (p=0.82) or altitude (p=0.17).

Climate data were downloaded from Worldclim v1.4 (Hijmans *et al.*, 2005) and CHELSA (Karger *et al.*, 2017a, 2017b) at 30 arc-second resolution. We used climate change projections for 2070 (average of 2061-2080, RCP4.5 and 8.5 emissions scenarios) from three General Circulation Models (GCMs): CCSM4, CNRM-CM5, and NorESM1-M were chosen because they have been shown to perform well in Latin America (Yin *et al.*, 2013; Hidalgo and Alfaro, 2015; Lovino *et al.*, 2018) and were available for both Worldclim and CHELSA at the desired resolution. Best practice in SDM construction advocates restricting inputs to biologically relevant climate factors rather than using the full set of bioclimatic variables (Fourcade, Besnard and Secondi, 2017). We selected six, based on the subset of all variables which yielded the lowest Bayesian Information Criterion (BIC): isothermality (bio3), minimum temperature of the coldest month (bio6), mean temperature of the coldest month (bio11), annual precipitation (bio12), precipitation seasonality (bio15) and precipitation of the driest quarter (bio17). Multidimensional scaling showed these variables were not closely correlated (for correlation statistics, see fig. S1), and they appear to be biologically relevant as Araucaria and MOF are associated with a constantly moist climate with no dry season, and constantly cool conditions with low minimum temperatures (Hueck, 1953; Alvares *et al.*, 2013; Oliveira-Filho *et al.*, 2014; Neves *et al.*, 2017).

Topographic variables (exposure to solar irradiation, exposure to prevailing winds, relative elevation) were derived from the 30m-resolution ASTER global digital elevation model, a product of METI and NASA, downloaded from https://earthexplorer.usgs.gov. These variables were chosen as MOF at high elevations has been observed to prefer sheltered valley slopes and river banks (Hueck, 1953; Robinson *et al.*, 2018), and because these areas are likely to represent colder and moister microclimates (Ashcroft, Chisholm and French, 2008; Dobrowski, 2011; Ashcroft and Gollan, 2012; McLaughlin *et al.*, 2017). The two exposure variables were calculated according to the methods in (Ashcroft, Chisholm and French, 2008) using azimuths of 315° (i.e. north-west) for solar irradiation (McCune and Keon, 2002; McCune, 2007) and 30°, 60° and 90°, subsequently averaged, for the region's prevailing winds (Camargo do Amarante *et al.*, 2001). A point's relative elevation has been shown to effectively predict the level of cold air pooling it experiences (Ashcroft and

Gollan, 2012); we followed Ashcroft and Gollan (2012) by calculating this as the difference between a pixel's elevation and the minimum elevation within a 500m radius. Although these variables are themselves static (i.e. will not change over the time scales studied here), they interact with changeable climate variables and so were included as explanatory variables in our CHELSA+ model (following Stanton *et al.*, 2012).

We did not include edaphic variables in the modelling process since Araucaria's distribution is better explained by climatic variables alone – SDMs of the species perform better when edaphic variables are excluded, and soil conditions do not appear to exert a strong influence on its occurrence (Müller *et al.*, 2012; Velazco *et al.*, 2017).

2.2. Model construction

Species distribution models (SDMs) were constructed using the 'biomod2' package (Thuiller *et al.*, 2016) in R v.3.4.2 (R Core Team, 2020). We created ensemble models by averaging high-performing model runs from seven (CHELSA+) or eight (Worldclim, CHELSA) algorithms: generalised linear models (GLMs), generalised additive models (GAMs), artificial neural networks (ANNs), maximum entropy (Maxent (Phillips *et al.*, 2017)), generalised boosting models (GBMs), random forests (RFs), classification tree analysis (CTA), and multiple adaptive regression splines (MARS). For computational reasons, Maxent was not run for CHELSA+. Each algorithm was run ten times, and assessed using the area under the receiver operating curve (AUC) and true skill statistic (TSS) metrics (Allouche, Tsoar and Kadmon, 2006). TSS varies from -1 to +1, with 0 signifying a model no different to random; AUC varies from 0 to 1, with a random classifier expected to score 0.5. Projections from model runs with TSS ≥0.65 and AUC ≥0.9 for both cross-validation and evaluation were averaged to produce 'hibar' ensembles; 'lobar' ensembles averaged model runs with TSS scores ≥0.6 and AUC ≥0.85 (table 1). These ensemble models were then projected into scenarios for 2070 (relatively optimistic RCP4.5 and pessimistic, business-as-usual RCP8.5) using climate data from each GCM for Worldclim and CHELSA, with an average prediction subsequently taken. Due to the computational demands of CHELSA+, only the CCSM4 scenarios were run – this GCM was chosen as it makes the most accurate predictions of temperature and precipitation in this region (Lovino *et al.*, 2018).

For subsequent analysis we categorised the continuous model output (probability of occurrence, p_{occ}) into four equal classes, with divisions at 25%, 50% and 75%. To guide conservation priorities, it is important to consider areas where Araucaria is most likely to be – and remain – present. Although it is likely to be found in some areas projected to have lower p_{occ} values, we can be highly confident of Araucaria's presence in areas with p_{occ} ≥75%; this makes these the most valuable foci. We therefore consider locations with p_{occ} ≥75% in all three modelled scenarios (present, RCP4.5 and RCP8.5) to be potential microrefugia. We also consider areas which have p_{occ} of ≥50% in all three scenarios, but which do not qualify as potential microrefugia, to have moderate climatic resilience – they are less climatically suitable for Araucaria than full microrefugia, but may provide important habitat if the species is able to tolerate relatively less suitable conditions.

		Model runs meeting hibar/lobar standard								
		GLM	GAM	Maxent	ANN	GBM	RF	CTA	MARS	Total
WC	hibar						2			2
	lobar	1				2	5			8

CH	hibar	5					3		1	9
	lobar	8	3		2	2	8		8	31
CH+	hibar	5		x		8	7		4	24
	lobar	10	2	x	5	10	10		10	47

Table 1: Model runs meeting 'hibar' and 'lobar' criteria for inclusion in ensembles (see fig. S2 for evaluation scores of all model runs).

2.3. Vegetation remnants and conservation areas

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

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

3. Results

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

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

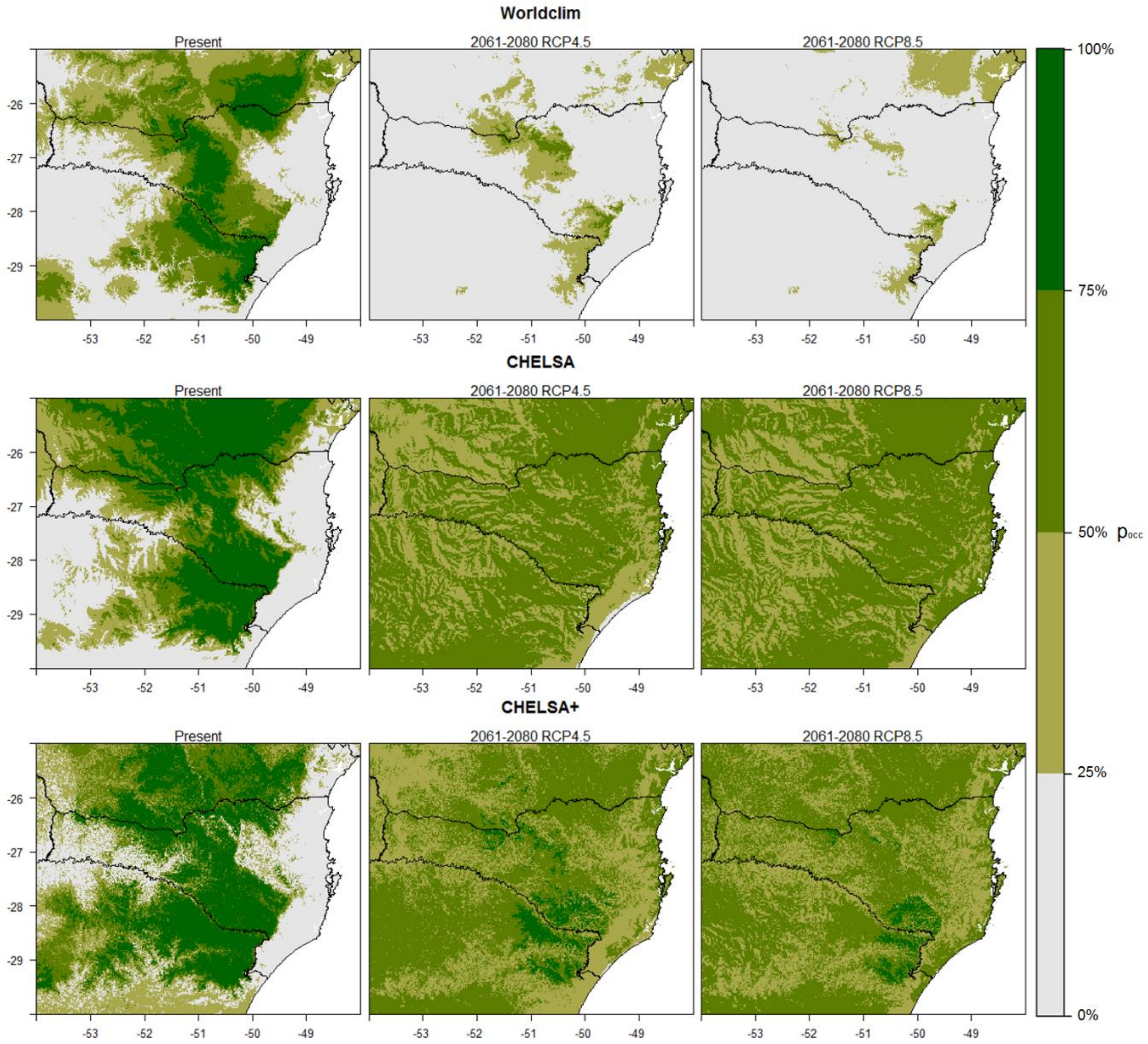

Figure 2: Ensemble predictions of habitat suitability for Araucaria using Worldclim (top), CHELSA (centre) and CHELSA+ (bottom) at present (left) and in 2070 under the RCP4.5 (centre) and RCP8.5 (right) scenarios.

CHELSA climate-only models predict 99.9%-100.0% loss of presently highly suitable habitat (p_{occ} ≥75%) in the future, but the incorporation of fine-scale topographic variables leads CHELSA+ to predict some persistence across the high elevation areas in the central and south-eastern areas of the plateau, much of it along river valleys (table S1, fig. 2). And although CHELSA+ still projects 85.3%-93.2% losses of this habitat class (table S1), it does identify 4,948 km^2 of potential microrefugia, as well as 24% more moderately resilient habitat (defined as p_{occ} ≥50% in all scenarios) than predicted by CHELSA alone (table 2). However, the impact of 20th-Century land use change can be seen, with 37.4% of potential microrefugia having lost their natural vegetation cover, rising to 82.4% of all moderately resilient habitat (table 2, fig. 3). These losses are particularly acute in forest remnants, which make up only 6.7% (333 km^2) of all Araucaria's potential microrefugia. This represents a climate-caused reduction of 96.5% from the 9,577 km^2 of forest where Araucaria is presently ≥75% likely to occur.

The majority of the most resilient habitat is predicted to occur in Campos. These naturally non-forested areas make up more than half of all potential microrefugia and 89.3% of those which have retained their natural vegetation, although CHELSA+ predicts that 71.6% of the presently most suitable Campos will be lost in future. The analysis of patches containing significant microrefugial areas shows that 679 patches of Campos, totalling 7,089 km^2 and covering on average 10.4 km^2 each, have ≥5% of their area covered by potential microrefugia or contain ≥100 microrefugial cells. By contrast, the 4,801 km^2 of forest patches which meet these criteria are found in 1,967 separate forest fragments, averaging only 2.4 km^2 per patch – a number which falls to 1.4 km^2 when excluding an outlier patch covering 41% of the total area (despite containing only 6.7 km^2 of microrefugia).

	Area (km^2)	Worldclim	CHELSA	CHELSA+
Microrefugia (p_{occ} ≥75% at present and in both future scenarios)	Total area	0	0	4,948.2
	In remnant forest	0	0	332.5
	In naturally non-forested area	0	0	2,763.7
Moderately resilient (p_{occ} ≥50% at present and in both future scenarios)	Total area	575.7	92,212.8	11,4416.4
	In remnant forest	250.1	13,561.9	11,438.3
	In naturally non-forested area	166.1	7,344.5	8,704.1

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

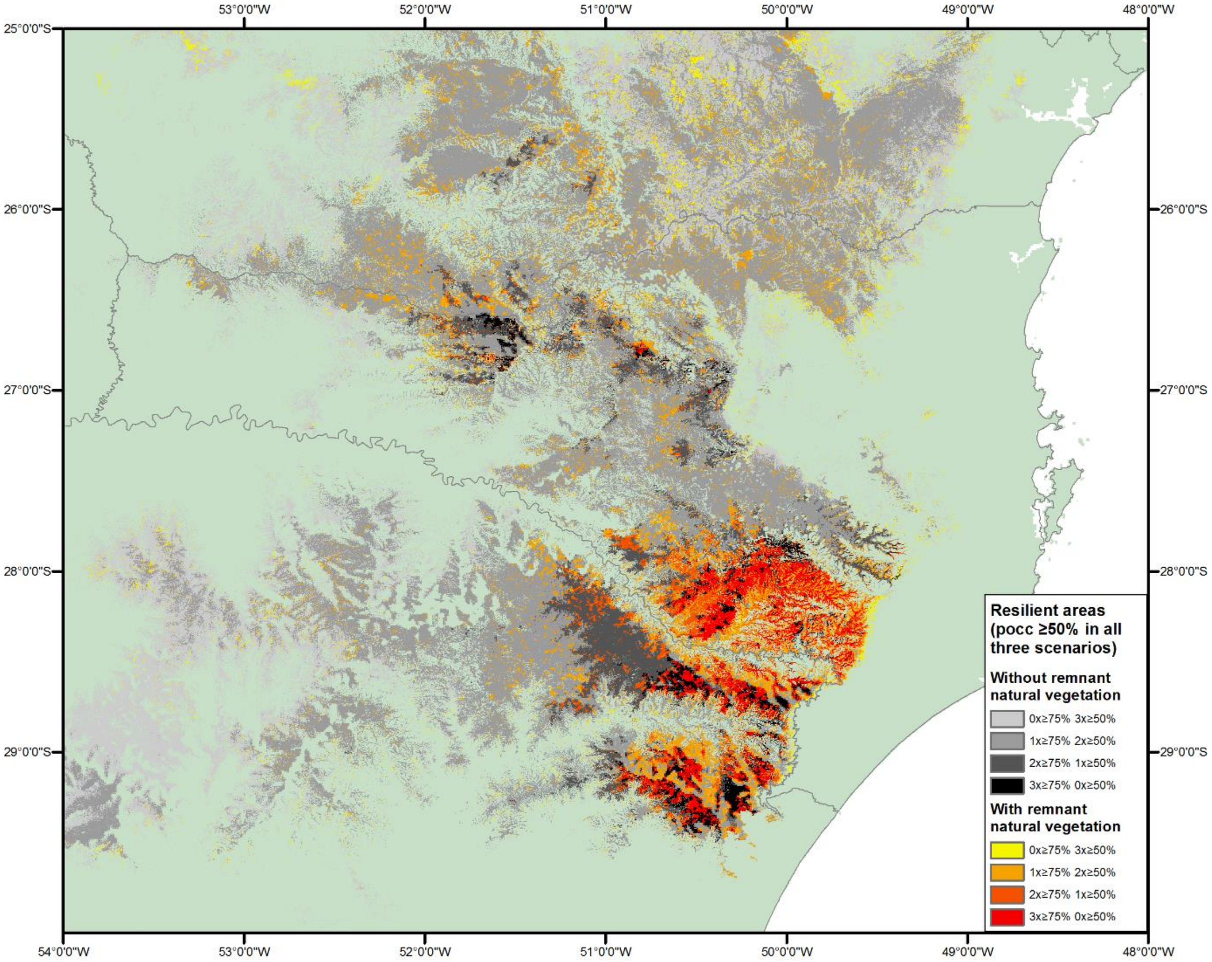

Figure 3: Map showing the loss of Araucaria's climatically resilient areas (from CHELSA+ ensemble model) to habitat change. Darker/redder areas are more climatically resilient, from light grey/yellow (p_{occ} 50%-75% in all three scenarios) to black/red (potential microrefugia, p_{occ} ≥75% in all scenarios).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

The great majority of microrefugia, and the habitat patches they reside within, are located outside existing conservation infrastructure (fig. 4). Of all Araucaria's microrefugia which still have natural vegetation cover, only 2.5% are in any protected area, with a higher proportion of microrefugia in remnant forest represented (5.6%, 18.6 km^2) than those in Campos (2.2%, 59.5 km^2). Two national parks (Aparados da Serra and São Joaquim) contain 83.3% of all the protected Campos microrefugia and the two largest areas of highly resilient forest (6.7 km^2 and 4.0 km^2, respectively). Nine other protected areas average 0.9 km^2 of forest microrefugia each, and four of these hold the remaining 9.9 km^2 of protected Campos microrefugia. And although natural vegetation patches holding significant microrefugial components are found in fifteen protected areas (with six more, far from microrefugial cells, in the east of the outlier forest fragment discussed above), half (50.8%) of the total protected area is concentrated in São Joaquim National Park, which holds 162.4 km^2 of forest patches containing microrefugia and 148.3 km^2 of similar patches in Campos.

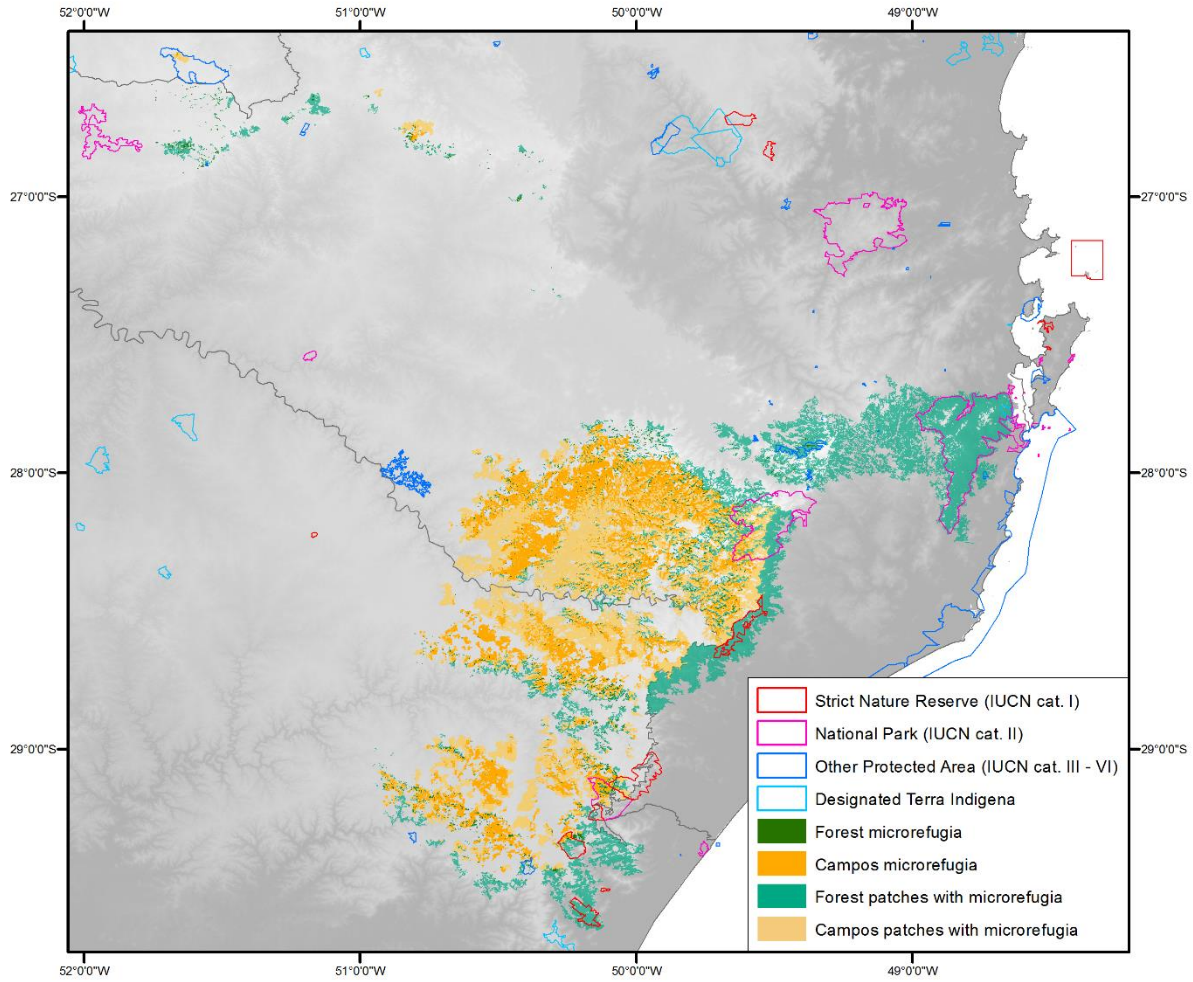

Figure 4: Map showing microrefugial cells in remnant vegetation (forest in dark green, Campos in orange), patches of remnant vegetation containing ≥100 microrefugial cells or which have ≥5% of their area covered by microrefugia (forest in pale green, Campos in buff), protected areas and designated Terras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

4. Discussion

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

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

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

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

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

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

Fine-scale species distribution models are known to predict patchier distributions and improved persistence compared to those conducted at coarser resolutions (Storlie *et al.*, 2013; Meineri and Hylander, 2017), an effect also found in this study. The concept of microrefugia is one with origins in palaeoecology (Petit, Hu and Dick, 2008; Rull, 2009; Dobrowski, 2011; Bemmels, Knowles and Dick, 2019) but which is increasingly recognised as highly relevant for conservation ecology (Ashcroft, 2010; McLaughlin and Zavaleta, 2012; Hannah *et al.*, 2014; Suggitt *et al.*, 2018). Our finding that some areas among the grasslands on southern Brazil's highlands are likely to shelter microrefugia for Araucaria echoes the species' past ecology: previous relatively rapid expansions of forest on the plateau are thought to have been facilitated by the expansion and persistence of gallery forests through the late Pleistocene and Holocene (Behling *et al.*, 2004; Costa *et al.*, 2017). Whether the patches of microrefugial vegetation we have identified in this study will similarly persist and act as sources of future forest expansion is far from certain, however, as our findings show that significant portions of this resilient habitat have either already been lost or currently lie outside formal protected areas. And, with the next century's climate likely to be highly novel compared to the present and recent past (Fischer *et al.*, 2018; Fitzpatrick *et al.*, 2018), an improved understanding of Araucaria's spatial dynamics throughout the Quaternary may be essential for truly long-term conservation planning.

Araucaria's long evolutionary history, its past and present cultural and economic significance, and its Critically Endangered status combine to make such planning an urgent task. Deforestation between 1870 and 1970 left less than 3% of Araucaria's former forest habitat standing by the late

20th Century (Thomas, 2013). Here we have shown that climate change is likely to repeat these losses within this century: of the 9,577 km^2 of forest fragments in our study region where Araucaria currently has ≥75% probability of occurring, only 3.5% will remain similarly suitable by 2070. However, by highlighting the areas whose climatic and topographic conditions give Araucaria the best chance of persisting, we hope to encourage the critical conservation measures needed for this iconic tree to see another century on the highlands.

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Author contributions

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

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Preface to Chapter 2: A quantitative study of modern pollen–vegetation relationships in southern Brazil's Araucaria Forest

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Overview

This paper marks the point where the research in this thesis pivots away from the present and future alone, and begins to incorporate the past. Using modern vegetation surveys and pollen rain from moss polsters, it establishes the relationships between Araucaria Forest taxa and their likely representation in fossil pollen records. This information lays important foundations for the chapters which follow, both of which rely on integrating species-level modelling data with palaeoecological proxy evidence; this chapter's research helps clarify the potentially skewed ways in which the former is represented in the latter. Additionally, by evaluating the extent to which compositional and structural changes in the forest can be seen in pollen records, this paper's findings are an important prerequisite to Chapter 4's efforts to identify evidence of pre-colonial Indigenous land use in Araucaria Forests using that very same proxy.

Contribution to the research

This paper is an addition to the three main chapters in this thesis. It was conceived and designed by a post-doctoral researcher in the research group, but is included here as it is relevant to my wider thesis and I made a substantial contribution to the study. When I was invited to join this paper as a co-author, an initial data analysis and draft were available; I was not involved in any of the vegetation data collection, processing or counting of pollen, and some decisions on the paper's framing and analytical approach had already been taken. However, I realised that the initial analysis did not support some arguments in the draft, so completely reanalysed the data (including applying some new approaches), wrote a new draft which reflected the updated findings, and led the rest of the authoring process. My contribution to this paper is estimated to be 40%. The published author contribution statement is below:

MLC and FEM conceived the study; MLC collected moss polsters; MLC and LAS collected vegetation survey data; MLC performed pollen analysis and counting; MLC and OJW analysed the data and interpreted the results; OJW, MLC and FEM drafted the manuscript; all authors commented on the manuscript before submission.

Chapter 2: A quantitative study of modern pollen-vegetation relationships in southern Brazil's Araucaria Forest.

Authors

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Abstract

Southern Brazil's highland Araucaria Forest is ancient, diverse and unique, but its future is under significant threat from 20th-Century habitat loss and 21st-Century climate change. Palaeoecological studies have revealed that it expanded rapidly over highland grasslands around 1,000 years ago, but whether this expansion was caused by human land use or climate change has been a topic of considerable debate. Discriminating between these potential drivers has so far not been possible with fossil pollen, however, as the palynological representation of floristic and structural differences in Araucaria Forest remains poorly understood. Here, we address this shortcoming using modern pollen rain from moss polsters and vegetation surveys in forest areas with minimal current human disturbance. We show that forest plots with evident structural differences lack consistent differences in their floristic composition and cannot be reliably distinguished by their pollen spectra. We quantify pollen-vegetation relationships for 27 key tree genera of Araucaria Forest, showing that, despite significant intra-taxon variability, 22 of these are under-represented or absent in the pollen record. These palynologically under-represented and silent taxa include many of the forest's most ecologically important tree species, with only *Araucaria*, *Lamanonia*, *Podocarpus*, *Myrsine* and *Clethra* being more abundant in the pollen rain than vegetation. Our results suggest that subtle structural changes in Araucaria Forest, as well as moderate to significant floristic changes, may not be clearly distinguished in fossil pollen records – an important limitation when attempting to identify past human and climatic impacts on Araucaria Forest via pollen analysis.

1. Introduction

1.1. Rationale

Disentangling the past effects of humans and climate on ecosystems requires a rigorous understanding of the vegetation changes that occurred, and how these are reflected in palaeoecological proxies. This is an important undertaking in Brazil's Araucaria Forest (also known as Mixed Ombrophilous Forest), an ancient, highly diverse and threatened ecosystem in the country's southern highlands. Studies have charted changes in the distribution of Araucaria Forest in relation to climatic variations since the late Pleistocene (Behling *et al.*, 2004; Ledru, Mourguiart and Riccomini, 2009), many finding rapid increases in its pollen abundance about 1,000 years ago which, in some sites, reached levels unprecedented for tens of thousands of years (Behling *et al.*, 2004; Gu *et al.*, 2017). This marked expansion ca. 1000 years ago was much more drastic than the steady expansion of Araucaria Forest over the previous few millennia, and has been attributed by some authors to ancient human land use, rather than climate change, due to the coincident expansion of the local southern proto-Jê culture (Noelli, 2000; Bitencourt and Krauspenhar, 2006; dos Reis, Ladio and Peroni, 2014; Lauterjung *et al.*, 2018; Robinson *et al.*, 2018), whose economy, spiritual beliefs and living space were closely linked to the forest (Iriarte and Behling, 2007; de Souza, Corteletti, *et al.*, 2016; Iriarte *et al.*, 2016).

Understanding the extent to which Araucaria Forest's late-Holocene expansion can be attributed to humans versus climate change will improve our understanding of the ecosystem's responses to prevailing climatic conditions – a particularly important endeavour in the face of continuing anthropogenic climate change. With regional temperatures forecast to become warmer, and precipitation more variable, as this century progresses (Chou *et al.*, 2014), the cold- and humidity-dependent Araucaria Forest is likely to contract (Wrege *et al.*, 2009; Bergamin, 2017). Understanding how this iconic forest responded to past variations in climate – and how humans may have altered this response – may help conservationists anticipate and ameliorate the effects of modern climatic changes upon its distribution. This is especially important as Araucaria Forest cover was much reduced by the 20th-Century logging boom in the states of Paraná, Santa Catarina and Rio Grande do Sul (de Carvalho and Nodari, 2010), with remnants now covering just 12.6% of the biogeographic region it previously dominated (Ribeiro *et al.*, 2009).

The main proxy used for reconstructing past dynamics of vegetation on the southern Brazilian highlands is fossil pollen from lake/bog sediments, the informed and accurate interpretation of which requires appropriate characterisation and quantification of modern pollen-vegetation relationships. This is currently poor for Brazil's Araucaria Forest. Existing pollen-vegetation studies (Behling, Bauermann and Neves, 2001; Garcia *et al.*, 2004; Jeske-Pieruschka *et al.*, 2010) are purely qualitative, identifying Araucaria Forest's key indicator taxa but giving little insight into the degree to which the floristic composition or structure of these forests can be resolved palynologically. In this study, we address this shortcoming, presenting the first quantitative examination of the modern pollen-vegetation relationship of Araucaria Forest and its constituent taxa.

1.2. Background

Araucaria Forest is found at the southern and south-eastern reaches of the Atlantic Forest biome, a global biodiversity hotspot (Myers *et al.*, 2000; Colombo and Joly, 2010). It occupies the biome's high-altitude and low-temperature extreme niches (Oliveira-Filho *et al.*, 2014; Neves *et al.*, 2017), mostly occuring above 500 m altitude (Hueck, 1953; Lacerda, 2016) in areas with high annual rainfall and climatic conditions classified as Cfb – humid subtropical oceanic climate, with temperate summers and no dry season (Alvares *et al.*, 2013) – under the Köppen-Geiger system (Hueck, 1953; Higuchi *et al.*, 2012). At more southerly latitudes in Brazil, some apparently natural stands of Araucaria Forest can also be found at elevations below 500 m (Behling *et al.*, 2016).

Araucaria Forest is home to over 1,500 species of plants, 6% of which are endemic to the Atlantic Forest biome (Neves *et al.*, 2017), and is characterised by the dominance of the conifer *Araucaria angustifolia* in its canopy (Leite and Klein, 1990; Meyer *et al.*, 2013; Duarte *et al.*, 2014). This species has the third highest EDGE score (a metric which combines evolutionary distinctiveness and global endangerment) of all the world's gymnosperms (Forest *et al.*, 2018), imperilled by logging and habitat loss which started in the late 19th Century and reduced the forests' area by 97% within three generations (de Carvalho and Nodari, 2010; Thomas, 2013). Other important arboreal species include *Dicksonia sellowiana, Podocarpus sellowiana, Matayba elaeagnoides, Lithraea brasiliensis, Clethra scabra, Ocotea porosa*, and *Prunus myrtifolia* (Meyer *et al.*, 2013; Duarte *et al.*, 2014).

Araucaria Forest is not floristically homogenous, however. Early studies differentiated eight types of Araucaria Forest (Klein, 1978), and the ecosystem's mixture of tropical and temperate elements varies with longitude, altitude, temperature, river basin, and distance to other forest types (Klein, 1975; Higuchi *et al.*, 2012; Duarte *et al.*, 2014; Gonçalves and Souza, 2014; Oliveira-Filho *et al.*, 2014;

Sevegnani *et al.*, 2016). At higher altitudes, under drier conditions and in areas of high fire frequencies and shallower soils, Araucaria Forest forms mosaics with Campos grasslands (Hueck, 1966; Müller *et al.*, 2012; Oliveira-Filho *et al.*, 2014), with other ecotones occurring with seasonally deciduous and dense ombrophilous forests at its western and eastern extents, respectively (Gonçalves and Souza, 2014; Oliveira-Filho *et al.*, 2014).

Fossil pollen records from the eastern edge of southern Brazil's highland plateau show that the area was dominated by Campos at the Last Glacial Maximum, with Araucaria Forest likely confined to river valleys (Behling, 2002; Behling *et al.*, 2004; Leonhardt and Lorscheitter, 2010). These forests subsequently expanded slightly 4,000-3,000 years ago, and then rapidly 1,500-900 years ago (Behling, 1995, 1997b; Behling *et al.*, 2004; Iriarte and Behling, 2007; Leonhardt and Lorscheitter, 2010; Silva and Anand, 2011; Jeske-Pieruschka and Behling, 2012), in some places replacing grasslands within a century (Behling *et al.*, 2004; Iriarte and Behling, 2007).

These changes have typically been attributed to climate change (Rodrigues, Behling and Giesecke, 2016b). However, recent speleothem data (Bernal *et al.*, 2016) show that, although the initial Araucaria Forest expansion at 4,000 yr BP does correlate with an increase in rainfall, no subsequent climate change accompanies the later, more significant forest expansion at 1,500-900 yr BP (Robinson *et al.*, 2018). This has led several authors to invoke humans as the most likely cause for this most recent, rapid expansion of Araucaria Forest (Noelli, 2000; Bitencourt and Krauspenhar, 2006; Iriarte and Behling, 2007; dos Reis, Ladio and Peroni, 2014), bolstered by evidence that, under natural conditions, expansion of forest patches into Campos grassland can be extremely slow (less than 100 m in 4,000 years (Silva and Anand, 2011)).

Before European arrival, the Indigenous people of the highlands, the southern Jê, had lifestyles that were at least semi-sedentary and practised a mixed economy that combined the cultivation of manioc (Manihot esculenta), maize (Zea mays), squash (Cucurbita sp.) and beans (Phaseolus sp.) with hunting, fishing, and gathering forest and riverine resources (Métraux, 1946; Henry, 1964; Corteletti *et al.*, 2015; de Souza, Robinson, *et al.*, 2016; Noelli and De Souza, 2017). Araucaria angustifolia seeds, known as pinhão, have long been a critical food source for the southern Jê (Métraux, 1946; Henry, 1964; Urban, 1985; Heineberg, 2014; Corteletti *et al.*, 2015; Loponte *et al.*, 2016), with one group traditionally defining a year as "one period with no pine nuts" (Henry, 1964, p. 68). Ethnographic studies of extant southern Jê groups have also highlighted the importance of Araucaria Forest – and A. angustifolia in particular – as a source of spiritual power and cultural identity (Haverroth, 1997; Silva, 2002; Hoffmann, 2011; Fernandes and Piovezana, 2015; Robinson *et al.*, 2017).

Archaeological records show that the southern Jê flourished around 1,000 years ago (Iriarte *et al.*, 2013, 2016; Noelli and De Souza, 2017; Robinson *et al.*, 2018), as changes in domestic architecture appeared (de Souza, Robinson, *et al.*, 2016), combining with the arrival of funerary mound-and-enclosure complexes (de Souza, Corteletti, *et al.*, 2016; Iriarte *et al.*, 2016) to form highly structured 'sacred landscapes' (Iriarte *et al.*, 2013) in the highlands. The temporal overlap of these changes with the most recent Araucaria Forest expansion suggests that more available forest resources likely helped underpin the cultural changes (Iriarte and Behling, 2007), and there is some evidence that the southern Jê may in turn have helped expand the forest (dos Reis, Ladio and Peroni, 2014; Lauterjung *et al.*, 2018; Robinson *et al.*, 2018), though this has not yet been tested with fossil pollen data.

1.3. Aims

Quantitative studies of the relationships between present-day Araucaria Forest and its constituent pollen assemblages are needed to improve the level of ecological detail that can be extracted from fossil pollen records, and thereby obtain a firmer basis for unravelling the relative roles of climate change versus human land use in driving this threatened forest's long-term dynamics over the past several millennia. We therefore conducted a study to quantitatively define the vegetation-pollen relationships of Araucaria Forest taxa. Specifically, we analysed floristic inventories from vegetation plots, and collected their constituent pollen assemblages from moss polsters, to determine: 1. whether structurally different Araucaria Forest patches can be differentiated by their pollen spectra, and 2. how the constituent species of these patches are represented in the modern pollen rain.

2. Methods

2.1. Study site

The Reserva Particular do Patrimonio Natural (RPPN) Emilio Einsfeld Filho (27°58'0.80"S, 50°49'20.03"W, 650-990 m a.s.l.), managed by the Florestal Gateados company, is located in the municipalities of Campo Belo do Sul and Capão Alto, southern Santa Catarina State, Brazil (fig. 1). RPPN Emilio Einsfeld Filho is located on the plateau of the Serra Catarinense, a gently undulating landscape. The reserve covers 6,329 hectares of native Araucaria Forest patches within a wider matrix of Campos grassland, with the largest density of forest along rivers, valleys and slopes. Forested areas have been protected from timber extraction since 1989 and cattle grazing since 1993 (Zeller, 2010).

The climate of the area corresponds to Cfb in the Köppen-Geiger classification: humid subtropical with temperate summers and no dry season, but with occurrence of severe frosts (Formento *et al.*, 2004; Zeller, 2010; Alvares *et al.*, 2013). Between 2005 and 2009 the reserve's average annual temperature was 16°C, with hottest months averaging 31°C, coldest months averaging 6.5°C and a lowest recorded temperature of -12°C; in this period annual precipitation varied between 1300 and 2400 mm, with an average of 129 rainy days a year (Zeller, 2010).

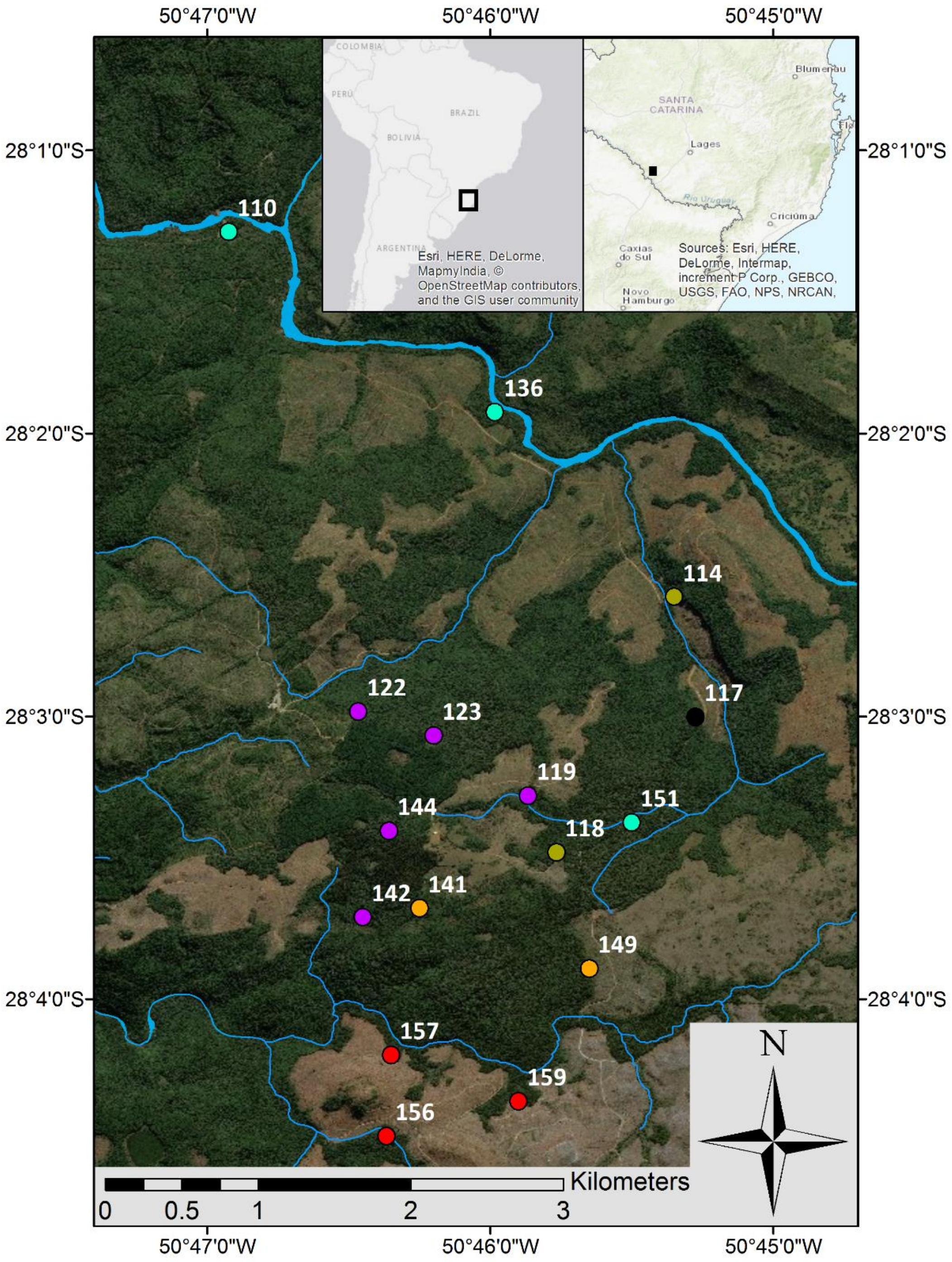

Figure 1: Map of forest plot locations; numbers refer to plot codes (see Table 1 below). Plot colours: Cyan: riverine; Olive: slope; Black: rock outcrop; Purple: open understorey; Orange: closed understorey; Red: disturbed.

2.2 Field sampling

2.2.1 Vegetation survey

The native Araucaria Forest at RPPN Emilio Einsfeld Filho has been subject to ecological studies for the last 20 years, with permanent plots of 10 x 50 m installed to perform floristic inventories and study forest dynamics under distinct geographic conditions. Within each plot all trees with d.b.h. (diameter at breast height) ≥ 10 cm have been recorded (Formento *et al.*, 2004; Maçaneiro *et al.*, 2018). Percentage abundances were calculated based upon all recorded stems surveyed within each plot.

The sixteen plots used in this study are located within the oldest and least disturbed areas of forest and incorporate the widest available range of vegetation form and physical setting (Table 1). Data on canopy openness, slope, animal disturbance, geographical feature associations and topographic position were collected during botanical surveys in 2015, and the plots classified into six structural categories according to their dominant feature:

- slope: forest patches in areas with > 25% inclination
- rock outcrop: forest patches where rock outcrops cover > 20% of plot surface
- riverine: forest patch bounded by, or entirely within 50 m of, a water course (river or creek)
- open understorey: forest with closed canopy and scarce understorey
- closed understorey: forest with closed canopy and dense understorey
- naturally disturbed: forest patches with evidence of ground disturbance by wild boars

Plot ID	Forest Plot category	Coordinates	Altitude (a.s.l.)
114	Slope	28° 2'34.70"S, 50°45'21.40"W	780 m
118	Slope	28° 3'28.80"S, 50°45'45.80"W	924 m
117	Rock outcrop	28° 3'0.10"S, 50°45'16.50"W	856 m
110	Riverine	28° 1'17.30"S, 50°46'55.50"W	721 m
136	Riverine	28° 1'55.50"S, 50°45'59.00"W	740 m
151	Riverine	28° 3'22.50"S, 50°45'29.60"W	874 m
119	Open understorey	28° 3'16.80"S, 50°45'51.70"W	929 m
122	Open understorey	28° 2'59.00"S, 50°46'28.10"W	921 m
123	Open understorey	28° 3'4.10"S, 50°46'11.60"W	935 m
142	Open understorey	28° 3'42.60"S, 50°46'26.60"W	922 m
144	Open understorey	28° 3'24.30"S, 50°46'21.50"W	953 m
156	Disturbed	28° 4'29.00"S,	850 m

		50°46'22.10"W	
157	Disturbed	28° 4'11.80"S, 50°46'20.90"W	851 m
159	Disturbed	28° 4'21.60"S, 50°45'53.60"W	868 m
141	Closed understorey	28° 3'40.70"S, 50°46'14.90"W	931 m
149	Closed understorey	28° 3'53.50"S, 50°45'39.20"W	891 m

Table 1: The studied forest plots, their structural category, and the location and altitude of each transect's starting point.

2.2.2 Modern pollen rain

Using moss polsters to study modern pollen rain has been widely used and recognized as a reliable technique (Hicks, 1977; Caseldine, 1989; Tonkov *et al.*, 2001; Pardoe, 2006; Atanassova, 2007; López-Sáez *et al.*, 2010; Pardoe *et al.*, 2010). Moss polsters can collect several years' pollen (Pardoe *et al.*, 2010), occur naturally within the forest on different substrates and at varied heights (allowing for effective capture of pollen rain) and do not need to be installed and managed before analysis (Hicks, 1985). Moss polsters were gathered every 10 m along the 50 m length of each forest inventory plot surveyed. At each collection point, polsters were obtained from ground level (including rocks), chest height (1.20 m) and overhead (1.80 m). The samples for each point of collection were mixed to form one homogeneous sample for each plot (following Pardoe *et al.*, 2010), placed in a labelled, sealed plastic bag, and stored at 4°C to preserve the material.

2.3. Laboratory methods

Subsamples of 1 cm^3 were extracted from each homogenised sample for pollen processing. Each subsample was centrifuged, washed with distilled water, centrifuged again, then treated with 10% NaOH and put in a hot-water bath to deflocculate the organics. Afterwards, acetolysis was carried out in the samples to dissolve cellulose material (Faegri and Iversen, 1989).

Samples were mounted on slides in silicone oil and counted at 400× and 1000× magnification using a Leica DME binocular microscope. Samples were counted to a minimum of 300 terrestrial pollen grains. Aquatic taxa and spores were also counted as is standard practice, but were excluded from the total terrestrial pollen (TTP) sum; non-native species (e.g. pine from recent plantations surrounding the reserve) were also excluded from the TTP sum. For pollen determination, the reference collection of the Tropical Palaeoecology Research Group of the University of Reading was used, along with several pollen atlases – Colinvaux *et al.* (1999), Hooghiemstra (1984), Roubik and Moreno (1991), Behling (1993) – and the online Neotropical Pollen Key (Bush and Weng, 2007). Diagrams of vegetation and pollen abundance were made using C2 v.1.7.7 (Juggins, 2016).

2.4. Data analysis

2.4.1 Vegetation data processing

Analysis of each plot's floristic inventory data used percentage abundance (relative to the total number of individual trees counted) and relative coverage value (RCV). RCV, expressed as a percentage, indicates the importance of a species within a forest plot, and is calculated as the average of its relative density (the percentage of all individuals in a plot which belong to that species) and relative dominance (the percentage contribution from individuals of that species to a plot's total basal area).

2.4.2 Statistical analysis of vegetation and pollen data

To investigate the extent to which structural differences between plots are reflected in their vegetation composition and pollen rain, we conducted cluster and Detrended Correspondence Analysis (DCA) multivariate analyses using PAST (Hammer, Harper and Ryan, 2001) v.3.19 (2018). Raw floristic inventory and pollen data were normalised using natural logarithm before running the analyses. Only taxa with abundance ≥ 2% in two or more plots were considered for cluster and multivariate analysis.

Cluster analysis was run with hierarchical clustering using the Unweighted Pair Group Method (UPGM) algorithm, which iteratively joins clusters based on the average distance between all members of the groups (Kent and Coker, 1992; Legendre *et al.*, 2012). The measure of similarity or distance measurements between samples (forest plots) was calculated using Bray-Curtis index of dissimilarity (Kent and Coker, 1992). The DCA uses the same algorithm as Decorana (Hill and Gauch, 1980), with modifications according to Oksanen and Minchin (1997). The DCA method was preferred as it allows the identification of the ecological variances amongst the forest plots (Correa-Metrio *et al.*, 2014).

To enable direct comparisons between taxa in the vegetation and pollen rain, which were mostly identified at different taxonomic levels, the vegetation-pollen analysis was performed at genus level, with congeneric species combined for the analysis (Burn, Mayle and Killeen, 2010).

To quantify the vegetation-pollen relationships of taxa in this study area, we calculated mean p/v (pollen/vegetation) values (Gosling *et al.*, 2009; Burn, Mayle and Killeen, 2010; Montade *et al.*, 2016), which are analogous to R values (Davis, 1963). We calculate the p/v value for taxon *i* as:

$$p/v_i = \frac{Pollen\ abundance\ (\%)\ averaged\ over\ all\ plots_{\,i}}{Vegetation\ abundance\ (\%)\ averaged\ over\ all\ plots_{\,i}}$$

Although more complex measures of pollen production exist (e.g. Parsons and Prentice, 1981; Sugita, 2007a, 2007b), p/v values provide a straightforward and intuitive index of the relationship between vegetation and pollen abundance and continue to be foundational for vegetation reconstruction (Mrotzek *et al.*, 2017).

To complement this metric and show the variability in pollen-vegetation relationships between plots, we also calculated a pollen-vegetation abundance differential for taxon *i*:

$$Abundance\ differential_i = Pollen\ abundance\ (\%)_i - Vegetation\ abundance\ (\%)_i$$

Plots where a taxon was absent from both the pollen rain and vegetation survey were not included in calculations of mean differentials. p/v values and abundance differentials could not be calculated for herbaceous taxa as these were not included in the vegetation survey. Data were plotted using R v.3.4.2 (R Core Team, 2020) and PAST (Hammer, Harper and Ryan, 2001) v.3.19 (2018).

3. Results

3.1. Vegetation

Across the 16 forest plots, 54 tree species with d.b.h. ≥ 10 cm were recorded, of which 33 had relative abundances of 2% or higher in at least two plots; the relative (percentage) abundance of these species within each plot is shown in fig. 2. The most consistently present species were

Lithraea brasiliensis (15 plots), *Cinnamodendron dinisii* (13 plots), *Myrsine coriacea, Ocotea pulchella* and *Araucaria angustifolia* (12 plots), undifferentiated *Eugenia* sp. (11 plots), and *Calyptranthes* cf. *concinna, Ilex theezans, Pera glabrata, Podocarpus lambertii* and *Zanthoxylum kleinii* (10 plots).

The taxa with the highest average abundance in the vegetation were *L. brasiliensis* (9.1%), *Cinnamodendron dinisii* (7.7%), *A. angustifolia* (7.3%), undifferentiated *Eugenia* sp. (6.7%), *O. pulchella* (5.7%), and *Calyptranthes* cf. *concinna* (5.0%). Of the common taxa, *L. brasiliensis* had the highest maximum abundance (34.2%), followed by *Eugenia* sp. (26.4%), *A. angustifolia* (26.1%), *E. uniflora* (25.7%) and *Cinnamodendron dinisii* (24.1%). Two less common species with high maximum abundances were *Matayba elaeagnoides* (found in three plots, max. 35.6%) and *Nectandra megapotamica* (three plots, max. 28.6%).

Generally, tree species that were more abundant also had higher relative coverage values (RCVs; fig. 3): the taxa with the highest RCVs averaged across all plots were *L. brasiliensis* (10.3%), *A. angustifolia* (10.0%), *O. pulchella* (7.8%), *C. dinisii* (6.1%), *Styrax leprosus* (5.3%) and undifferentiated *Eugenia* sp. (5.2%). Some species were found in few plots, but had high RCVs where they were present: the less frequent species with the highest RCVs averaged across the plots in which they were found were *M. elaeagnoides* (15.6%, four plots), *Luehea divaricata* (9.2%, three plots), *N. megapotamica* (9.0%, three plots), *Vernonanthura discolor* (7.4%, five plots), *Sebastiania commersoniana* (7.0%, six plots), *Prunus myrtifolia* (5.7%, six plots), *Piptocarpha angustifolia* (5.2%, two plots), *Myrceugenia* sp. (5.1%, five plots) and *Myrsine umbellata* (5.0%, two plots).

3.2. Pollen

170 pollen and spore types were found in the 16 forest plots. Of these, 118 could be identified to family level, 95 of which could be refined to genus, one to species (*Ilex theezans*). We also assign species names to *Araucaria angustifolia* and *Podocarpus lambertii* because no other species of these genera occur in our study area. The plots' pollen spectra are summarised in fig. 4, where abundant and important taxa are shown.

Eight pollen types were found in all 16 plots: *A. angustifolia*, Asteraceae (others total), *Eugenia* type, 'cf. *Lithraea* a (Anacardiaceae)', *Myrsine*, Poaceae, *P. lambertii*, and Pteridophyta. Additionally, Araceae pollen was found in 15 plots, and *Lithraea, Vernonanthura*-type and *Calyptranthes*-type in 14; *Sebastiania* and undifferentiated Myrtaceae pollen was found in 12 plots, and *Clethra*, *I. theezans* and *Pteris* each in 10 plots. Additionally, *Alchornea* pollen and *Cyathea*-type spores were found at very low levels (average abundance 0.27% and 0.2% respectively) in 11 plots, with *Senecio*-type (average 0.35%) and *Mimosa scabrella*-type (average 0.25%) present in 10 plots.

Myrsine pollen was the most abundant across all plots (averaging 19.5%), followed by *A. angustifolia* (16.6%), Pteridophyta (13.2%), *Podocarpus lambertii* (7.9%) and Poaceae (5.2%). *Eugenia*-type, 'cf. *Lithraea* a (Anacardiaceae)', Asteraceae (others total), *Lamanonia*, *I. theezans, Calyptranthes*-type, *Vernonanthura*-type and *Clethra* pollen all had average abundances between 1% and 5%.

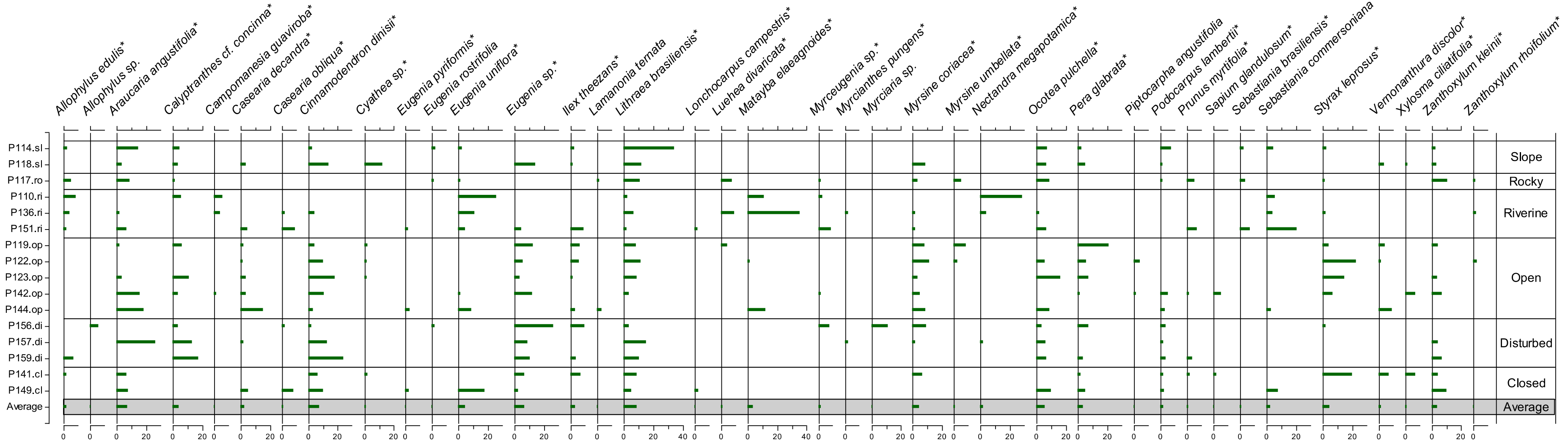

Figure 2: Relative abundance (%) of selected tree species in the vegetation survey. Species included in the cluster analysis and DCA are indicated with an asterisk.

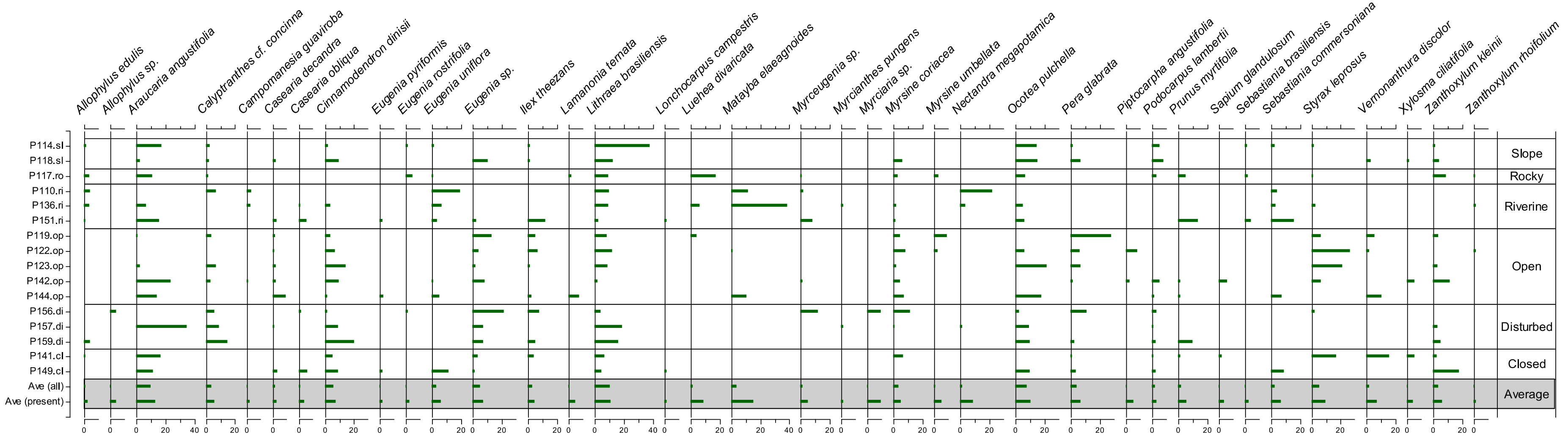

Figure 3: Relative Coverage Values (RCVs, %) of selected tree species in the vegetation survey. 'Ave. (all)' = sum of RCVs/total number of plots; 'Ave. (present)' = sum of RCVs/number of plots in which taxon was present.

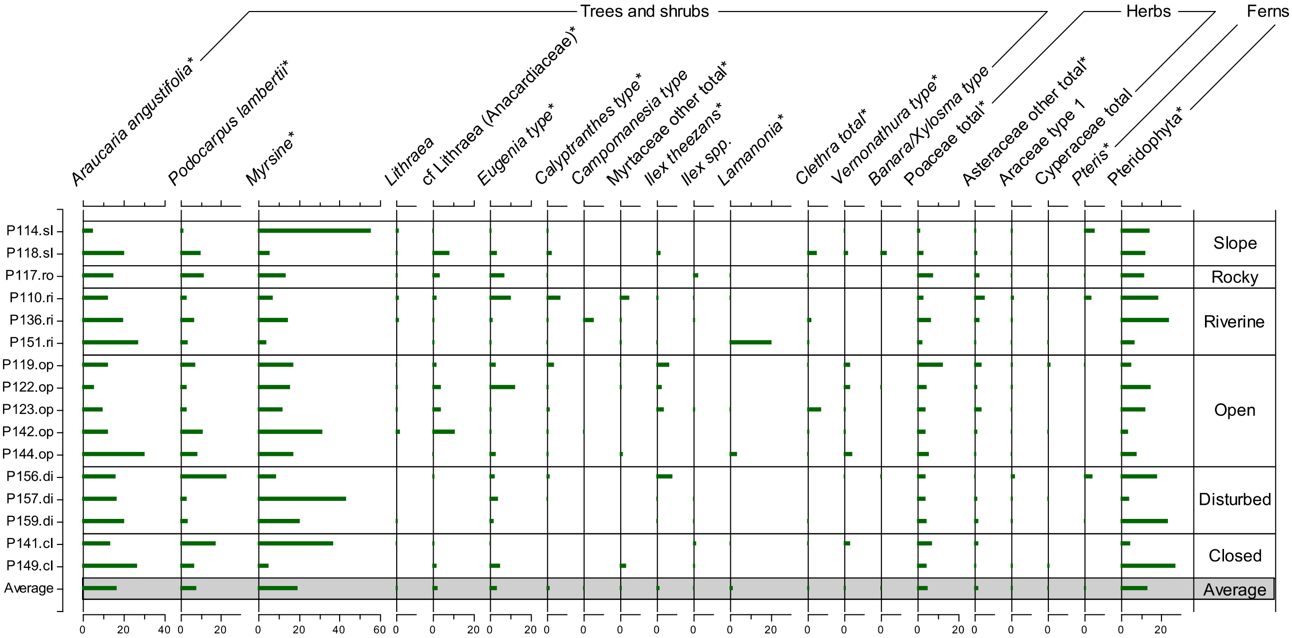

Figure 4: Relative abundance (%) of selected pollen types. Taxa included in the cluster analysis and DCA are indicated with an asterisk

3.3. Plot differentiation

33 taxa from the vegetation survey and 15 pollen types met the 2% abundance threshold for inclusion in the plot differentiation analysis (see section 2.4.2); these are identified with asterisks in the summary diagrams (figs. 2 and 4).

In the cluster analysis of vegetation data (fig. 5a), similarity scores range from ~0.25 to > 0.75. Two plot groupings that are somewhat structurally consistent can be highlighted. One such cluster contains three of the five open-understorey plots (P119, P122 and P123) with the lone slope plot P118 (similarity score > 0.65); the other is the pairing of riverine plots P136 and P110 which, despite having similarity scores < 0.6 relative to each other, are together highly dissimilar to all other plots.

In the DCA of vegetation data (fig. 5b), most variation is explained on axis 1 (eigenvalue 0.3781), with values ranging from -196 (*Cyathea* sp.) to 365 (*Nectandra megapotamica*). The majority of sample plots are clustered between 0 and 143 on axis 1, with the riverine plots P136 (202) and P110 (255) more distinguished. The values on axis 2 (eigenvalue 0.1268) range from -337 (*Sapium glandulosum*) to 388 (*Myrsine umbellata*); sample plots are all clustered between 0 and 140 on this axis.

In the pollen cluster analysis (fig. 5c), plots' similarity scores range from ~0.5 to > 0.85. Two small clusters dominated by open understorey forest plots were found: P122 and P123 (both open; similarity > 0.7), and P144 and P119 (both open) with the rocky forest plot P117 (similarity > 0.7). These two groupings are quite dissimilar from each other, however, and the cluster that contains them both also contains seven non-open plots, and excludes the final open plot (P142).

In the DCA of pollen spectra (fig. 5d) axis 1 (eigenvalue 0.2454) ranges from -72 (*Pteris*) to 305 (*Lamanonia*), with 15 of the plots clustered between 0 and 119; P151 is located at 184. The forest plots are less well distinguished on axis 2 (eigenvalue 0.07194), sitting between values of 0 and 110 on an axis that ranges from -233 (Myrtaceae others total) and 426 (*Clethra* total).

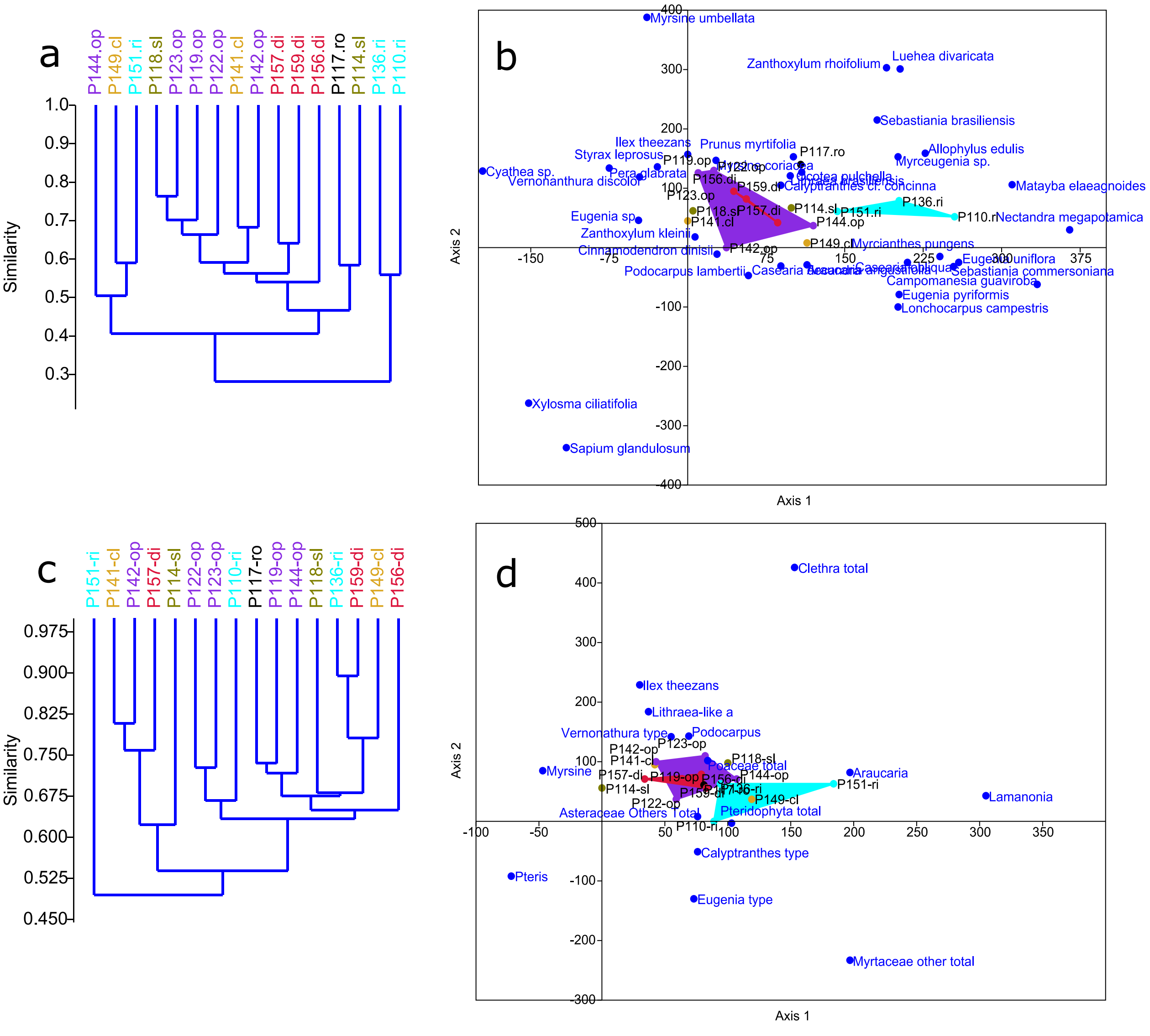

Figure 5: Cluster analyses (left; a, c) and DCAs (right; b, d) of plots by vegetation (top; a, b) and pollen (bottom; c, d) taxa found in ≥2 plots at ≥2% abundance. In the DCAs, convex hulls are delimited for structural categories containing three or more plots. Plot types are identified by colour and two-letter code (op: open; cl: closed; ri: riverine; di: disturbed; ro: rock; sl: slope; see Table 1).

3.4. Vegetation-pollen relationships.

We examined the vegetation-pollen relationships of 27 arboreal genera. Four of these (*Myrceugenia*, *Nectandra*, *Ocotea* and *Piptocarpha*) were present in the vegetation but with no identifiable pollen produced or preserved (p/v = 0), and one (*Clethra*) was frequent in the pollen record without being recorded in the vegetation survey (giving it a mathematically infinite p/v value). Four other genera had higher average abundances for pollen than vegetation (p/v > 1), and 18 were more abundant in the vegetation than pollen (p/v < 1) – see fig. 6.

Of the taxa found in both pollen and vegetation datasets, the most over-represented genus is *Lamanonia*, followed by *Podocarpus*, *Myrsine* and *Araucaria*. In plot P151 *Lamanonia* was not recorded in the vegetation but its pollen made up 20.3% of the total; with this data point excluded from the average calculations, *Lamanonia*'s p/v value is 1.25. The most under-represented genera found in the pollen rain are *Cinnamodendron*, *Allophylus*, *Prunus*, *Styrax*, *Luehea* and *Zanthoxylum* (p/v < 0.05); *Casearia*, *Matayba*, *Pera* and *Lithraea* also have p/v scores < 0.1. *Calyptranthes, Campomanesia, Eugenia, Sapium, Sebastiania* and *Xylosma* all have p/v values between 0.1 and 0.5. The pollen type 'cf. *Lithraea* a (Anacardiaceae)' was three times more common than pollen that could be confidently identified to the *Lithraea* genus; assigning these grains to *Lithraea* changes the genus's p/v score from 0.09 to 0.39.

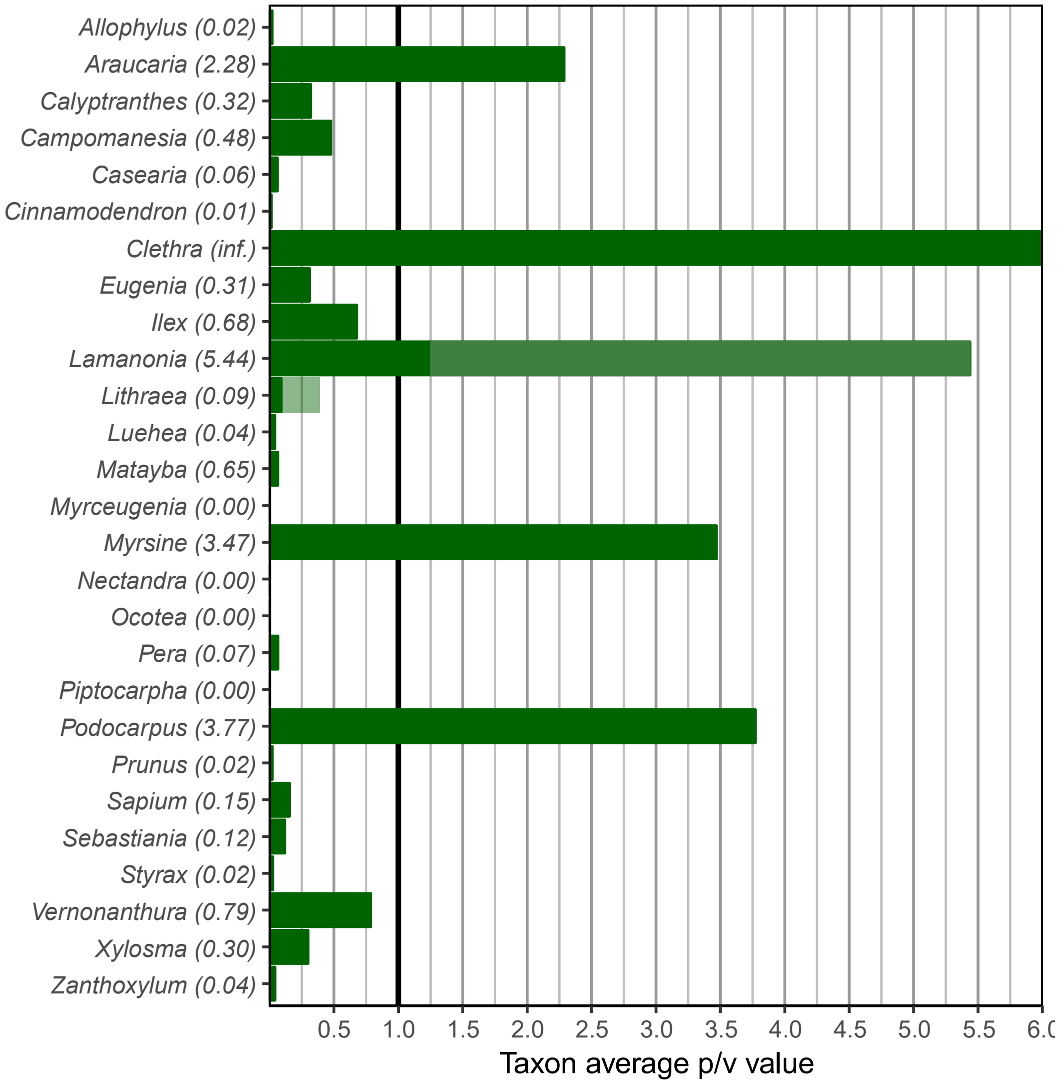

Figure 6: p/v values of key genera of Araucaria Forest in this study. Clethra has an infinitely high p/v value; faint sections in the bars of Lamanonia and Lithraea reflect alternate calculations of their p/v values (see section 3.4).

Between-plot variability in vegetation-pollen relationships is not well demonstrated by p/v values, as their calculation requires a taxon to be present in both vegetation and pollen records for a plot. The only taxon for which this occurs in all plots is *Eugenia*, whose plot-specific p/v scores varied between 0.04 (P141) and 2.26 (P122), with 14 plots having p/v values < 1. This variability is more evident with pollen-vegetation abundance differentials (Table 3 and fig. 7). *Myrsine, Araucaria* and *Podocarpus* had the most positive mean values (all above +5%); *Nectandra, Eugenia, Lithraea, Cinnamodendron, Styrax, Ocotea,* and *Matayba* had the most negative mean values (all below -5%). *Lithraea*'s mean differential changes to -5.52% if 'cf. *Lithraea* (Anacardiaceae)' pollen is included in the calculation.

Myrsine had the most extreme positive values: +55.75% (P114, slope), +41.25% (P157, disturbed), +30.70% (P141, closed understorey), +26.38% (P142, open understorey) and +20.48% (P159, disturbed). Values above +20% also occurred twice for *Araucaria* (+20.63% in P151, riverine, and +20.30% in P159, disturbed) and once for *Lamanonia* (+20.32% in P151, riverine). Similarly negative values (below -20%) were more evenly spread among taxa, with two cases in *Styrax* (-22.86% in P122, open understorey, and -20.00% in P141, closed understorey) and one each in *Matayba* (-34.14% in P136, riverine), *Lithraea* (-32.56% in P114, slope), *Nectandra* (-28.57% in P110, riverine), *Eugenia* (-25.92% in P156, disturbed), *Sebastiania* (-25.85% in P151, riverine), *Cinnamodendron* (-24.14% in P159, disturbed), and *Pera* (-21.04% in P119, open understorey).

Genus	**Mean**	**Min**	**Max**	**Range (Max-Min)**
Allophylus	-4.13	-8.57	0.20	8.77
Araucaria	+9.36	-9.48	20.63	30.11
Calyptranthes	-3.44	-17.06	1.09	18.15
Campomanesia	-2.08	-5.71	0.81	6.52
Casearia	-4.17	-13.84	0.45	14.29
Cinnamodendron	-8.08	-24.14	0.44	24.57
Clethra	+1.76	0.37	6.68	6.31
Eugenia	-8.47	-25.92	7.17	33.09
Ilex	-1.07	-8.73	2.93	11.66
Lamanonia	+2.69	-1.16	20.32	21.49
Lithraea	-8.25	-32.56	0.26	32.82
Luehea	-4.89	-8.89	0.18	9.07
Matayba	-6.29	-34.14	0.36	34.50
Myrceugenia	-4.61	-9.09	-1.75	7.34
Myrsine	+13.88	-3.05	55.75	58.80
Nectandra	-11.73	-28.57	-2.17	26.40
Ocotea	-7.25	-16.36	-1.75	14.61
Pera	-4.83	-21.04	1.21	22.25
Piptocarpha	-3.02	-4.29	-1.75	2.53
Podocarpus	+5.78	-5.73	19.24	24.97
Prunus	-3.21	-6.82	0.23	7.04
Sapium	-1.27	-5.05	0.44	5.49

Sebastiania	-4.35	-25.85	0.55	26.40
Styrax	-7.52	-22.86	0.45	23.31
Vernonanthura	-0.38	-4.89	1.83	6.72
Xylosma	-2.16	-7.02	1.49	8.51
Zanthoxylum	-4.76	-12.73	0.20	12.93

Table 3: Pollen-vegetation abundance differential values (%) for key genera of Araucaria Forest in this study.

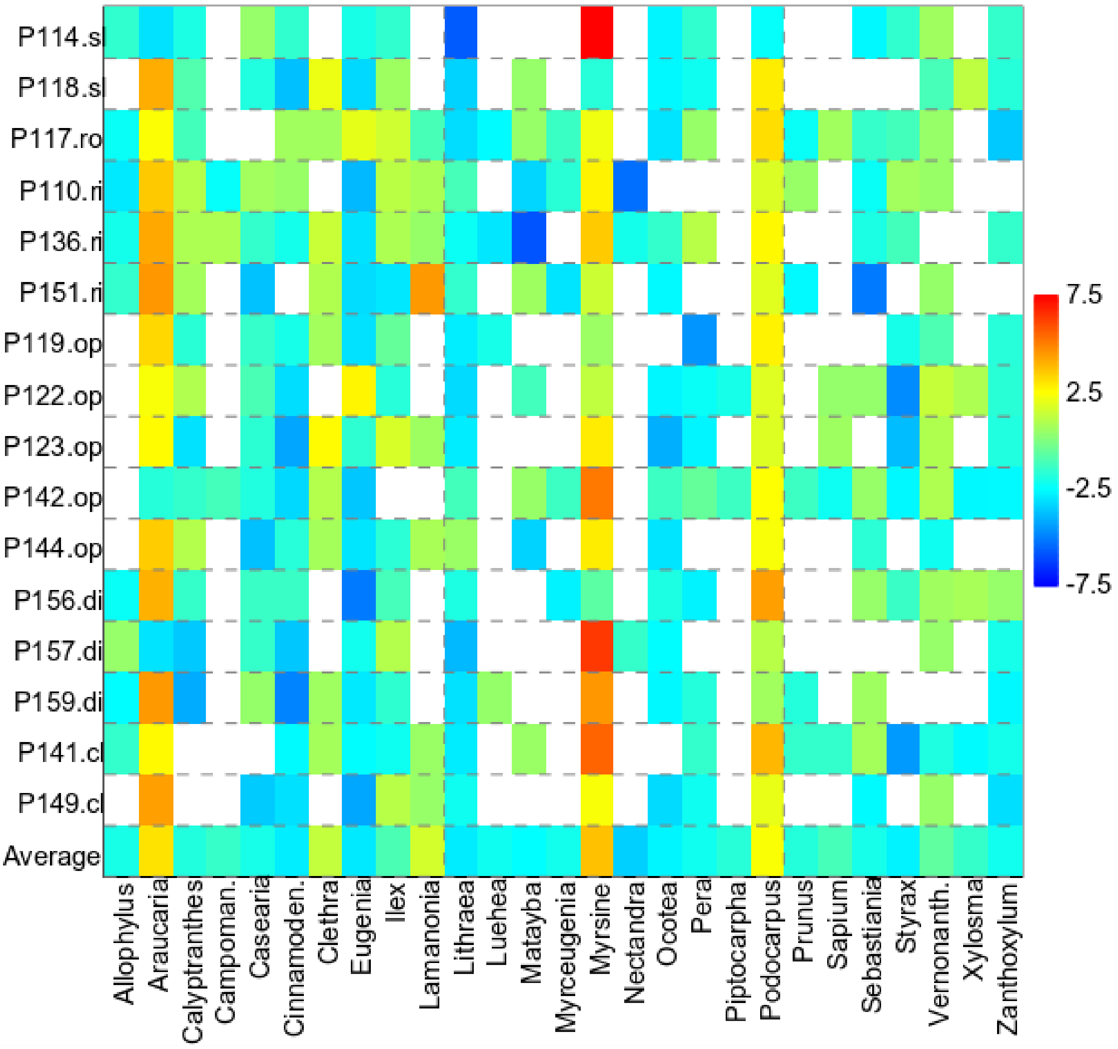

Figure 7: Pollen-vegetation abundance differentials (square-root transformed) for selected genera. Positive values denote plots where a taxon's pollen was more abundant than its vegetation; negative values reflect vegetation being more abundant than pollen. Blank cells denote plots where a taxon was absent from both pollen and vegetation data.

The genus with the greatest difference between maximum and minimum abundance differentials is *Myrsine*, with wide variation (> 30%) also found in *Matayba*, *Eugenia*, *Lithraea* and *Araucaria*; *Nectandra*, *Sebastiania*, *Podocarpus*, *Cinnamodendron*, *Styrax* and *Lamanonia* had differences between 20 and 30%. Most genera had both positive and negative abundance differentials, with the exceptions being *Clethra* (all positive) and *Myrceugenia, Nectandra, Ocotea and Piptocarpha* (all negative). However, few taxa (*Araucaria*, *Eugenia*, *Ilex*, *Myrsine*, *Podocarpus*) had differentials > 2% in both positive and negative directions.

4. Discussion

4.1. Detecting structural differences in Araucaria Forest

The vegetation of the studied forest area is characteristic of Araucaria Forest, containing 19 of its 30 most important tree species (Schorn *et al.*, 2012). Three of the predominant species in this study (*A. angustifolia, O. pulchella*, *P. lambertii*), as well as others found at lower levels (*Matayba elaeagnoides*, *Lamanonia ternata*), are key indicator species (Gonçalves and Souza, 2014). *Lithraea brasiliensis*, the most common, abundant and dominant species in our sample plots, is the fifth most important tree across Santa Catarina's Araucaria Forest, especially significant below 1200 m a.s.l (Schorn *et al.*, 2012; Meyer *et al.*, 2013).

The floristic composition of the plots is somewhat variable, with no pair of plots having a similarity score above 0.8 (fig. 5a), but this variability in composition does not generally reflect the structural differences between the plots. This can be seen in the cluster analysis (fig. 5a): three of the open understorey plots (P119, P122, P123) are clustered together along with the slope plot P118, but the remaining two open plots (P142 and P144) are far removed; the cluster that would include all five open plots would have 14 members. Similarly, the disturbed plots P157 and P159 are closely paired, but the cluster that would also include the third disturbed plot (P156) would encompass nine plots in total. The riverine plots P110 and P136 are distinct from the rest of the plots but cannot be grouped with the third member of the riverine group (P151) without including all sampled plots in the cluster.

This pattern is further shown in the DCA (fig. 5b), of which only axis 1 has an eigenvalue > 0.3 (0.3781), which would be suggestive of ecological relevance (Peterson and Gale, 1991; Rezende *et al.*, 2015). Here again P110 and P136 are the only plots that are clearly distinguished by their vegetation. Their floristic difference to the other studied plots may partly result from their location at the northern end of the studied area, > 1.5 km from the other plots. Their regeneration stage could also be an explanatory factor: these plots have the highest RCVs for *Matayba elaeagnoides*, as well as the highest recorded abundances of the pioneer *Nectandra megapotamica*, two of the three highest abundances of *Allophylus edulis*, and the presence of *Sebastiania commersoniana*, all of which are important taxa in regenerating Araucaria Forest patches (Schorn *et al.*, 2012; Meyer *et al.*, 2013).

The most common and abundant tree pollen in our study sites came from *Araucaria angustifolia*, Myrtaceae (mainly *Eugenia*), Anacardiaceae cf. *Lithraea*, *Myrsine* and *Podocarpus*, with *Lithraea*, *Vernonanthura*-type, *Sebastiania*, *Ilex* and *Clethra* found in the majority of plots at generally low abundances (fig. 4). Pteridophyte spores were both common and abundant, and Poaceae was the most prevalent herbaceous pollen taxon, with Asteraceae and Araceae pollen also common but less abundant. The sum of all herbaceous pollen varies from 5-20%, averaging 10% – similar to the 5-15% found by Garcia *et al.* (2004) in a study of Araucaria Forest peat deposits in Sao Paulo state, but lower than the 24-60% found by Jeske-Pieruschka *et al.* (2010) in a forest patch surrounded by Campos grassland. The herbaceous pollen counts in the latter were likely increased by influx from the grasslands surrounding the forest, and as a result of disturbance from grazing in the studied forest patch (Jeske-Pieruschka *et al.*, 2010).

The plots are less well differentiated by pollen than by their vegetation, as shown by their generally higher cluster similarity scores (fig. 5c). As with the vegetation there are some potential pairings of open understorey plots (P122 and P123; P119 and P144 with the rocky plot P117), but these are quite distinct from each other – the cluster that would encompass all five open plots would only exclude the riverine plot P151. No potential groupings in the pollen cluster analysis mirror clusters of the plots' vegetation (fig. 5a,c), and there are no consistent groupings of structurally similar plots. This is also seen in the DCA (fig. 5d), where the eigenvalue for axis 1 (0.2454) may indicate the separation is not ecologically relevant (Peterson and Gale, 1991; Rezende *et al.*, 2015). Here, as in the cluster analysis, the only plot that is clearly distinguished is P151, due in large part to its exceptionally high abundance of *Lamanonia* pollen.

Although it was not explicitly examined, a plot's distance to open areas (fig. 1) does not appear to have any consistent relation to its vegetation composition or its pollen signal (figs. 2-4). This can be demonstrated by comparing the riverine plots P136 (close to edge) with P110 and P151 (further from edge) or the open plots P119 and P122 (close to the edge) with P123, P142 and P144 (further from edge) – none form coherent groups in the clustering analyses in fig. 5. Contributions of exotic pollen such as *Pinus* (excluded from this palaeoecology-focused analysis) also appear largely unrelated to plots' distance from open areas (data not presented).

These results show that the notable structural differences between the different forest plot categories are not echoed in the composition of their woody taxa. Since there are no consistent floristic differences between plot types, it is unsurprising that these structural differences cannot be detected by their pollen signals – especially as pollen's sensitivity is affected by relatively coarse taxonomic resolution and differential pollen production and preservation between taxa.

4.2. Vegetation-pollen relationships

The pollen records of the studied forest plots did not consistently reflect large variations in a taxon's abundance in the vegetation (fig. 6 & 7). *L. brasiliensis*, for example, makes up 2.9% of the vegetation in P110 and 34.1% in P114 (fig. 2), but *Lithraea* pollen is equally abundant in each plot (1.6%) (fig. 4); its abundance in the vegetation is intermediate in P117 (10.9%) and P118 (12.3%) but its pollen makes up just 0.9% and 1.0% of those plot totals, respectively. This variability in vegetation-pollen relationships can also be illustrated with *Myrsine*: its pollen made up more than half of all counted grains (55.8%) in P114, despite no individuals from the genus being recorded in the vegetation survey; it was also significantly over-represented in P157 (pollen abundance 43.4%, vegetation abundance 2.2%), but proportionately represented in P119 (17.3% of the pollen; 17.0% of the vegetation) and under-represented in P118 (5.7% of the pollen, 8.8% of the vegetation).

However, general patterns of over- or under-representation of each taxon in the pollen record could be determined – only *Araucaria, Eugenia, Ilex, Myrsine* and *Podocarpus* had both positive and negative abundance differentials above 2% (Table 3). The majority (22 of 27) of the arboreal genera examined were under-represented in the pollen record (p/v values <1; fig. 6), with four (*Myrceugenia, Nectandra, Ocotea* and *Piptocarpha*) being palynologically silent. These under-represented taxa include many of the most abundant tree species in the plots, as well as some of the most ecologically important taxa in Araucaria Forest (*Lithraea, Matayba, Cinnamodendron, Ocotea, Prunus* and *Nectandra*) (Sevegnani *et al.*, 2013). The highest p/v value among these key genera is *Lithraea*'s 0.09 (i.e. less than one tenth as abundant in the pollen record as in the vegetation), and no pollen which could be reliably identified as *Ocotea* or *Nectandra* was counted at all.

Under-representation in the pollen record is common in the Neotropics (Bush, 1995; Bush and Rivera, 1998; Gosling *et al.*, 2009; Haselhorst, Moreno and Punyasena, 2013). This is partly due to the relative rarity of anemophilous plants – generally the most over-represented taxa – in tropical forests, although entomophilous plants are less under-represented in tropical pollen spectra than in temperate regions (Whitehead, 1983; Bush, 1995; Viera, Fonseca and Araújo, 2012). Our results fit this general pattern: of the under-represented taxa in our study, *Nectandra* and *Ocotea* are pollinated by thrips (Thysanoptera) (Souza and Moscheta, 2000; Danieli-Silva and Varassin, 2013), and *Lithraea, Ilex, Matayba, Prunus, Eugenia* and *Cinnamodendron* depend on bees and other small insects (Tomlinson, 1974; Imperatriz-Fonseca, Kleinert-Giovannini and Ramalho, 1989; Wilms *et al.*, 1997; Hermes and Köhler, 2006; Montalva *et al.*, 2011; de Deus *et al.*, 2014). Additionally, *Ocotea* pollen is fragile, with a thin exine that means it preserves poorly (Behling, 1993). By contrast, the over-represented taxa *Araucaria* (Bittencourt and Sebbenn, 2007, 2008) and *Podocarpus* (Midgley, 1989; Wilson and Owens, 1999; Negash, 2003) are anemophilous, as are South American members of *Myrsine* (Otegui and Cocucci, 1999; Albuquerque *et al.*, 2013), and therefore produce abundant pollen.

Lamanonia was over-represented in the pollen record (p/v 5.44; 1.25 when excluding P151) despite being insect-pollinated (Wilms *et al.*, 1997; Hermes and Köhler, 2006; de Deus *et al.*, 2014). Its relative abundance of pollen in this study may be explained by its mass-flowering habit (Hermes and Köhler, 2006), so it is possible that *Lamanonia*'s pollen-vegetation relationship varies significantly year-on-year. *Clethra* is another entomophilous taxon (Freitas and Sazima, 2006) with over-represented pollen in this study: its pollen was found in 10 of the 16 plots at an average abundance of 1.10% (0.37-4.58%), but no individuals were recorded in the vegetation (fig. 2) despite *C. scabra* being the third most important tree species in Araucaria Forest (Schorn *et al.*, 2012). Given *Clethra* pollen is not adapted for long-distance travel, it is unlikely to have originated outside the plots; potentially, individuals from this genus were present but too small to be included in the survey (i.e. d.b.h. < 10 cm), making it difficult to make a true assessment of the taxon's pollen-vegetation relationship.

It is important to note that some of the variability in our data may be more the result of methodological choices rather than reflecting ecological truth. The forest plots used in this study (50 x 10 m) are relatively small, so it is possible that some of the variability in vegetation-pollen relationships would be reduced if considering a wider area of contributing vegetation (Duffin and Bunting, 2008; Piraquive Bermúdez, Theuerkauf and Giesecke, 2021). This has (subsequently) been shown elsewhere in south-eastern Brazil's highlands, although the closest relationship between vegetation and pollen spectra was found for the smallest examined radius (50 m) around pollen traps (Guarinello de Oliveira Portes *et al.*, 2020). Different methods of collecting pollen (moss polsters vs pollen traps vs bog or lake surface sediments) can also contribute variability to the relationship between vegetation cover and pollen (Tonkov *et al.*, 2001), though an increasing number of studies in the southern Atlantic Forest, embracing a wider range of survey methods, is becoming available (Montade *et al.*, 2019; Guarinello de Oliveira Portes *et al.*, 2020; Piraquive Bermúdez, Theuerkauf and Giesecke, 2021). These demonstrate that, as in our study, variability between sites is often large, but they also help to narrow down the plausible range of values for species' and vegetation types' representation in modern pollen rain.

4.3. Implications for palaeoecology

Our findings have important implications for the interpretation of fossil pollen records. Many of the key taxa used to reconstruct past Araucaria Forest dynamics were identified palynologically in this study, but two were largely missing. Pollen from *Mimosa scabrella* and *Weinmannia* is commonly cited as evidence of Araucaria Forest (Behling, 1995, 1997b; Behling *et al.*, 2004; Leonhardt and Lorscheitter, 2010) but *M. scabrella* pollen was not abundant (present in 10 of the 16 plots, maximum abundance 0.89%) and *Weinmannia* pollen was absent; neither species was recorded in the vegetation survey. *M. scabrella* is a species which is especially encouraged by anthropogenic forest disturbance, so its absence here may be connected to the relatively long time since the last anthropogenic disturbance of our studied plots. Moreover, both taxa (especially *Weinmannia*) are much more floristically important at elevations above 1,200 m a.s.l. (Sevegnani *et al.*, 2013) so their absence here is unsurprising, and highlights the biases of existing palaeoecological studies towards high-altitude regions along the eastern edge of the highland plateau (Behling, 1995, 1997b; Behling *et al.*, 2004; Behling, 2006; Leonhardt and Lorscheitter, 2010; Jeske-Pieruschka *et al.*, 2013; Scherer and Lorscheitter, 2014).

The geographical bias of existing studies can further be seen in the classifications proposed by Rodrigues *et al*. (2016a) for distinguishing woodland types in southern Brazil based on pollen spectra. Although our sites (721-953 m a.s.l.) have vegetation which is most similar to that in the 'low Poaceae subtropical forest' (LPSF) category (Behling *et al.*, 2004; Jeske-Pieruschka and Behling, 2012; Jeske-Pieruschka *et al.*, 2013; Behling and de Oliveira, 2018), they are excluded from this group due to their absence of *Weinmannia* pollen. Instead, our plots would likely be included in the disparate 'low Poaceae subtropical-tropical' (LPST) group, along with two sites in Santa Catarina's coastal tropical forest (9-10 m a.s.l.) (Behling, 1995, 1997a), one in northern Argentina at the westernmost limit of Araucaria Forest taxa (604 m a.s.l.) (Gessert *et al.*, 2011), and another at low altitude in south-central Rio Grande do Sul (176 m a.s.l.) (Santa Mônica, unpublished, cited in Rodrigues, Behling and Giesecke, 2016a) . The significant altitudinal, geographical and floristic differences between these sites suggests LPST may not be a true grouping, and that the classification of southern Brazil's forests by their pollen spectra will improve as more westerly plateau sites, with different assemblages of Araucaria Forest, are studied.

Most of the taxa widely used in palaeoecological studies were here found to be over-represented in the pollen record (*Araucaria, Myrsine, Podocarpus, Lamanonia*) or under-represented but very abundant in the vegetation (Myrtaceae, such as *Eugenia* and *Calyptranthes* which are rarely distinguished to genus in fossil pollen). Fossil *Lithraea* pollen is quite often identified (Behling, Pillar and Bauermann, 2005; Behling, 2006; Gessert *et al.*, 2011; Behling *et al.*, 2016) or grouped with *Schinus* (Behling, 1997a, 1997b; Behling *et al.*, 2004; Jeske-Pieruschka *et al.*, 2010) but rarely treated as important (but see Behling, 1997b; Gessert *et al.*, 2011); given the floristic importance of *L. brasiliensis* (Schorn *et al.*, 2012; Meyer *et al.*, 2013) and its under-representation in the pollen rain (p/v 0.09-0.39, pollen 8.25% less abundant than vegetation on average), the presence and dynamics of *Lithraea* pollen may warrant more detailed examination in future studies. *Lithraea* is one of several key Araucaria Forest taxa we have shown to be either significantly under-represented (*Matayba, Cinnamodendron, Prunus*) or absent (*Ocotea, Nectandra*) in the pollen record, even when quite abundant in the vegetation. This suggests that some significant changes in past forest composition may not be reflected in fossil pollen, highlighting a potentially important limitation of pollen as a palaeoecological proxy for determining this ecosystem's responses to past millennial-scale human land use and climate changes.

The importance of fossil pollen's limited sensitivity to compositional changes in Araucaria Forest is reinforced when considering that structural differences between plots were not clearly reflected in their pollen signals. Although the plots had notably different structural characteristics to one another, this was only weakly echoed in the floristic composition of their arboreal component, and even less so in their pollen spectra, which were more similar to each other than the vegetation. This implies that pollen records may not clearly detect structural changes in Araucaria Forest, especially when these are not accompanied by significant or long-term alterations in floristic composition. Further investigations of the sensitivity of pollen rain to larger-scale changes in composition and structure of Araucaria Forest might involve integration with the state-wide plot network of the Santa Catarina forest floristic inventory (Vibrans *et al.*, 2010) or palynological examination of forest fragments with relatively intense present human land use, such as caívas, faxinais or ervais (Mello and Peroni, 2015; Fichino, Pivello and Santos, 2017; dos Reis *et al.*, 2018). Such research would aid the interpretation of fossil pollen records which do show significant changes with climatic changes and human land use (e.g. Behling *et al.*, 2004), permitting shifts in pollen composition to be more accurately related to changes in the vegetation.

The difficulty of detecting structural and compositional changes in Araucaria Forest with pollen records has implications for the reconstruction of past human impacts on the forest. Before European arrival, the Indigenous southern Jê people lived in semi-subterranean dwellings in the forest, practising swidden cultivation and exploiting *Araucaria angustifolia* nuts and Myrtaceae fruits (Iriarte and Behling, 2007; Corteletti, 2012; dos Reis, Ladio and Peroni, 2014; Corteletti *et al.*, 2015). It has been suggested that their lifestyles helped to spread Araucaria Forest more quickly than natural drivers, such as climate change, and even beyond the forest's natural limits (Noelli, 2000; Bitencourt and Krauspenhar, 2006; Iriarte and Behling, 2007; Lauterjung *et al.*, 2018; Robinson *et al.*, 2018), but our findings raise the question of whether, and how, more subtle impacts within the forest – especially structural and compositional changes – would be represented in fossil pollen sedimentary archives. There is significant ongoing debate over the extent to which pre-Columbian peoples altered the floristic composition of Amazonian forests (Shepard and Ramirez, 2011; Barlow *et al.*, 2012; Levis *et al.*, 2017, 2018; McMichael *et al.*, 2017) and the limitations of fossil pollen analysis in identifying such impacts are well known (e.g. Carson *et al.*, 2016), with recent simulations showing that pollen sites in tropical forest-grassland mosaics (like those between Araucaria Forest and Campos grasslands) may be insensitive to large changes in forest cover (Whitney *et al.*, 2019). The forest plots in our study have been free of human disturbance for several decades, so their present condition is unlikely to mirror the full range of southern Jê land use. Nevertheless, our findings highlight potential limitations of pollen analysis as a tool for investigating and reconstructing the role of the southern Jê in shaping the Araucaria Forest's floristic composition and structure – the absence of evidence of human impacts may not equate to evidence of their absence.

5. Conclusions

In this study, the pollen rain from 16 structurally different Araucaria Forest plots has been characterised and compared with floristic inventory data, and 27 tree genera have had their vegetation-pollen relationships quantified.

Our results show that the structurally different plots do not exhibit consistent differences in the floristic composition of their tree taxa. Correspondingly, their structural differences cannot be clearly detected in their pollen rain, with pollen spectra more similar than vegetation between plots.

On average, the most abundant tree species in the plots are *Lithraea brasiliensis*, *Cinnamodendron dinisii*, *Araucaria angustifolia*, *Eugenia* sp., *Ocotea pulchella* and *Calyptranthes* cf. *concinna*, representing the typical composition of Araucaria Forest at this altitude. As well as these, *Styrax leprosus* has a high average relative coverage value (RCV) across all plots, and species including *Matayba elaeagnoides*, *Nectandra megapotamica*, *Vernonanthura discolor*, *Prunus myrtifolia*, *Piptocarpha angustifolia*, *Myrceugenia* sp. and *Myrsine umbellata* have high RCVs in the (relatively few) plots in which they occur. The modern pollen rain of Araucaria Forest in our study area (720-920 m a.s.l.) is characterised by *Myrsine* (19.5%), *A. angustifolia* (16.6%), Pteridophyta (13.2%), *Podocarpus lambertii* (7.9%) and Poaceae (5.2%), along with *Eugenia*-type, Anacardiaceae cf. *Lithraea*, Asteraceae (others), *Lamanonia*, *Ilex theezans*, *Calyptranthes*-type, *Vernonanthura*-type and *Clethra* at lower abundance.

Vegetation-pollen relationships vary between plots but general patterns of over- or under-representation could be identified for the majority of taxa. *Araucaria*, *Lamanonia*, *Podocarpus*, and

Myrsine are over-represented in the pollen record (average p/v >1), and *Clethra* pollen was frequently identified but the genus is absent from the vegetation survey. All of the other 22 genera analysed are under-represented, with *Myrceugenia*, *Nectandra*, *Ocotea* and *Piptocarpha* palynologically silent.

The palynological under-representation of ecologically key Araucaria Forest taxa and the lack of clear differentiation of structural differences in the forest's pollen spectra have important implications for the interpretation of fossil pollen records, highlighting the challenges of resolving past human impacts and ecological changes within Araucaria Forest using this proxy. This quantitative analysis of vegetation-pollen relationships for key Araucaria Forest taxa is a key tool for interpreting fossil pollen records and understanding past vegetation dynamics on the highlands of southern Brazil.

Author contributions

MLC and FEM conceived the study; MLC collected moss polsters; MLC and LAS collected vegetation survey data; MLC performed pollen analysis and counting; MLC and OJW analysed the data and interpreted the results; OJW, MLC and FEM drafted the manuscript; all authors commented on the manuscript before submission.

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Preface to Chapter 3: Floristic change in Brazil's southern Atlantic Forest biodiversity hotspot: From the Last Glacial Maximum to the late 21st Century

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Overview

This chapter, more than any of the others in this thesis, straddles the temporal divide between past and future resilience to climate change among southern Brazil's ecosystems. In order to capture compositional changes as species reassort themselves under shifting climates, it considers Araucaria Forests as well as the other main ecosystems of the southern Atlantic Forest (Campos, Seasonally (semi-)Deciduous Forests and Atlantic Rainforests) with which they have floristic continuity. It builds on Chapter 2's modern pollen-vegetation calibration to bring together palaeoecological proxies with ecological niche model (ENM) predictions (themselves an evolution of the process begun in Chapter 1) for insight into how the region's ecosystems have changed since the Last Glacial Maximum. This information is used to set in 21,000 years of context the climate-driven ecological changes which could take place in the 21st Century, providing a corollary to the results from Chapter 1.

Contribution to the research

I undertook all relevant aspects of the research for this paper: I conceived the study, built the ENMs (using locality data provided by Débora Lingner and Alexander Vibrans), processed the results, prepared the palaeo-vegetation proxy comparison, analysed the two strands of evidence together, and led the writing-up process. My contribution to this paper is estimated at 95%. The published author contribution statement is below:

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

Chapter 3: Floristic change in Brazil's southern Atlantic Forest biodiversity hotspot: From the Last Glacial Maximum to the late 21st Century

Authors

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Abstract

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

1. Introduction

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

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

One key approach for predicting the impacts of climate change is to use species distribution models (SDMs, also known as ecological niche models). However, significant uncertainties about the planet's longer-term climate trajectory under anthropogenic forcing, as well as the spectre of increasing climate novelty, mean that no SDM study can make precise forecasts beyond the current century (Fitzpatrick et al., 2018; Williams & Jackson, 2007). Palaeoecology is valuable in this context, illuminating vegetation responses to wide ranges of past climates which may present useful analogues for future scenarios (Barnosky et al., 2017; Dietl et al., 2015; Jackson & Blois, 2015; McElwain, 2018). These insights can come from palaeoecological proxies (e.g. fossil pollen, soil carbon isotopes, phytoliths) and/or distribution modelling. These approaches are complementary: proxy studies provide rich, empirical records on individual sites' vegetation histories; SDMs can provide high spatial- and taxonomic-resolution predictions for times, taxa and places poorly covered by proxy data; integrating the two therefore yields highly detailed, generalisable, ground-truthed insights into palaeoecological dynamics (Svenning et al., 2011).

Southern Brazil's late-Quaternary vegetation history has been better studied than much of the Neotropics, especially with fossil pollen and, to a lesser extent, soil carbon isotopes and phytoliths (synthesised in Smith & Mayle, 2017). There are limits, however, to the insights available from these proxies. The overwhelming majority of studied sites have small catchments recording local-scale vegetation changes (Smith & Mayle, 2017), and their uneven spatial distribution (skewed towards the plateau's (south-)eastern edges and the southern part of the coastal lowlands) mean that large parts of the region are unstudied (fig. 3). Temporal coverage is similarly uneven, with few sites providing continuous records from the Last Glacial Maximum (LGM, ca. 21,000 years ago). Finally, each proxy has significant limits on the taxonomic resolution it can provide for vegetation reconstructions. Soil carbon isotopes ($\delta^{13}C$) distinguish C_4-dominated (sub-tropical/tropical grassland) and C_3-dominated (generally, but not always, woody) vegetation (Dümig et al., 2008; L. C. R. Silva & Anand, 2011); phytoliths can effectively differentiate herbaceous or monocotyledonous taxa, and fossil pollen discriminates between woody dicots (Daniau et al., 2019; Plumpton et al.,

2019) – yet despite its higher taxonomic resolution, fossil pollen records under-represent or omit significant parts of southern Brazil's flora (Behling & Negrelle, 2006; Cárdenas et al., 2019), leaving their dynamics unrecorded.

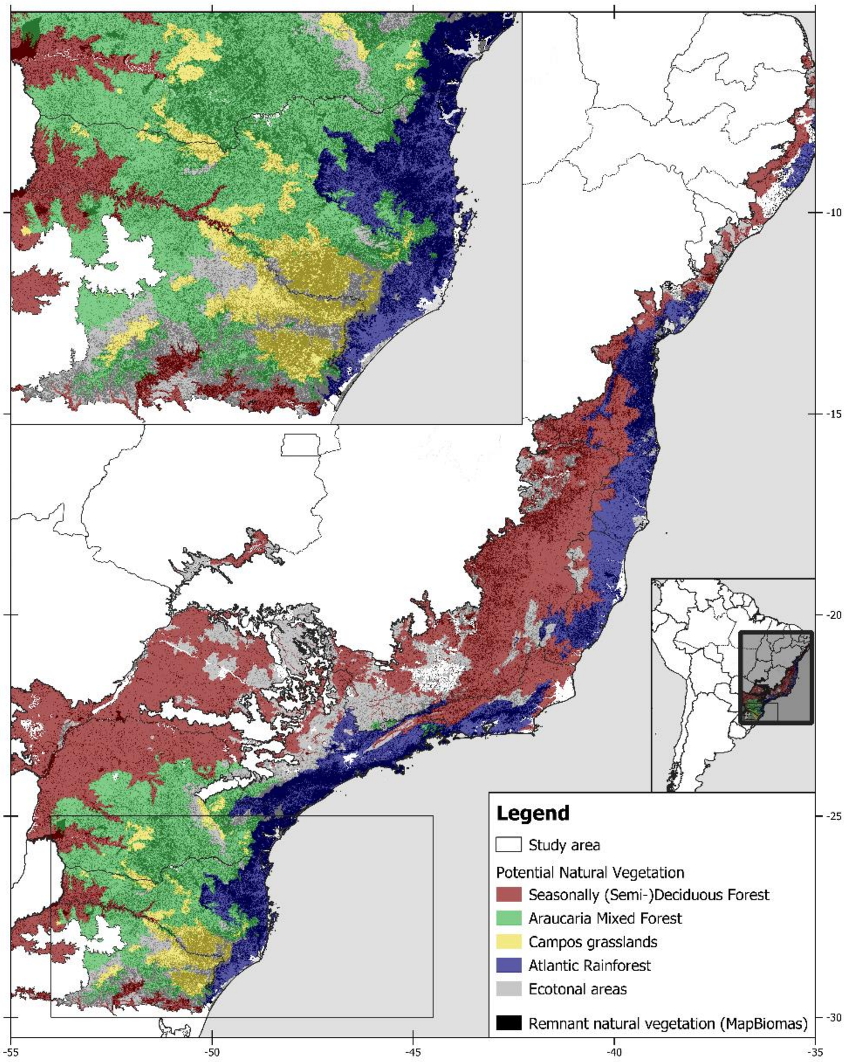


Figure 1: Brazil's Atlantic Forest vegetation (IBGE, 2012) and its natural remnants in 2018 (shaded; Souza et al., 2020)*; ecosystems not prominent in our study area are not shown in colour.*

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

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

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

2. Methods

2.1. Overview

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

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

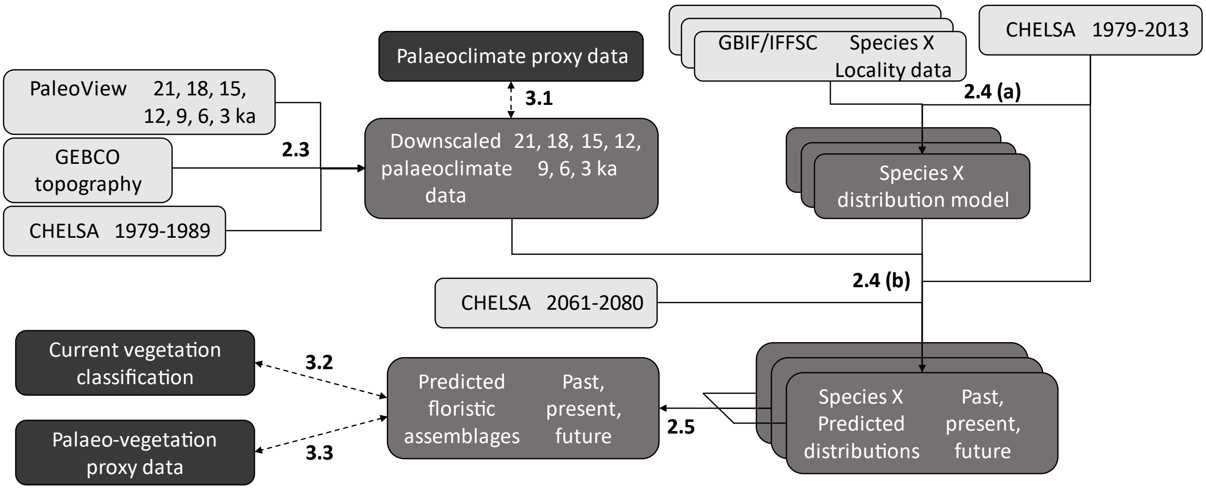


Figure 2: conceptual overview of this study showing input data (light grey), generated outputs (mid grey), and data for model intercomparisons (dark grey). Segment labels highlight where in the text relevant sections are discussed. For data generation methods (solid lines): palaeoclimate data downscaling (Section 2.3), model fitting and projection (Section 2.4 – labelled a and b respectively), combining individual species predictions into floristic assemblages (Section 2.5). For model-data intercomparison results (dashed lines): palaeoclimate data and proxies (Section 3.1), current mapped and modelled vegetation (Section 3.2), and predicted floristic assemblages and palaeo-vegetation proxies (Section 3.3).

2.2. Modern ecosystems of the southern Atlantic Forest

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

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

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

Campos share the highest and coldest parts of the plateau with Cloud Forest, especially along the escarpment's upper edge where orographic fog is common (Falkenberg & Voltolini, 1993). These forests contain a mix of cold-adapted species from both AMF and ARF, but despite being floristically distinct they are often treated as high-montane expressions of these larger forest formations (Bertoncello et al., 2011; Falkenberg & Voltolini, 1993; Higuchi et al., 2013; Oliveira-Filho et al., 2014; Scheer et al., 2011).

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

2.3. Climate data

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

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

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

2.4. Species distribution modelling

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

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

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

Clethra scabra (Clesca; Clethraceae)		Y	Y	Y						Y
Cupania vernalis (Cupver; Sapindaceae)	Y	(Y)	(Y)					(Y)		
Danthonia secundiflora (= *D. montana*) (Dansec; Poaceae)					Y					
Dicksonia sellowiana (Dicsel; Cyatheaceae)		Y	Y	Y			(Y)			Y
Drimys brasiliensis (Dribra; Winteraceae)			(Y)	Y		Y				Y
Eragrostis polytricha (Erapol; Poaceae)					Y					
Euterpe edulis (Eutedu; Arecaceae)							(Y)	Y	Y	
Hypochaeris lutea (Hyplut; Asteraceae)					Y					
Ilex microdonta (Ilemic; Aquifoliaceae)						Y				Y
Lithraea brasiliensis (Litbra; Anacardiaceae)		Y	Y							Y
Luehea divaricata (Luediv; Malvaceae)	Y									(Y)
Matayba elaeagnoides (Matela; Sapindaceae)	Y	Y	Y							Y
Mikania decumbens (Mikdec; Asteraceae)					Y					
Mimosa scabrella (Mimsca; Fabaceae)			(Y)	Y		(Y)				Y
Myrocarpus frondosus (Myrfro; Fabaceae)	Y									
Ocotea catharinensis (Ococat; Lauraceae)						Y	Y	(Y)		
Ocotea puberula	Y	Y								

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

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

Locality data for these species were drawn from two sources: the Santa Catarina Forest Floristic Inventory (IFFSC) (Alexander Christian Vibrans et al., 2010, 2020), and the Global Biodiversity Information Facility for records outside Santa Catarina (https://doi.org/10.15468/dl.ol64p1, https://doi.org/10.15468/dl.o97owq, https://doi.org/10.15468/dl.nxy2cp). GBIF records were taken from 15-45° S and 67.5-35°W, where present-day conditions generally encompass those experienced by our study area over the last 21,000 years, then coordinates were cleaned and thinned. Because true absences were only available from the IFFSC, which covers only a subset of the geographic and climatic space our models were trained on and lacks data on Campos species, we added 1,000 randomly located pseudo-absence points for each species.

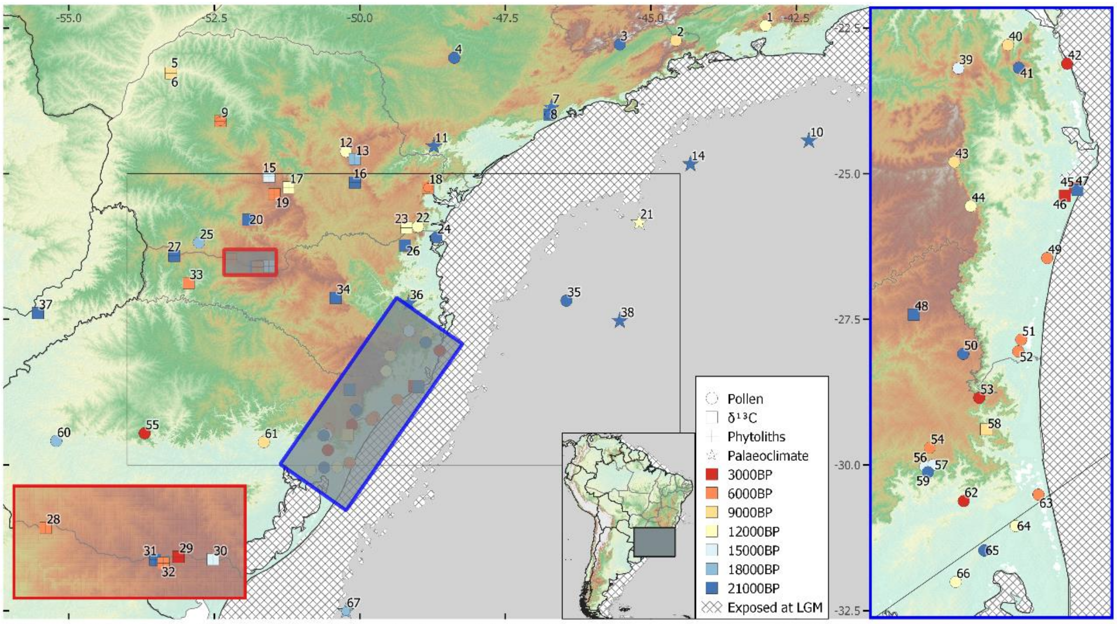
Modelling used the package 'biomod2' in R v3.5 (R Core Team, 2018; Thuiller et al., 2016). For each species a randomly selected 25% of the location data was set aside for model evaluation, with the remaining 75% used for training and cross-validating the models. We used an ensemble modelling approach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

2.5. Floristic assemblage analysis

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

2.6. Palaeo-data - model comparison

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



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

Figure 3: Map showing palaeo-data sites included in this study. Symbol shapes represent the palaeo-proxies included in each record, and their colour indicates the oldest time period covered. The hatched area illustrates the

maximum extent of land which was exposed at the LGM (sea levels ca. 130 m below modern). For further details on the sites, see table S2.

3. Results

3.1. Palaeoclimate data validation

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

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

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

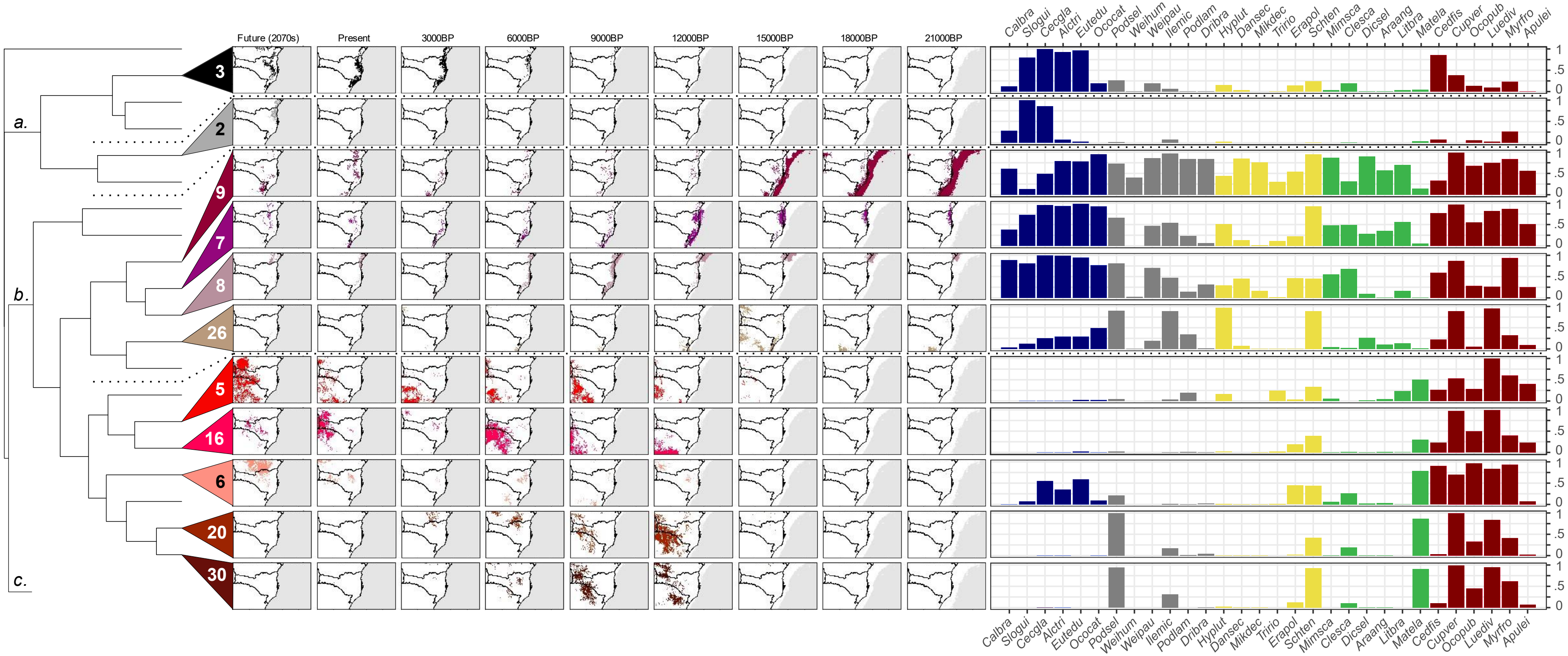
The Köppen-Geiger climate classification system (fig. S8) shows that southern Brazil's highlands have retained a subtropical climate with warm summers and no dry season since the LGM. This Cfb climate type covered almost all of southern Brazil's current land area at the LGM. Increasing temperatures since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

3.2. Modelled species and modern-day ecosystems

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

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

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


Future (2070s)
Present
3000BP
6000BP
9000BP
12000BP
15000BP
18000BP
21000BP
Calbra
Slogui
Cecgla
Alctri
Eutedu
Ococat
Podsel
Weihum
Weipau
Ilemic
Podlam
Dribra
Hyplut
Dansec
Mikdec
Tririo
Erapol
Schten
Mimsca
Clesca
Dicsel
Araang
Litbra
Matela
Cedfis
Cupver
Ocopub
Luediv
Myrfro
Apulei
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2
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1
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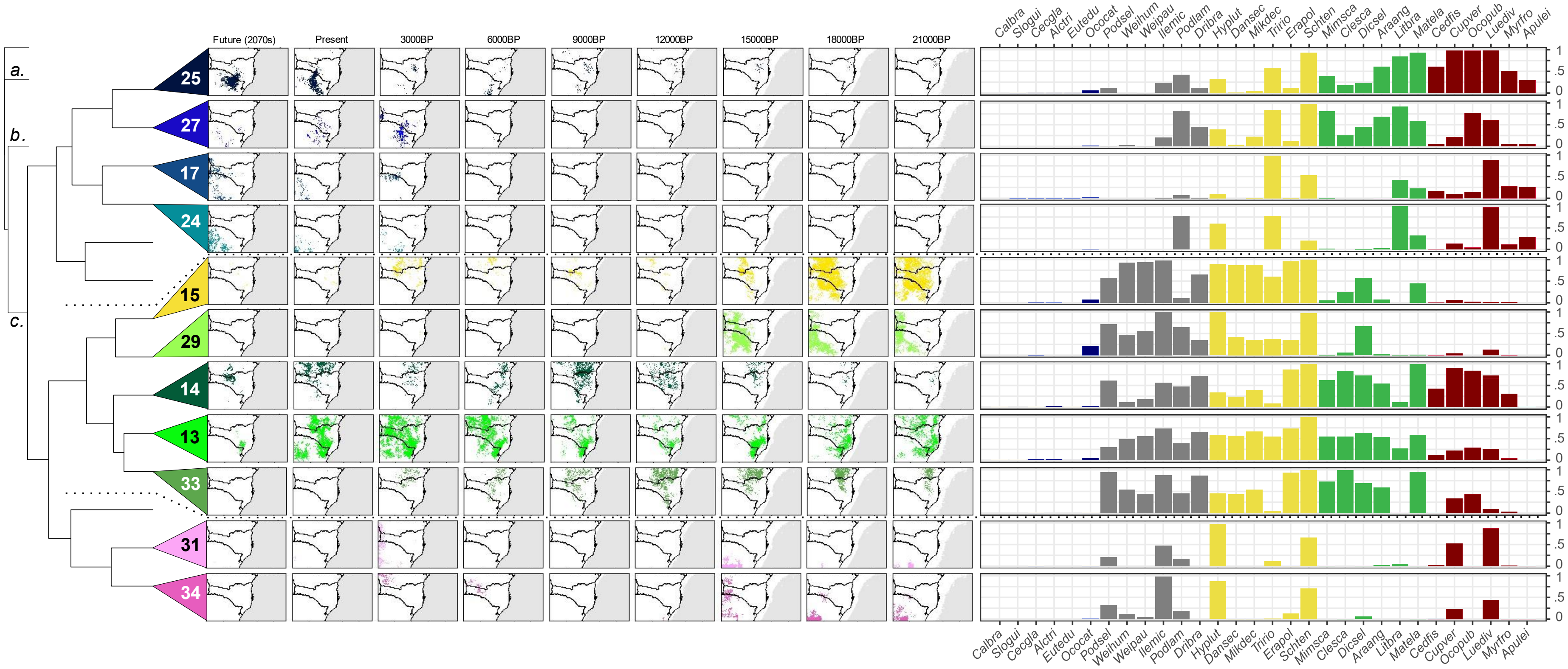


Figure 4: relationships (left; see also fig. S2), distributions (centre; see also fig. 6), and floristic compositions (right; each species' average predicted prevalence) of predicted assemblages used in this study (top, clusters a and b; bottom, cluster c). The right-most panel shows species' average predicted prevalence in each assemblage, using species' six-letter codes from table 1 and colours from the ecosystems in which each species is currently most important (see table 1 and fig. 1). Dendrogram branches without additional detail represent

assemblages which never reach 5% of the land area in any time slice and which are excluded from further analysis (see fig. S2).

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

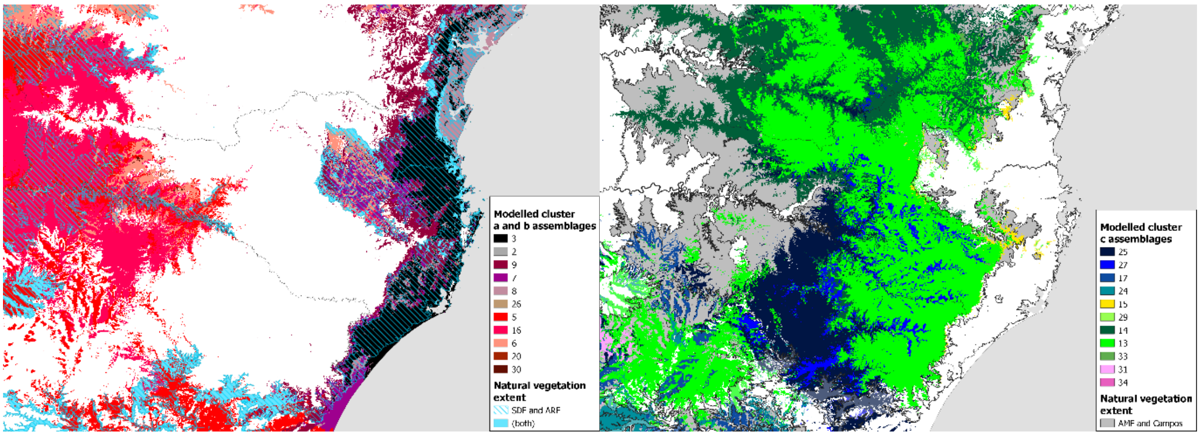


Figure 5: overlay maps of modelled floristic assemblages and official vegetation (IBGE, 2012; see fig. 1). Left: assemblages from clusters a and b compared with SDF and ARF (blue). Right: assemblages from cluster c compared with grassland and AMF (dark grey). See fig. S12 for ecotonal areas and comparison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

3.3. Changes through time and proxy comparison

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

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

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

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

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

3.3.2. Late Glacial Period (15,000 BP)

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

Most of the predicted changes between the LGM and Late Glacial occur in areas not covered by palaeo-data sites, making it difficult to discern their accuracy. Most sites in our study area do show modest increases in forest pollen between 18,000 and 15,000 BP, in line with predictions of more range expansions for forest species than herbs, though fossil pollen from the growing cluster of south-eastern plateau sites remains ≥90% grassland taxa. The largest increases in forest pollen are found in GeoB2107 and Curucutu, reaching 33% of the total in each. GeoB2107's arboreal pollen also becomes more diverse, with notable increases of Moraceae/Urticaceae, Melastomataceae and *Celtis*, while previously established taxa such as *Alchornea, Araucaria* and *Podocarpus* are maintained. This might support the predicted development of assemblage 7 at the expense of assemblage 9 on the north-central continental shelf: the former is more dominated by warm-adapted tropical trees, with cold-adapted Campos, Cloud Forest and AMF species less prevalent than in assemblage 9. A notable proxy site which first covers the 15,000 BP time slice is Buriti (Bertoldo et al., 2014): at this time period, 91% of Buriti's pollen comes from tree taxa – a proportion far higher than any other site at this period – with *Araucaria* (ca. 20%), *Ilex* and *Podocarpus* (15-20%) the main contributors. This would suggest that at least some western areas in our study area – around assemblages 29, 26 and 34 – had AMF-like forest cover at 15,000 BP.

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

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

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

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

The cold-adapted assemblages of cluster *c* also experience significant changes between the late glacial and early Holocene. Here again, however, few palaeoecological sites can test these predictions. Phytoliths and soil carbon isotopes at Aroeiras (D. W. Silva, 2018), Guarapuava (Calegari, 2008) and another nearby site (D. W. da Silva et al., 2016; no precise location) suggest the presence of woody AMF-like vegetation in the early Holocene, which subsequently declined. Further soil profiles at CPCN Pro Mata (Dümig et al., 2008; L. C. R. Silva & Anand, 2011) show that smaller-than-modern forest blocks were also found in the highlands' south-east by 9,000 BP, but any changes in their composition are invisible in the region's grassland-dominated pollen records. Further north, there is little change in the grassland-dominated pollen record from Serra do Aracatuba (Behling, 2006), but a short buried peat sample near the Cerro do Touro Watershed (M. A. T. de Oliveira et al., 2008) shows a 30% decline in Campos pollen within a few centuries of 12,000 BP as *Weinmannia,* Myrtaceae, *Myrsine* and *Dicksonia sellowiana* pollen increase. Combined with changes in AMF taxa from GeoB2107 (*Araucaria, Schinus/Lithraea, Podocarpus* and *Myrsine* all respond differently), this may provide general support for predicted compositional changes in highland vegetation through the early Holocene, though forest coverage apparently remained patchy.

3.3.4. Mid-Holocene (6,000 BP)

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

Most palaeo-proxy sites in the region's west are dominated by grassland/C4 signals at the mid-Holocene, apart from Trincheira Reserva (Alcantara dos Santos, 2013) to the north-west, where phytoliths and $\delta^{13}C$ records show dominant woody C3 vegetation, and Buriti, where forest pollen increases to make up 70% of the total. As before, there is compositional change in Buriti's arboreal pollen with *Araucaria*'s contribution decreasing, being overtaken by *Alchornea*. There are also increases in *Dicksonia sellowiana* spores and pollen from *Drimys, Podocarpus* and *Luehea*, with

Sloanea occurring at 6,000 BP for the first time in several millennia. This combination of AMF and more warm-adapted tropical taxa may suggest a no-analogue forest assemblage at Buriti in the mid-Holocene; although our modelled species do not cover the location well at this period, this could support our prediction of the site occurring between floristic assemblages resembling tropical forest and AMF 6,000 years ago.

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

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

3.3.5. Late Holocene (3,000 BP)

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

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

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

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

3.3.6. Future (2070s)

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

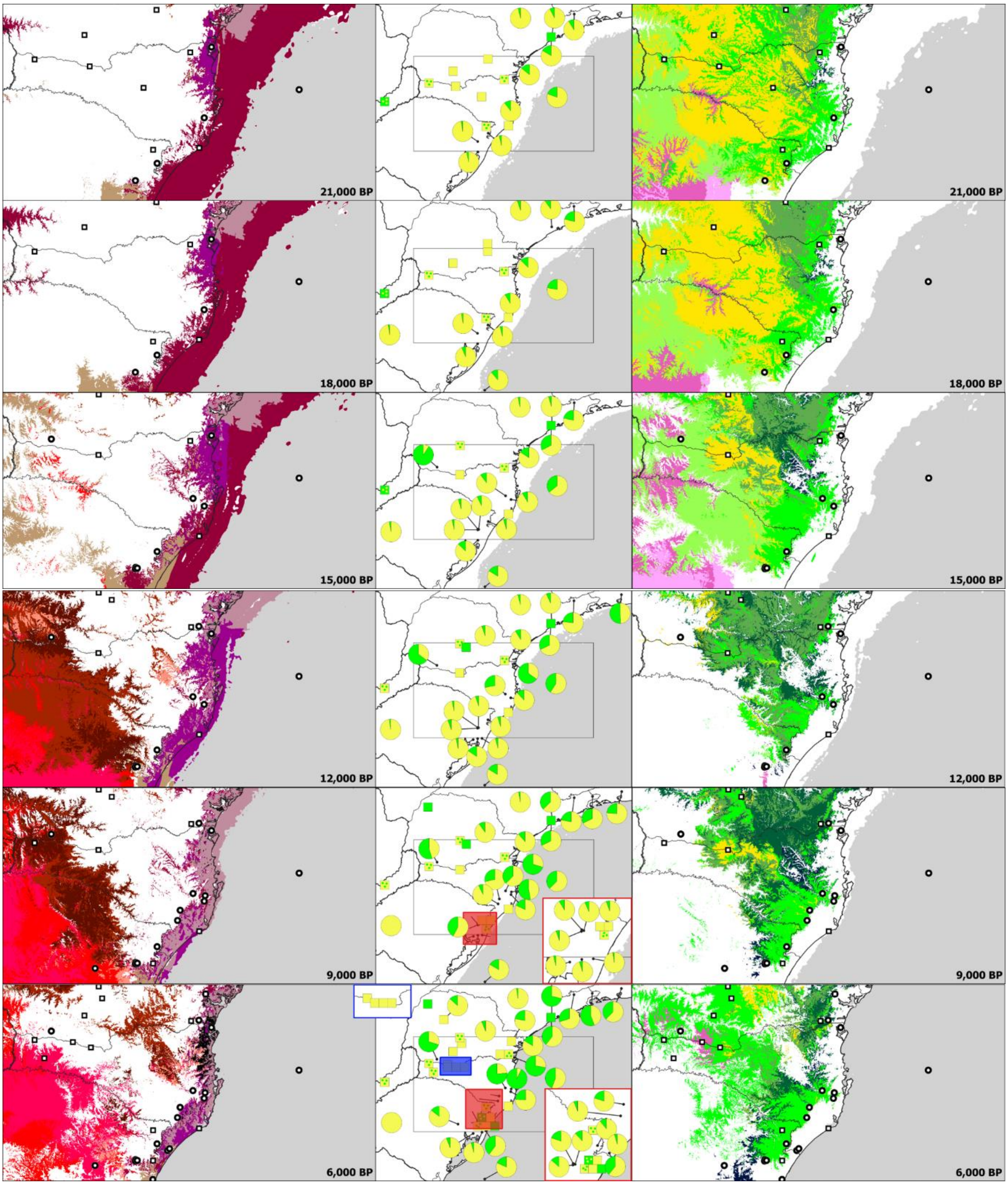
In our study area's west, assemblages 17 and 24, presently rare and scattered in the south-west, become widespread. Assemblage 24, the more southerly of the two, is characterised by a mixture of SDF and AMF/SDF species, with some presence of the few cold-adapted species to experience westward range expansions (*Podocarpus lambertii*, *Trifolium riograndense* and *Hypochaeris lutea*). Fewer species characterise assemblage 17, found along parts of the Uruguay and Iguazu river valleys, and, still further to the north-west, other parts of the Iguazu valley are predicted to be unsuitable for all our modelled species by the 2070s. These assemblages are interspersed with the SDF-like assemblage 5, dominated here by *Luehea divaricata* and other SDF species with some

Lithraea brasiliensis and *Matayba elaeagnoides*, which occupies large parts of present-day AMF/SDF ecotones.

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

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

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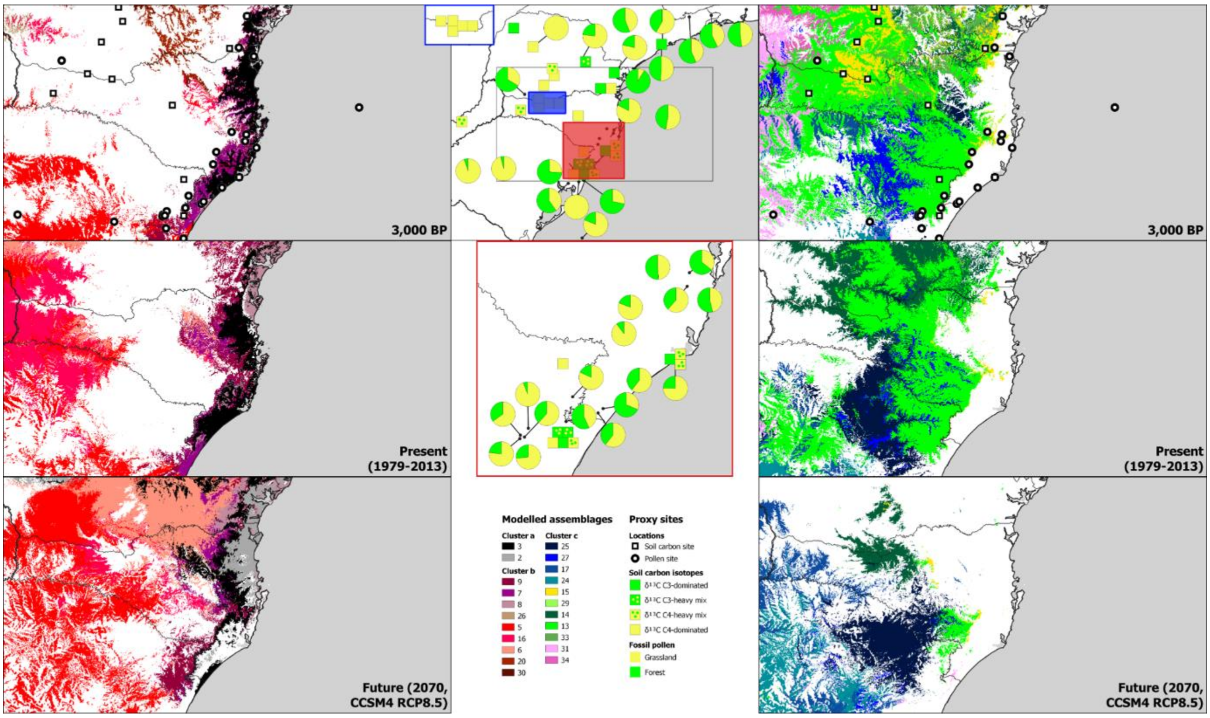

Figure 6: predicted floristic assemblages (clusters a and b, left, and cluster c, right) and palaeo-proxy values (centre) for our study area through time. For maps of individual assemblages, see fig. 4 or Supplementary Information.

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

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

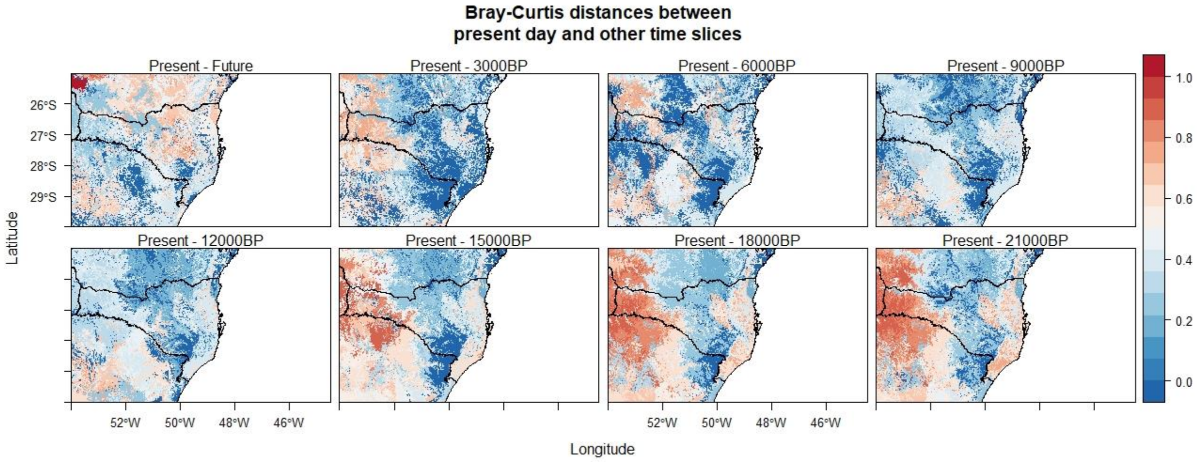

Figure 7: the (dis)similarity of present-day floristic assemblages to those of past and future time slices – red denotes assemblages which are more dissimilar and blue those which are more similar.

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

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

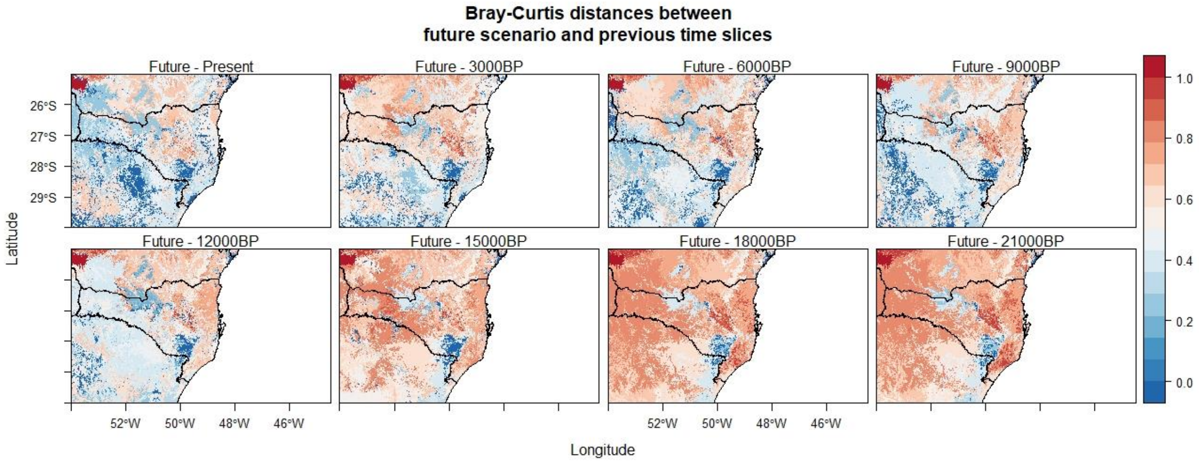

Figure 8: The (dis)similarity of future floristic assemblages to those of past and present time slices – red denotes assemblages which are more dissimilar and blue those which are more similar.

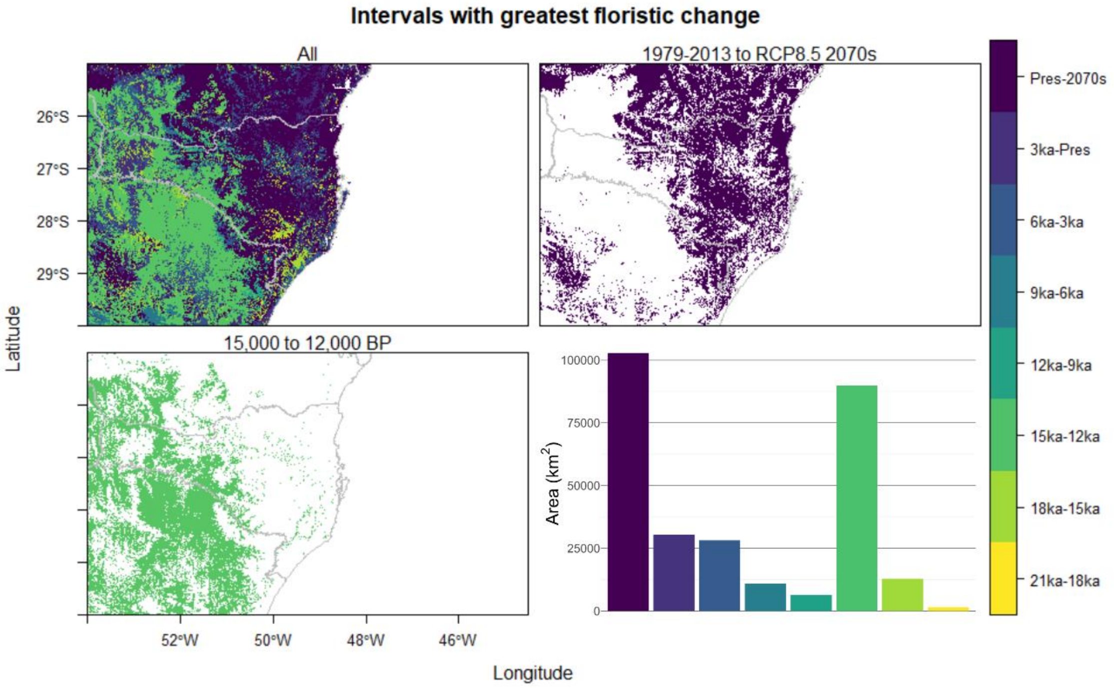

Figure 9: Between-time slice intervals during which the greatest floristic change is predicted. For figures underpinning column chart, see table S3. For past time slices only (i.e. excluding the future scenario), see fig. S13. For change between all intervals, see fig. S14.

4. Discussion

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

4.1. Plant community change since the LGM

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

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

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

4.2. Grassland-forest mosaics across space and time

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

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

One consequence of non-climatic influences on vegetation physiognomy is that modelled assemblages may have manifested quite differently in the past than in the present (e.g. assemblages 9, 15 and 13, detailed above). At the LGM and subsequently, many plant communities predicted to have co-occurring herbaceous and tree taxa may have been grassland landscapes with embedded forest (micro)refugia. Such formations have previously been inferred in southern Brazil from modelling (Barros et al., 2015; Costa et al., 2017; Stefenon et al., 2019), palynology (Behling et al., 2004; M. A. T. de Oliveira et al., 2008; Ledru et al., 2007, 2016) and phylogeography (Auler et al., 2002; de Sousa et al., 2020; Lauterjung et al., 2018; Ledru et al., 2007; Stefenon et al., 2007, 2008, 2019). Direct evidence can also be observed in our synthesised palaeo-proxy sites: a valley's base sheltering more woody vegetation than its head during the Last Glacial (Paisani et al., 2019); 7,500 years of forest and grassland respectively occupying opposing sheltered and exposed aspects of valley slopes (Robinson et al., 2018); and 15,000 years of continuous forest pollen in Buriti's topographic depression, while surrounding soil profiles show grasslands (Bertoldo et al., 2014). The buffering effect of small-scale topography (beyond our climate data's spatial resolution) may also have permitted species to persist in apparently unsuitable areas – Buriti records *Araucaria angustifolia* pollen 15,000 years ago, for instance, when our SDMs suggest it should have been absent (though this could also be because each sediment subsample covers a longer period than our palaeoclimate time slices). Refugia such as these will have played important roles in AMF's late-Holocene expansion across the plateau, and explain the development of *A. angustifolia's* western populations more parsimoniously than long-distance human-mediated dispersal in the late Holocene (cf. Lauterjung et al., 2018).

Compared to the plateau, inferring past vegetation physiognomies from meso-scale SDM predictions and finer-scale topographic data is much more difficult for the coastal lowlands, where detailed palaeo-topography is poorly known, due to submerged LGM coastlines. The prevalence of grassland pollen (and the near-absence of tropical forest pollen) in coastal proxy sites between the LGM and early Holocene has led some to suggest that grasslands replaced Atlantic Rainforest wholesale, with tropical tree species' southern limits found several hundred kilometres further north than at present (Bauermann, 2003; Behling, 2002; Behling & Negrelle, 2001) – a Pleistocene 'Forest Refuge Hypothesis' supported by early palaeo-distribution modelling (Carnaval & Moritz, 2008). However, a subsequent 'Atlantis Forest Hypothesis' argues that continental shelf exposed by lower LGM sea-levels could have supported large areas of forest (Leite et al., 2016). Our modelling and palaeo-data synthesis support an intermediate scenario of subtropical forest patches in a matrix of cold-adapted grassland/Campos (Bauermann, 2003; Behling & Negrelle, 2001; Gu et al., 2017). Our results suggest that the coastal lowlands and continental shelf had temperatures and rainfall suitable for both tropical trees (cf. Leite et al., 2016) and highland Campos species (cf. Behling & Negrelle, 2001), but available palaeoecological records show much more herb than forest pollen (Bauermann, 2003; Behling & Negrelle, 2001; Carvalho do Amaral et al., 2012; Gu et al., 2017), indicating that non-climatic factors likely dictated the distribution of these patches as they did with AMF and Campos on the highlands. However, without detailed topographic data for the presently submerged LGM coastal area, the precise spatial configuration of this LGM vegetation mosaic cannot be determined.

4.3. Context for a high-emissions future

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

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

4.4. Implications for Conservation

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

Our palaeoecological insights provide invaluable baselines which can help inform restoration or conservation strategies, but they must be explicitly (and rationally) chosen and many historical baseline landscapes may become unviable under future conditions (Barnosky et al., 2017; Dietl et al., 2015; Loughlin et al., 2018; Rick & Lockwood, 2013; Willis et al., 2010). Under a high-emissions scenario, future floristic assemblages in the southern Atlantic Forest will have few close analogues from the last 21 millennia, possibly favouring ‘taxon-free’ conservation measures – prioritising biodiversity *per se* or ecosystem function, structure or services, rather than the protection or restoration of specific, historically known landscapes (Barnosky et al., 2017). Drastic increases in atmospheric CO_2 concentrations will make structure-preserving measures particularly difficult in Araucaria Mixed Forest-Campos mosaics – which, in contrast to our LGM reconstruction, will increasingly favour forest over grassland (Fair et al., 2020; McElwain, 2018) – and will also impact the structure, function and biodiversity of the biome’s other forests (Esquivel-Muelbert et al., 2019). But regardless of the conservation approaches taken, a key task will be facilitating species’ individualistic movements in response to climate changes, including through forest restoration (Rezende et al., 2018; Zwiener et al., 2017). This too will come with challenges, however: increasing landscape connectivity amid anthropogenic climate change may erode endemic-rich marginal habitats and aid biotic homogenisation across the Atlantic Forest (Neves et al., 2017; Zwiener et al., 2018), and risks introducing competitor and antagonist species to populations sheltering in microrefugia (Ashcroft et al., 2012).

4.5. Conclusions

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

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Author contributions

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

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Preface to Chapter 4: How climate, fire and Indigenous people shaped Brazil’s Araucaria Forests through the Late Holocene

Publication status

This paper has been submitted to Nature Ecology and Evolution (February 2022).

Overview

Chapter 2 began to consider the past, which Chapter 3 continued and on which it focused, forging links with the future-focused predictions of Chapter 1. This arc culminates here in Chapter 4. The following paper considers two key non-climatic factors which affected Araucaria Forests’ past dynamics over the last 6,000 years: the mosaic’s fire ecology and long human occupation.

The work in this chapter builds on the research in all its predecessors. It uses topography-informed ecological niche models (ENMs, Chapter 1) to investigate how Campos and Araucaria Forest shared the highlands through time; as in Chapter 3, this study considers compositional change through time, again using new sources of palaeoclimate data to make prediction for important (but understudied) time periods. Chapter 3, applying insights from Chapter 2, demonstrated that combining ENMs with a detailed synthesis of palaeoecological data could provide novel insights into past vegetation changes, and here this approach is further focused and intensified. In addition to the comparison between ENM projections and palaeo-vegetation proxies used in Chapter 3, this chapter incorporates syntheses of palaeoclimatological and archaeological data, as well as examining new multiproxy palaeoecological records. Triangulating these diverse strands of multidisciplinary evidence provides the best evidence yet on the role of Indigenous people in shaping pre-colonial Araucaria Forests.

Contribution to the research

I conceived the design of this paper, and undertook all components of the research except the production of the new palaeoecological records – the three sites’ fossil pollen and charcoal were analysed by Macarena Cárdenas and their $\delta^{13}C$ by Claudio Latorre. I analysed the Botuverá palaeoclimate data; compiled, digitised and analysed the existing palaeoecological records; modelled the ecosystems’ changing distributions and compositions through time; led the synthesis of the different strands of data and the writing-up of the results. My contribution to this paper is estimated at 70-75%. The submitted form of the author contributions statement is below:

The overall aim of the study was conceived by FEM and OJW. The project design and methodological approach was devised by OJW. OJW undertook the ENM development, palaeoclimate analysis, and syntheses of palaeoecological and archaeological data. FEM collected the study’s new sediment cores which were prepared and analysed for palaeo-proxies by MLC (pollen, charcoal) and CL (δ13C). OJW and FEM interpreted the results with MLC. OJW drafted the manuscript, which all authors reviewed before submission.

Chapter 4: How climate, Indigenous people and fire shaped Brazil's Araucaria Forests through the Late Holocene

Authors

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Abstract

For millennia, climate changes and Indigenous people have influenced Earth's tropical ecosystems; their relative importance affects our understanding of the ecosystems' resilience to current anthropogenic changes, so is subject to intensive research and debate. Brazil's Atlantic Forest, a global biodiversity hotspot, has been largely absent from this conversation. Here we focus on this biome's most iconic, ancient and threatened formation – the highland mosaic of Araucaria Forest and Campos grasslands. Using novel integrations of palaeo-data and ecological modelling, we assess how climatic and human drivers shaped these landscapes over the last 6,000 years. We show that expansions of Araucaria Forest cover over the last several thousand years were predominantly natural, driven by non-linear responses of fire-forest feedback loops to minor climatic shifts. However, within Araucaria Forests Indigenous people profoundly affected vegetation structure and composition in areas they occupied and used more intensely. Our results challenge simplistic narratives of climate- versus human-driven past vegetation change. Climate, humans and fire all shaped these landscapes through space and time in complex combinations, all of which must be considered to understand or effectively conserve them.

Introduction

Few places on Earth are more threatened by human-driven land use pressure and climate change than tropical forests (Lewis, Edwards and Galbraith, 2015). Understanding how these ecosystems are likely to react to these intersecting drivers of change is crucially important because of their disproportionate contribution to global biological diversity, carbon sequestration and climate regulation (Lewis, Edwards and Galbraith, 2015; Ferreira *et al.*, 2018). Though predicting the future is inherently uncertain, understanding how tropical forests have been modified in the past – responding to natural climate changes since their formation, and to human occupations over the past several millennia – can provide critical clues as to their potential pathways through this century and beyond (Barnosky *et al.*, 2017; Roberts *et al.*, 2017; Fordham *et al.*, 2020; Ellis *et al.*, 2021; Roberts, Hamilton and Piperno, 2021). The interwoven contributions of Indigenous people and climatic conditions to shaping tropical and sub-tropical ecosystems over millennia have been studied from Australia and Asia to Africa, Amazonia and the Andes (e.g. Duvall, 2007; Rangan *et al.*, 2015; Morin-Rivat *et al.*, 2017; Loughlin *et al.*, 2018; Nogué *et al.*, 2018; Åkesson *et al.*, 2020; Fletcher, Hall and Alexandra, 2021; Hall *et al.*, 2021), with various lines of evidence showing that humans induced profound changes in their environments (Levis *et al.*, 2017, 2018) – promoting and dispersing culturally important species (Shepard and Ramirez, 2011; S Yoshi Maezumi *et al.*, 2018; Odonne *et al.*, 2019), altering soil properties (S. Yoshi Maezumi *et al.*, 2018; Levis *et al.*, 2020), and even preventing natural ecosystem changes (Carson *et al.*, 2014, 2015; Watling *et al.*, 2017).

The contributions of pre-colonial Indigenous societies to Amazonia's biogeographic patterns have been intensely studied and debated (e.g. Denevan, 1992; Bush and Silman, 2007; Barlow *et al.*, 2012; Clement *et al.*, 2015; Levis *et al.*, 2017), befitting the largest tropical forest biome in our planet's most biologically diverse continent (Antonelli *et al.*, 2018; Raven *et al.*, 2020). By comparison, these issues have received little attention in South America's other major tropical forest region, the Atlantic Forest. Yet the Atlantic Forest biome, which covers >3,000 km of Brazil's coast and stretches inland to Argentina and Paraguay, is a global biodiversity hotspot (Myers *et al.*, 2000). The Atlantic Forest has lost far more of its natural vegetation than Amazonia [63-88% (*MapBiomas Trinational Atlantic Forest Project*; Ribeiro *et al.*, 2009; Rezende *et al.*, 2018) vs. 17% (*MapBiomas Amazon Project*)] but contains 26% more known seed plant species [15,004 vs. 11,902 (Brazil Flora Group, 2015)], three times more of which are endemic [49.5% vs. 16.0%; species numbers for Brazil only (Brazil Flora Group, 2015)] – indeed, one in every 50 seed plant species on Earth is unique to the Atlantic Forest (Myers *et al.*, 2000; Brazil Flora Group, 2015; Lughadha *et al.*, 2016; S1). Considering likely trajectories of climatic disruption and land cover changes, the Atlantic Forest is the most threatened biodiversity hotspot in the world (Bellard *et al.*, 2014).

The impending threats from changing land use and climate conditions are most acute in the Atlantic Forest's ever-wet southern region, at the biome's highest elevations and under its coldest conditions (ca. 500-2,000 m above sea level; annual average temperatures ca. 15-21°C; annual precipitation ca. 1,250-2,250 mm) (Neves *et al.*, 2017). The ancient mosaic of Araucaria Forests and natural Campos grasslands found here is unique, iconic, and vanishing. Araucaria Forests comprise a variable mix of warm-adapted tropical species and cold-adapted Gondwanan relicts, with a phylogenetic signature that distinguishes them from other forests in the Atlantic Forest (Duarte *et al.*, 2014; Oliveira-Filho *et al.*, 2014). Campos, one of the very few non-forest ecosystems in the biome, are old-growth grasslands (Veldman *et al.*, 2015) which have been continuously present in southern Brazil for over 40,000 years (Behling *et al.*, 2004); about a quarter of their flora is endemic (Iganci *et al.*, 2011; Plá *et al.*, 2020). Both ecosystems have been heavily degraded by human activities in the 20th Century – Araucaria Forests are Endangered (Ferrer-Paris *et al.*, 2019), with some of the biome's worst trends in forest cover loss and increasing fragment isolation (Rosa *et al.*, 2021), and >25% of Campos was lost in three decades (Overbeck *et al.*, 2007). The mosaic's defining feature is the Araucaria tree (*Araucaria angustifolia,* also known as Brazilian or Paraná Pine) (Oliveira-Filho *et al.*, 2014), a member of the 'living fossil' Araucariaceae family which dominated South America's Cretaceous tropical forests before the extinction of non-avian dinosaurs (Panti *et al.*, 2012; Forest *et al.*, 2018; Carvalho *et al.*, 2021). Brazil's Araucaria trees are now at the brink of extinction themselves, after devastating losses from unsustainable 20th-Century logging and habitat conversion, which are being exacerbated by 21st-Century anthropogenic climate changes (Ribeiro *et al.*, 2009; Thomas, 2013; Wilson *et al.*, 2019, 2021; Tagliari, Vieilledent, *et al.*, 2021). As a result, *A. angustifolia* is among the most evolutionarily distinct and globally endangered tree species on the planet (Forest *et al.*, 2018).

Araucaria trees have multifaceted importance to the natural world and to human societies. *A. angustifolia* seeds (pinhão) are large, nutritious, abundant, and consistently produced, a keystone plant resource (Bogoni, Muniz-Tagliari, *et al.*, 2020) – food for more than 70 mammal and bird species (Dénes *et al.*, 2018; Bogoni, Batista, *et al.*, 2020; Bogoni, Muniz-Tagliari, *et al.*, 2020), commercially valuable to southern Brazil's rural communities (IBGE, 2018), and a crucial food resource for Indigenous people long before European arrival (Corteletti *et al.*, 2015), traded from the highlands to communities on the distant coast more than 1,000 years ago (Scheel-Ybert and Boyadjian, 2020). Araucaria's importance to Indigenous people past and present gives it many hallmarks of a cultural keystone species (Coe and Gaoue, 2020): the tree "could be considered the ritual object par excellence" for its role in the Kaingang Kiki ceremony (Fernandes and Piovezana, 2015, p. 120), its fruiting defined Xokleng territories and seasonal movements (Henry, 1964; Moura, 2021), and the highest level in Kaingang shamanic territory – the domain of glory, where God lives – is named after, characterised by, and can be reached by climbing Araucaria trees (Réus Gonçalves Da Rosa, 2005).

Through their multi-millennial association, Araucaria Forests significantly shaped Indigenous societies (Iriarte and Behling, 2007), but did people similarly influence Araucaria Forests? Are the southern Atlantic Forest's highland ecosystems principally cultural relics, previously domesticated landscapes? The question is critical for understanding the potential for their sustainable use and resilience to 21st-Century climate changes and has been the subject of speculation for decades (Aubreville, 1948; Bitencourt and Krauspenhar, 2006), but has remained unresolved (reviewed in S2). In many tropical regions, in particular Amazonia, the extent, intensity and durability of human and climatic ecosystem transformations is the subject of a long-standing polarised debate (Denevan, 1992; Bush and Silman, 2007; Barlow *et al.*, 2012; Clement *et al.*, 2015; Levis *et al.*, 2017), with research generally focusing on one driver over the other and requiring centennial- to millennial-scale extrapolations from present-day floristic patterns, in the frequent absence of proxy data on past human, climatic and environmental changes. By contrast, there is far greater potential for resolving the respective, and interactive, roles of Holocene human land use and climate change in shaping contemporary biodiversity patterns in the southern Atlantic Forest, because of the much richer dataset of palaeoenvironmental and archaeological data available for this region (Smith and Mayle, 2017; Wilson *et al.*, 2021).

Southern Brazil's Holocene climate history is recorded at sub-annual temporal resolution in a speleothem rainfall proxy record spanning the last 9,000 years (Bernal *et al.*, 2016). South America's densest collection of palaeoecological vegetation proxy records show how Campos and Araucaria Forest developed in time and space, with forest expansions recorded around 4,000–3,000 and 1,500–500 years ago (fig. 1, S4.2). The more recent episode of Araucaria Forest encroachment coincides with a period of population growth and cultural change reflected in the southern Jê archaeological record, whose cultural continuity with historical and contemporary Indigenous groups like the Kaingang and Xokleng is very clearly established (Urban, 1985; Robinson *et al.*, 2017; de Souza, 2018; de Souza and Riris, 2021). The southern Jê practised a mixed economy among Araucaria Forests and Campos: alongside hunting and cultivation of crops such as maize (*Zea mays*), squash (*Cucurbita* spp.) and beans (*Phaseolus* spp.), pinhão (*A. angustifolia* seeds) were an important food source (Corteletti *et al.*, 2015; Loponte *et al.*, 2016). Almost uniquely among useful and culturally important tropical trees (Bush and McMichael, 2016), *A. angustifolia* is clearly identifiable in both the palaeoecological and archaeological records: its pollen is distinctive, and diagnostic phytoliths and starch grains can also allow it to be identified in dental calculi and ceramic residues from archaeological sites (Corteletti *et al.*, 2015; Scheel-Ybert and Boyadjian, 2020).

The underlying driver(s) for the Late Holocene expansion of Araucaria Forest remain(s) contentious, with some arguing for an anthropogenic cause, based on coeval expansion of the southern Jê culture in the Common Era (Bitencourt and Krauspenhar, 2006; dos Reis, Ladio and Peroni, 2014; Robinson *et al.*, 2018), whereas others argue for climatic drivers (Behling *et al.*, 2004; Jeske-Pieruschka and Behling, 2012; Rodrigues, Behling and Giesecke, 2016). There are many compelling reasons to argue that Araucaria Forests could have been profoundly shaped by pre-colonial Indigenous communities (Bitencourt and Krauspenhar, 2006; dos Reis, Ladio and Peroni, 2014), but the few studies to have examined the subject have not produced definitive evidence (Lauterjung *et al.*, 2018; Robinson *et al.*, 2018; Pereira Cruz *et al.*, 2020; reviewed in S2). Close integration of high-quality archaeological, palaeoecological and palaeoclimate data is a necessary first step for robustly differentiating between human versus climatic causes of pre-colonial vegetation change, but it is not always sufficient. Relating Late Holocene vegetation dynamics to spatial gradients of human land use (cf. Robinson *et al.*, 2018) can only elucidate human drivers if the potentially confounding effects of natural ecological factors are adequately controlled for. Ecological niche models (ENMs) can perform this vital function by producing spatially explicit predictions of ecosystem change driven by climatic variables alone (Svenning *et al.*, 2011). Deviations in observed past vegetation dynamics from the expectations from these 'null' ecological models can point to non-climatic causes for such changes. Where these can be spatially, chronologically and causally linked to observed patterns of human occupation, this technique can provide much clearer evidence for anthropogenic drivers of vegetation change than is possible from empirical palaeo-proxy data alone.

In this study we investigate when, where and how climatic changes and human actions shaped Brazil's Araucaria Forest-Campos mosaic over the last 6,000 years, by integrating five independent strands of evidence. We use ENMs to predict climate-driven changes to ecosystems' distributions and compositions through space and time (figs. 1b-c, 2; S4.4), and synthesise proxy data from 46 existing palaeoecological sites – including every adequately dated record in southern Brazil's highlands (fig. 1d) – to reveal observed changes in past Araucaria Forest-Campos dynamics and fire regimes (fig. 3d-g, S4.2). Potential climatic drivers for these changes are examined by analysing a high-resolution speleothem rainfall proxy record (fig. 3a-b), and 311 archaeological radiocarbon dates show the temporal dynamics of human occupations across the landscape (fig. 3c). Finally, we describe three new multiproxy palaeoecological records, all in close proximity to well-researched southern Jê archaeological sites – the region's first fossil pollen and charcoal records designed to capture the effects of past human land use on the Araucaria Forest-Campos mosaic (cf. Mayle and Iriarte, 2014; figs. 1d, 3g, S4.3). Together, these lines of evidence reveal the complex ways in which climatic changes, Indigenous communities and fire combined to shape Brazil's Araucaria Forests through the Late Holocene.

Results

Our multistranded approach reveals three main findings: i) that Late Holocene Araucaria Forest expansions over Campos grasslands had primarily natural drivers (i.e. climate and fire); ii) that those expansions were transitions between alternative ecosystem stable states, caused by apparently minor climatic changes altering fire-forest feedbacks; and iii) that the southern Jê profoundly shaped the structure and composition of the landscapes among which they lived.

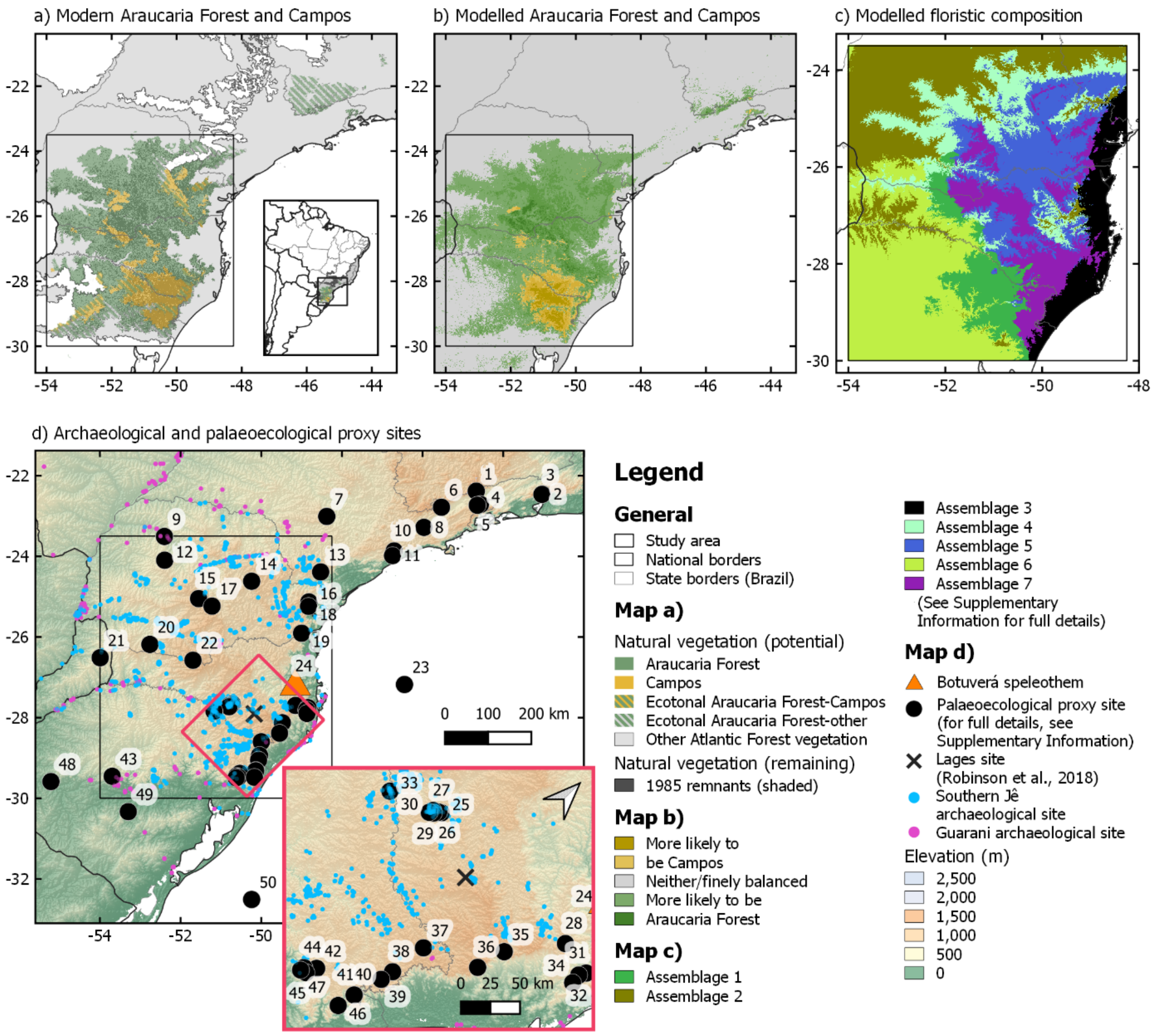

Figure 1: Maps showing a) the natural potential extent of Araucaria Forest and Campos, and their remnant natural vegetation from 1985 (Souza et al., 2020), *b) ecosystem-level ENM for the present-day (see S4.4), c) modelled floristic composition for the study area (see S3.23 and S4.4), and d) palaeoecological proxy sites synthesised for this study, with southern Jê and Guarani* (Bonomo *et al.*, 2015; Iriarte *et al.*, 2017) *archaeological sites. The new palaeoecological records in this study are sites 26 (Abreu e Garcia), 29 (Amaral) and 33 (Pinhal da Serra), in inset. For more information on the synthesised palaeoecological records, see S3.3.*

Natural causes for Araucaria Forest expansions

Various lines of evidence suggest that climatic changes made significant contributions to Late Holocene expansions of Araucaria Forest over Campos. The Botuverá speleothem record (Bernal *et al.*, 2016) highlights periods of increased rainfall for much of the period between 4,000 and 2,500 cal BP [calibrated years before radiocarbon present, 1950 AD], and even more so from 2,000 to ca. 800 cal BP (fig. 3a-b). These are the main periods in which proxy sites record increases in Araucaria Forest and/or *Araucaria angustifolia* pollen, and/or transitions to more C3-dominated (likely woody) vegetation (fig. 3d-f, S4.2). (Forest expansions in the Common Era tend to be larger and more pronounced than those in the preceding millennia, correlating with the relative magnitudes of the periods' rainfall increases.) With three notable exceptions (see S4.1), *A. angustifolia* pollen reaches its highest proportions in the last 2,000 years, though it is rarely abundant or an apparent driver of forest expansions; in a number of cases it only becomes a noticeable component of the pollen spectrum in the last two millennia. [This may be partly due to *A. angustifolia's* under-representation in some pollen records (Cárdenas *et al.*, 2019; Piraquive Bermúdez, Theuerkauf and Giesecke, 2021).]

These findings alone are insufficient to attribute Common Era expansions of Araucaria Forest and/or *A. angustifolia* to natural causes: the timings and magnitudes of vegetation changes are correlated with changes in both rainfall and the intensity of human occupation of the highlands (fig. 3a-c) (Robinson *et al.*, 2018; de Souza and Riris, 2021). Our ecological niche models (ENMs) provide the necessary evidence for any attribution to natural drivers. Driven by climatic variables alone, these ENMs tend to predict relative increases in the probability of Araucaria Forest compared to Campos, and/or changes to floristic composition, at the same times and locations that proxy records show vegetation changes (fig. 2, S4.2, S4.4). This strongly suggests that the observed changes were indeed largely driven by natural climatic fluctuations.

Several sites can be used to illustrate this. Serra das Pedras Brancas (Roth, Luisa Lorscheitter and Masetto, 2021), Banhado Amarelo (Scherer and Lorscheitter, 2014), Ciama 2 (Jeske-Pieruschka *et al.*, 2013) and CPCN Pro Mata (Dümig *et al.*, 2008; Silva and Anand, 2011) all record increases in Araucaria Forest pollen or C3 vegetation in the Common Era, at locations and times when Araucaria Forest is also predicted by our ENMs to increase its likelihood of occurring (in absolute terms and/or relative to Campos; S4.2). Looking at wider regions surrounding proxy sites (necessary because of our high-resolution ENM predictions and the wide and varied catchments for pollen records; fig. 2), we see areas predicted to transition from Campos to Araucaria Forest around Cambará do Sul (Behling *et al.*, 2004) and São Jose dos Ausentes (Jeske-Pieruschka *et al.*, 2010) in the last millennium, when both record increases in Araucaria Forest pollen. Notably, from 1,000 cal BP onwards, our ENMs also predict expansions in Araucaria Forest at the expense of Campos around archaeology-rich Campo Belo do Sul and stability at archaeology-free Lages (fig. 2). The former experienced increases in C3 vegetation in the last millennium, whereas vegetation distributions were stable over the long term at the latter, a difference Robinson *et al.* (2018) attribute to the spatial gradient in past southern Jê occupation. Instead, our ENMs suggest a greater contribution to these differences came from natural climatic changes: in Lages, Campos is predicted to have remained much more likely than Araucaria Forest over the last 6,000 years, whereas the two ecosystems are finely balanced in Campo Belo do Sul (S4.2). We also find that the two areas have different predicted floristic compositions which, with the results of the ecosystem-level ENMs, may help to explain the different spatial configurations of Araucaria Forest in the landscapes in both regions (Robinson *et al.*, 2018).

These findings strongly suggest that climate changes were the largest single cause of Araucaria Forest expansions in the synthesised palaeo-proxy sites (fig. 1d). Potential human contributions cannot be entirely ruled out, as these natural climate-driven trajectories of forest expansion could conceivably have been slowed (e.g. to maintain open areas for hunting) or exacerbated (e.g. to promote forest resources) by human actions, which could also have resulted in other changes that did not impact Araucaria Forest's extent (e.g. structural or compositional changes; S5.2). However, our findings reveal that it is not necessary to invoke anthropogenic causes to explain any of the previously identified expansions of Araucaria Forest over Campos.

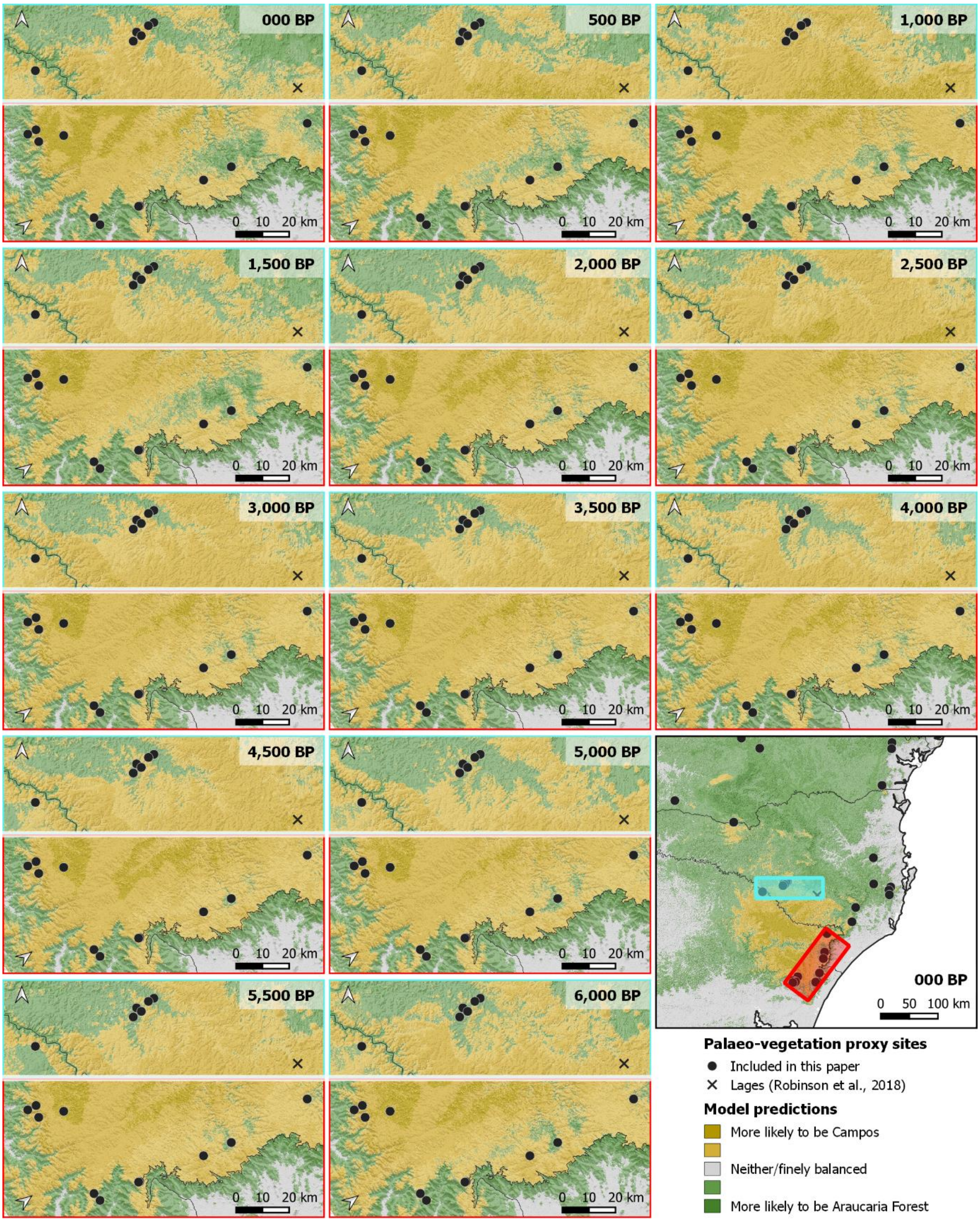

Figure 2: Maps showing modelled changes in the relative probabilities of Araucaria Forest and Campos over space and time, focusing on the areas with the most palaeoecological proxy sites. From left to right, the sites in the upper/blue panels are Pinhal da Serra, Luis Carlos, Baggio, Amaral, Abreu e Garcia, Heraldo, and Lages (cross – excluded from this study because it has only one date) (all from this study or Robinson *et al.*, 2018) *and in the lower/red panels, the sites are Alpes de São Francisco 2* (Leonhardt and Lorscheitter, 2010) *and 1* (Scherer and Lorscheitter, 2014), *Rincão das Cabritas* (Jeske-Pieruschka and Behling, 2012), *Fazenda do Pinto* (Behling, Bauermann and Neves, 2001), *CPCN Pro Mata (the two bottom dots)* (Dümig *et al.*, 2008; Silva and Anand, 2011), *Serra das Pedras Brancas* (Spalding and Lorscheitter, 2015) *and Banhado Amarelo* (Scherer and

Lorscheitter, 2014) *(not distinguishable at this scale), Cambará do Sul* (Behling *et al.*, 2004)*, and Cachoeira do Puma* (Fischer, 2015).

Natural fire-forest feedbacks drove Araucaria Forest expansions

A number of proxy records show somewhat sudden, relatively large increases in Araucaria Forest pollen at certain time periods in the past 4,000 years (fig. 3d-f, S4.2). These abrupt changes are not clearly associated with precipitation changes of similar magnitude in the Botuverá speleothem (Bernal *et al.*, 2016), though they do occur at times of increased rainfall (fig. 3a); similarly, while our ENMs predict relative gains for forest at many of these sites and time periods, they nonetheless frequently project that Campos would have remained more likely than Araucaria Forest (S4.2). However, a clear, consistent and close negative relationship between fire and forest can be observed at almost all sites which record both pollen and charcoal (fig. 3d-f, fig. 4, S4.2). High concentrations of charred particles are associated with decreases or low levels of forest pollen throughout the region, and in previously published cores, pollen from Araucaria Forest (and especially *A. angustifolia*) only increases after charcoal concentrations have declined to low levels. Three of the best exemplars of this pattern are Rincão das Cabritas (Jeske-Pieruschka and Behling, 2012), Cambará do Sul (Behling *et al.*, 2004), and Serra Campos Gerais before about 700 cal BP (Behling, 1997) (fig. 3d-f). In each, sharp declines in charcoal are accompanied by increases in Araucaria Forest in general and *A. angustifolia* in particular.

Fire is a natural part of the Araucaria Forest-Campos mosaic (Behling *et al.*, 2004; Overbeck *et al.*, 2018). Ecological and palaeoecological observations have highlighted that Campos and Araucaria Forest are alternative ecosystem stable states, with their boundaries maintained by natural and anthropogenic fire (and grazing, which is less relevant in the pre-colonial Late Holocene) (Beisner, Haydon and Cuddington, 2003; Oliveira and Pillar, 2005; Jeske-Pieruschka *et al.*, 2010; Müller *et al.*, 2012; Innes, Anand and Bauch, 2013; Blanco *et al.*, 2014; Henderson, Bauch and Anand, 2016; Sühs, Giehl and Peroni, 2020; Sühs *et al.*, 2021). Campos species are generally resilient to burning but tree seedlings are fire-sensitive, so fires prevent forest expansions (Jeske-Pieruschka *et al.*, 2010; de Oliveira Portes, Safford and Behling, 2018; Overbeck *et al.*, 2018; Sühs *et al.*, 2021). Established Araucaria Forest areas, however, are largely fire-resistant and generally do not burn under natural conditions. The observed fire and forest dynamics can therefore be explained by a positive feedback loop: relatively minor climate changes (rainfall or temperature increases) slightly favoured forest species and depressed natural fires, which also helped promote some forest expansion; since forest areas are less susceptible to burning, larger forest areas meant fires became less frequent, which allowed further forest expansion, and so on (van Nes *et al.*, 2018) (fig. 5). Such fire-forest feedbacks neatly explain how small changes in rainfall or modelled likelihood of Araucaria Forest could lead to disproportionately fast and large increases in forest pollen. Adding support to this hypothesis, the abrupt system changes in fire and forest proxies in Rincão das Cabritas, Cambará do Sul and Serra Campos Gerais are all slightly preceded by gentle increases in forest pollen (fig. 3d-f); these initial responses to more forest-favourable conditions probably initiated the positive feedback loops.

Climatic changes provide a more likely explanation for these changes than human land use. Conceivably, human actions which increased forest cover could have helped activate or accelerate the fire-forest feedbacks, but climatic changes co-occurred with the threshold shifts more consistently than did human activities. Additionally, an anthropogenic mechanism, beside the promotion of forest, is difficult to envision – pre-colonial human land use in forest ecosystems is generally correlated with increases in fire activity, not its decline (see de Oliveira Portes, Safford and Behling, 2018 and below, but also S5.2). Overall, therefore, the simplest explanation for these observed pattens is that they were predominantly driven by shifts to more forest-suitable climate conditions.

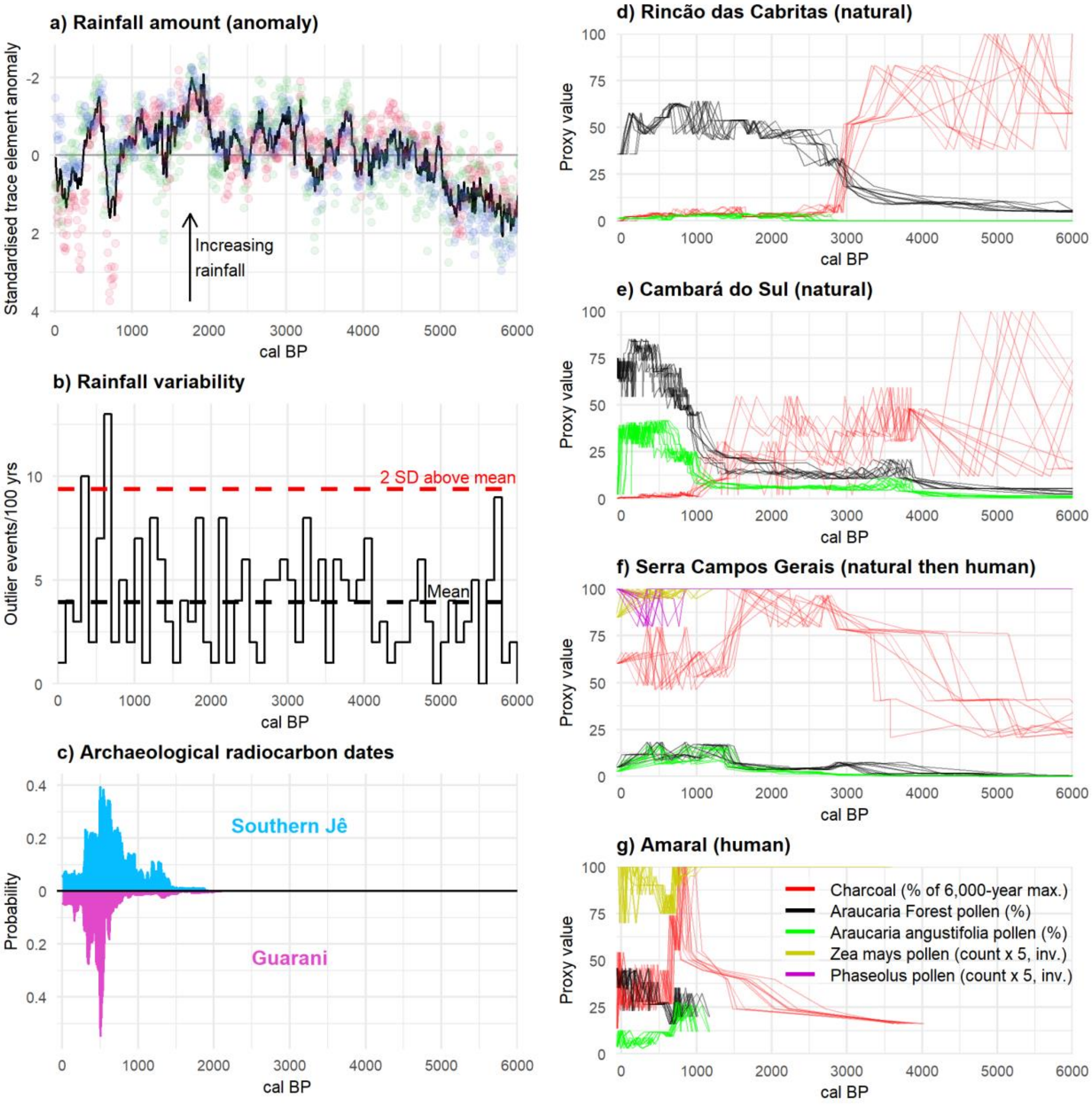

Figure 3: a-b) Proxy record for past precipitation amount [a), Mg/Ca, Ba/Ca and Sr/Ca as red, green and blue circles, respectively, and their mean as the black line] and variability [b), MAD outlier events per 100-year bin] from Botuverá trace element ratios (Bernal *et al.*, 2016). *c) Summed probability distributions of calibrated archaeological radiocarbon dates from southern Jê (195 dates) and Guarani (116 dates) contexts* (de Souza, Mateos and Madella, 2020). *d-g) Multiproxy palaeoecological records illustrating changes driven by natural climate changes [Rincão das Cabritas* (Jeske-Pieruschka and Behling, 2012), *site 45 in fig. 1d, and Cambará do Sul* (Behling *et al.*, 2004), *site 39], human land use (Amaral, site 29) and a mixture of both [Serra Campos Gerais* (Behling, 1997), *site 14]. Proxy time series are plotted against ten random iterations of each site's age-depth model. (Micro-)charcoal concentration is scaled to its 6,000-year maximum in each record. Cultigen pollen (maize, yellow, and beans, purple) is plotted inverted with 5x exaggeration.*

Indigenous communities shaped Araucaria Forests

The great majority of palaeo-proxy records we examined demonstrated a consistent negative relationship between charcoal concentrations and pollen from Araucaria Forest taxa (especially *A. angustifolia*), which fits well with their natural ecological dynamics (fig. 4a-b, S4.2). Four sites, however, display a systematic departure from – indeed an inversion of – these patterns: at Abreu e Garcia, Amaral, Pinhal da Serra, and Serra Campos Gerais (after about 700 cal BP), increases in charcoal are associated with increases of pollen from both Araucaria Forest and *A. angustifolia* (fig. 3f-g, fig. 4a-b, S4.2). Abreu e Garcia, Amaral and Pinhal da Serra are all in very close proximity to known southern Jê archaeological sites and all four sites have clear evidence of crop cultivation (pollen from *Zea mays* at all sites and from *Phaseolus* at Serra Campos Gerais) from the same time periods as these inverted fire-forest relationships. In these sites, therefore, southern Jê fire use is associated with both cultivation and modest anthropogenic increases in *A. angustifolia* and Araucaria Forest.

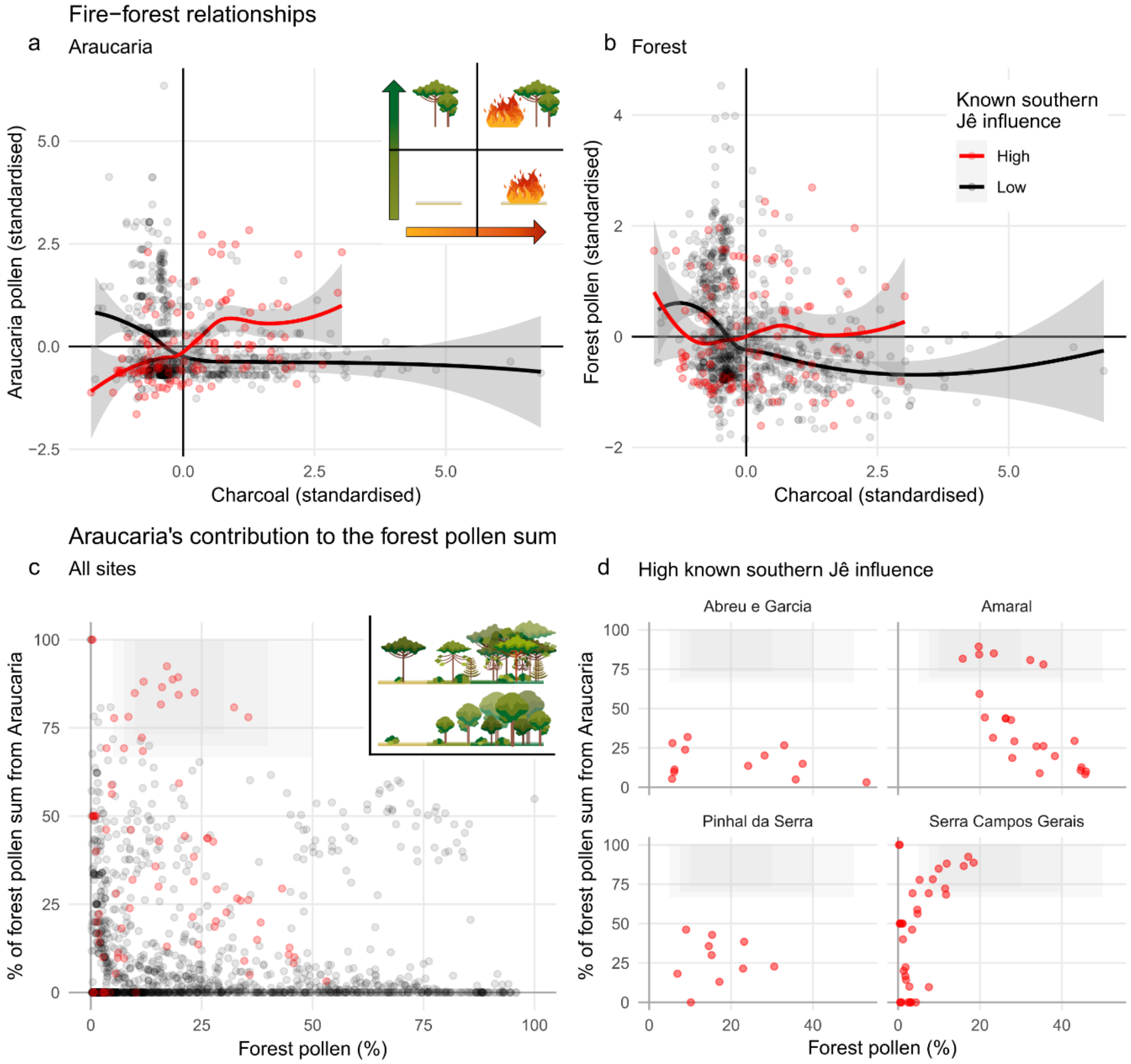

Figure 4: The differences between sites with high (red – Abreu e Garcia, Amaral, Pinhal da Serra, Serra Campos Gerais) and low (black) known southern Jê influence. Top: Araucaria (a) and (Araucaria) forest (b) vegetation against charcoal concentrations. For each site, charcoal concentrations and pollen proportions were standardised before plotting; lines are loess curves fitted to the points. Bottom: contribution of Araucaria pollen to (Araucaria) forest pollen sum for all sites (c) and those with high southern Jê influence (d). Data are taken from the records' entire lengths (i.e. not just the Late Holocene). For per-site comparisons, see S4.2.

In addition to their non-natural fire regimes, most of these human-altered landscapes are also distinguished by their forest pollen composition, with *Araucaria angustifolia* pollen generally relatively high and making up a greater proportion of the forest pollen than in predominantly natural sites (fig. 4c-d). The clearest example of this is found in the early part of the Amaral record (from about 950 to 770 cal BP), where *A. angustifolia* is 13-28% of the total terrestrial pollen (TTP) sum and 78-89% of the Araucaria Forest pollen (AFP) sum; despite declining subsequently, it remains >40% of the FP sum for another 350 years (figs. 3g, 4d). At Serra Campos Gerais, *A. angustifolia* pollen makes up 6-16% of the TTP, and 72-92% of the AFP sums for almost the entire millennium from 1,300 cal BP (though other tree taxa are quite well represented in other pollen groups; figs. 3f, 4d). *A. angustifolia* pollen makes up respectively 4-9% and 30-46% of the TTP and AFP sums at Pinhal da Serra between about 1,750 and 350 cal BP (fig. 4d, S4.2, S4.3). The pattern is not clear in the more variable Abreu e Garcia record. Several other sites show components of this signal, but in none of them can they be clearly attributed to human land use (S4.2, S5.1).

The landscape at Amaral between about 950 and 770 cal BP is particularly notable – pollen assemblages dominated by *A. angustifolia* (13-28%), Asteraceae (38-50%) and Poaceae (12-24%), and a C3-dominant $\delta^{13}C$ signature (-24 to -25‰ (Dümig *et al.*, 2008; Silva and Anand, 2011)). Nothing similar has previously been observed (fig. 4c-d, S4.3). The catchment around Amaral therefore seems likely to have been a type of parkland, with *A. angustifolia* canopy above Asteraceae shrubland or grassland, kept open with fire. (The presence of other Araucaria Forest taxa cannot be ruled out, since many are poorly represented in the pollen record (Cárdenas *et al.*, 2019; Piraquive Bermúdez, Theuerkauf and Giesecke, 2021), but most previous studies have more diverse tree pollen than this part of the Amaral record. The relatively high proportions of *A. angustifolia* are unlikely to be the result solely of its over-representation in the pollen record (Cárdenas *et al.*, 2019; Piraquive Bermúdez, Theuerkauf and Giesecke, 2021). Pollen-vegetation relationships also complicate our ability to understand the extent of such a system, since pollen from different taxa and ecosystems have different source areas (Duffin and Bunting, 2008; Guarinello de Oliveira Portes *et al.*, 2020), and its spatial patterning, since pollen discrete vegetation units becomes mixed (Bunting and Middleton, 2009; Bunting *et al.*, 2018; Whitney *et al.*, 2019). Nuances of forest structure can also be blurred or missing in comparably insensitive pollen data (Cárdenas *et al.*, 2019), though the confluence of different indicators here – including non-pollen $\delta^{13}C$ – increases our confidence that the bog's catchment likely had a relatively open structure.) This unusual floristic composition and assumed structure, accompanied by maize pollen, high macro- and micro-charcoal concentrations, and independent evidence of nearby human activity (charcoal from a fire pit at the Baggio 1 site has been dated to this period; de Souza, 2018), all suggest this landscape formed as a result of land use by southern Jê groups. This Araucaria parkland could have been used and/or managed for hunting game and harvesting pinhão – according to Xokleng-Laklãnõ elders, before intense contact with colonial society, these activities took place in forests that were 'taller and more open' than now (Gomes, 2018, p. 129).

The Amaral record also shows a change in the local landscape between 720 and 620 cal BP (fig. 3g, S4.2, S4.3). Peaks in macro-charcoal and maize, sudden declines in micro-charcoal and *A. angustifolia* and Araucaria Forest pollen, and a temporary change to a more open landscape, as inferred from the $\delta^{13}C$ record, all point to the founding of the Baggio 1 pit house settlement (de Souza, 2018) during a period of significantly variable rainfall (fig. 3b). This village was continuously occupied from the mid-14th Century to the late 18th Century AD, during which time the site's surroundings were burned less frequently (lower micro-charcoal concentrations), local fires continued (sustained high macro-charcoal concentrations) for domestic, ritual (de Souza *et al.*, 2016; de Souza, 2018) and/or for small-scale land management purposes, and maize cultivation was maintained or intensified. A marked change in forest composition from this time sees *A. angustifolia* begin to decline (though still >10% of the TTP sum until ca. 350 cal BP), replaced by *Mimosa* and *M.*

scabrella pollen. *M. scabrella* in particular is a short-lived early successional species favoured by disturbances, especially fire, so much of its increase may have been incidental (Machado *et al.*, 2006; Steenbock *et al.*, 2011). It does, however, produce much-valued firewood and material for construction and woodworking (Schallenberger and Machado, 2013; Cruz, 2014; Mello and Peroni, 2015; Serviço Florestal Brasileiro, 2018a, 2018b), forming near-monodominant forest blocks under (modern) management (Machado *et al.*, 2006; Steenbock *et al.*, 2011), so its proliferation could also have been encouraged and/or managed. The steady decrease in the Amaral record's macro-charcoal concentrations after about 260 cal BP was probably caused by Baggio 1 entering a period of decline (1670-1790 AD), in turn most likely the indirect result of European presence in the region (de Souza, 2018).

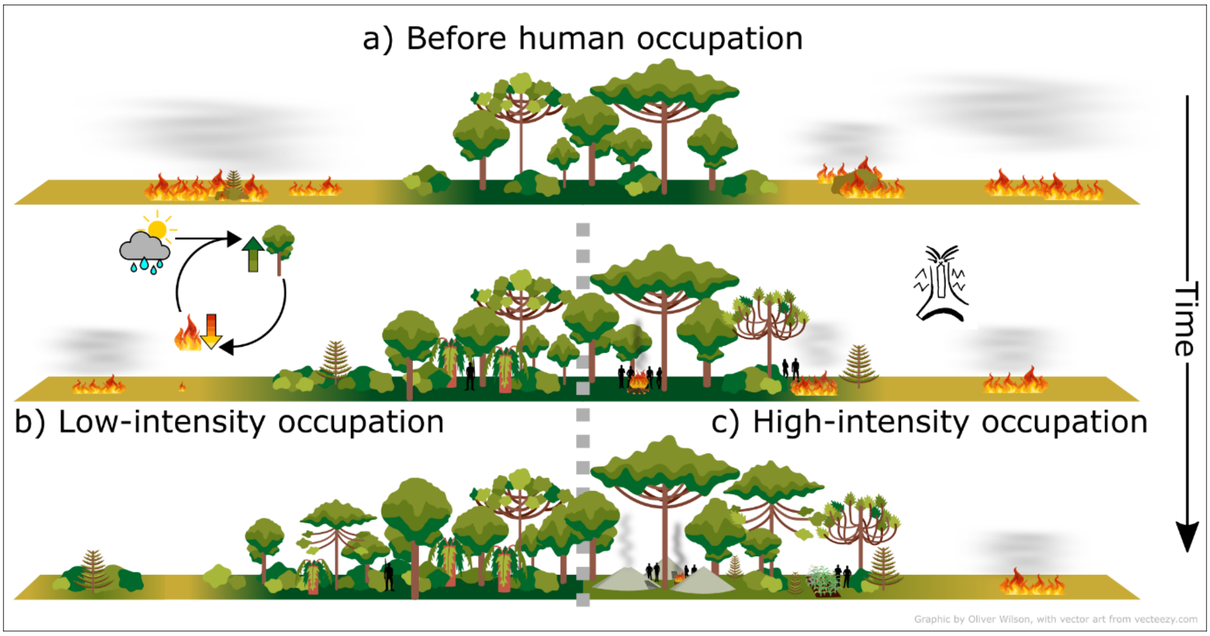

Figure 5: A schematic summary of our main results. In southern Brazil, fires in Campos prevent Araucaria Forest expansion, but established forest areas rarely burn. Before human occupation (a), these dynamics maintain the mosaic. In areas with less intense pre-colonial human occupation (b), climate changes altered fire-forest feedback loops – by helping forest areas expand, they reduced fires, which allowed more forest expansion, and so on. In areas they occupied intensely (c), southern Jê Indigenous people transformed the landscape, cultivating crops and setting more fires, which was associated with modest forest expansion and more Araucaria trees.

Discussion

The multidisciplinary approach used in this paper sheds unprecedented light on 6,000 years of natural and human activity on southern Brazil's highlands. It allows us to compare expected (modelled) and observed changes in both climate and vegetation, examine regional and local patterns, and probe differences across spatial and temporal gradients from intense to (apparently) light pre-colonial human impact. We find that climate and humans, each working through alterations to fire regimes, both played significant roles in shaping Araucaria Forest and Campos landscapes in the Late Holocene, and that these factors combined in complex, heterogeneous and interconnected ways (fig. 5).

Our results show that parts of Brazil's Araucaria Forests were significantly influenced by the southern Jê. Following their arrival, after 1,300-1,400 cal BP the highlands experienced pronounced and exponential population growth, which is associated with increases in the numbers of recorded archaeological sites and radiocarbon dates (fig. 3c; Robinson *et al.*, 2018; de Souza and Riris, 2021).

(These population changes were significantly more pronounced than concurrent demographic trajectories in Amazonia or other parts of the southern La Plata basin (Arroyo-Kalin and Riris, 2021; de Souza and Riris, 2021).) Locally, intense occupation by southern Jê groups – marked by crop cultivation and increases in burning – was associated with modest expansions of Araucaria Forest and apparent enrichment of *A. angustifolia*, both contrary to expected ecosystem responses to nearby fire. With local variations, these impacts may have been widespread, and are observed in four sites across two areas 350 km distant from one another (S5.1). We suggest that these proxy signatures are signals of intense southern Jê land use and occupation; the areas in which they occur correspond to the 'casa' (home) and 'espaço limpo' (clean space) domains in contemporary southern Jê ethno-landscapes, where villages and cultivated areas are found and daily activities occur (Réus Gonçalves Da Rosa, 2005; Moura, 2021). The most extreme manifestations of these domesticated ecosystems can be found at Amaral, where two anthropogenic landscapes, unlike any others in the palaeoecological record, were apparently maintained for a millennium.

In areas with apparently less intense Indigenous land use, we find that Araucaria Forest-Campos dynamics – which have often been attributed entirely or largely to interventions from the southern Jê (e.g. Bitencourt and Krauspenhar, 2006; Lauterjung *et al.*, 2018; Robinson *et al.*, 2018; others in S2) – generally follow expected natural patterns. Compared to archaeologically dense areas, these locations saw more pronounced Araucaria Forest expansions in the Common Era, associated with declines (rather than increases) in burning and changes to climate conditions more conducive to forests. These patterns were originally considered the result of significant increases in rainfall or temperature – climatic changes which directly hindered Campos and favoured Araucaria Forest (Behling *et al.*, 2004; Rodrigues, Behling and Giesecke, 2016). However, their disproportionate speed and magnitude are better explained by non-linear effects of relatively slight natural climatic changes on fire-forest feedback loops. It is important to note, though, that although the largest Araucaria Forest expansions appear to have been predominantly natural, these findings cannot fully exclude contributions from low-intensity Indigenous land use. Plausible mechanisms for such changes exist, the process has been observed in similar ecosystems elsewhere in the tropics, and Indigenous ecological knowledge suggests it may have occurred in southern Brazil's highlands too (S5.2). The question of pre-colonial human impacts in areas less intensely occupied or used by Indigenous people – perhaps corresponding to the ethno-landscape domain contemporary southern Jê groups call 'floresta virgem' (a space for hunting, ritual activity and contact with spirits) (Réus Gonçalves Da Rosa, 2005; Moura, 2021) – therefore remains open.

Our findings provide important historical context for conserving the Araucaria Forest-Campos mosaic in the face of acute present and impending threats. The destruction of the highland landscape through the 20th Century has generally been countered with the establishment of strictly protected areas (Tagliari, Levis, *et al.*, 2021), though they cover far less of this region than in other parts of the Atlantic Forest (Ribeiro *et al.*, 2009). These effectively conserve biodiversity, biomass and Araucaria Forest cover (de Lima *et al.*, 2020; Tagliari, Levis, *et al.*, 2021), but an alternative paradigm of collaborative conservation management with a holistic socio-ecological focus could enhance the system's general resilience (dos Reis *et al.*, 2018; Zechini *et al.*, 2018; Tagliari, Levis, *et al.*, 2021). We find that centuries of Indigenous occupation frequently had positive impacts on forest coverage, and on *A. angustifolia* in particular, so there are compelling historical grounds to view some modern Araucaria Forest areas as part of a long-established socio-ecological system. However, intense land use in the past occasionally led to marked changes in forest composition – their occupation history does not make these areas immune to negative impacts from contemporary human activity. Effective conservation measures are especially important because natural, non-linear Araucaria Forest expansions over Campos in recent millennia demonstrate the mosaic's vulnerability to anthropogenic climate change. Apparently minor increases in rainfall and/or temperature did, and will, significantly alter self-reinforcing feedbacks between fire and forest cover, pushing the landscape over a threshold between alternative stable states – a transition which, under Late Holocene climates, appears to be naturally irreversible. The tipping points for these changes are extremely hard to predict and cannot be precisely identified from palaeoecological data (van Nes *et al.*, 2018; Whitney *et al.*, 2019; Piraquive Bermúdez, Theuerkauf and Giesecke, 2021), but anthropogenic climate changes, CO_2 fertilisation, and fire suppression in protected areas (for forest-focused conservation) all serve to bring them closer (Overbeck *et al.*, 2007, 2018; de Oliveira Portes, Safford and Behling, 2018; Sühs, Giehl and Peroni, 2020). The benefits of fire for Campos are well known; our finding that pre-colonial southern Jê fire use could also assist Araucaria Forest may lead to new management approaches with positive impacts for both components of this ancient mosaic landscape.

Are southern Brazil's Araucaria Forests domesticated landscapes? Or were their Late Holocene dynamics principally driven by natural climate changes? As in so many tropical ecosystems, previous research, focusing on only parts of these questions, has tended to provide partial answers which can become simplistic – even polarised – narratives. The multiple strands of complementary evidence we present provide the most complete insight yet into how the southern Atlantic Forest was shaped over the last 6,000 years. Our results caution against sweeping generalisations; the interplay of climate, humans, forests and fire is complex and variable through space and time. Apparently minor climate changes could have outsized impacts. There is no neat, single correlation between more intense southern Jê land use and greater abundance or expansion of Araucaria Forest. The link between known archaeological sites and the intensity of human impacts on the landscape is imperfect. Anthropogenic causes cannot be assumed for floristic differences across spatial gradients of human land use. And the ways in which the southern Jê interacted with their land were not uniform, differing within, between and beyond archaeological sites. Ultimately, the Late Holocene formation of southern Brazil's Araucaria Forest-Campos mosaic is a tale of climate and Indigenous people, fire, forests and grasslands; without considering each element's contributions, and the complex ways they are woven together, this iconic landscape can be neither fully understood nor successfully conserved. These findings, and the approaches used to uncover them, are relevant to ecosystems throughout the tropics – such insights from the past must play an important role in the urgent quest to understand the resilience and vulnerability of tropical landscapes to contemporary climate and land use changes.

Methods

Overview

We used several complementary techniques to investigate the changes in climate, vegetation, fire, and human occupation in southern Brazil's highlands over the last 6,000 years. The following sections describe our analysis of independent rainfall proxy data from the Botuverá speleothem; ecological niche modelling of Araucaria Forest, Campos, and their species composition; the synthesis of existing palaeo-vegetation proxy data; the generation of multi-proxy data from three new palaeoecological records in close proximity to well-known archaeological sites; and the synthesis of archaeological dates in the region. Additional detail is available in S3.

Palaeoclimate data

Data on past rainfall comes from the Botuverá speleothem (Bernal *et al.*, 2016), whose trace element ratios (Sr/Ca, Mg/Ca, Ba/Ca) relate to rainfall quantity (Cruz *et al.*, 2007, 2009). Botuverá data are available from https://www.ncdc.noaa.gov/paleo-search/study/21060. Each record of trace element ratios was standardised so that its mean over the last 6,000 years was 0 and its standard deviation was 1; the mean rainfall anomaly was then taken from the three standardised ratios. To quantitatively assess the variability of southern Brazil's rainfall since the mid-Holocene, we calculated the Median Absolute Deviation (MAD) of Botuverá's trace element ratios, following Riris and Arroyo-Kalin (2019) (see S3.1 for further detail). MAD is a robust measure of climate (here, precipitation) variability, identifying sudden or large-amplitude deviations from a moving normal. Sub-annual trace element ratio data from Botuverá were first aggregated to decadal resolution, since MAD is sensitive to the number of observations in a time window. (Relatively coarse, multi-decadal stable isotope ratios were therefore not used.) Observations that were at least three times above or below the 100-year moving median proxy value were treated as outliers, a conservative threshold for extreme outliers (Riris and Arroyo-Kalin, 2019). The anomaly count in 100-year bins was summed across the three trace element proxies, and this anomaly count was compared to the standard deviation of the dataset mean. Riris and Arroyo-Kalin (2019) suggest time bins with an anomaly count more than two standard deviations above the mean represent periods with significantly more variable rainfall than normal.

Ecological niche modelling

Overview

We undertook two modelling sub-studies using ecological niche models (ENMs, also called species distribution models). The first modelled the distributions of Araucaria Forest and Campos as units using meso-scale climate (ca. 800 m resolution) and high-resolution (100 m) topography. This allows the changes in each ecosystem's distribution to be observed at both local and landscape level, and for factors such as topoclimate and interactions between forest and grassland to be analysed. The second set of models examined the distributions of 40 forest and grassland species in response to mesoclimate alone, allowing us to examine changes in the composition of Araucaria Forest through time and complementing the first set of models, since palaeoecological research has shown that species turnover within ecosystems can be at least as significant a contributor to past vegetation change as ecotonal shifts (e.g. Wilson *et al.*, 2021). Further details on our ENM methods are found in section S3.2.

Locality data

Locality data for both sets of models were drawn from the area 20-33°S and 43-58°W. For ecosystem-level models we compared a regular 0.1°-spaced grid of points against data on the region's potential natural vegetation (IBGE, 2019) and natural remnants in 1985 (Souza *et al.*, 2020); for areas outside Brazil not covered by these datasets, we used maps of WWF ecoregions (Olson *et al.*, 2001) and the Forest Landscape Integrity Index (Grantham *et al.*, 2020). Points with remnant natural grassland or forest which lay within areas of potential Araucaria Forest or Campos were assigned as presence records for their relevant ecosystem. Random Forest (RF) models require 'true' absence records as well as presences; we used two approaches to selecting these (S2.2.1) – either all points not meeting the criteria for presence records ('all absence'), or only points with other natural vegetation or which fell outside the ecosystem's potential natural area ('natural absence'). Figures in the main text show results from natural-absence RF models; results from the other approaches are available in S4.4. To model compositional change, we identified 40 key species from Araucaria Forest (20 spp.), Campos (10 spp.), Atlantic Rainforest and Seasonally Deciduous Forest (5 spp. each) (S3.2.1). Together, these provide a view of changes within and between these ecosystems' floristic continuum (Oliveira-Filho *et al.*, 2014; Wilson *et al.*, 2021). Locality data for tree species were taken from the Neotropical Tree Communities database (de Lima *et al.*, 2015) via (Zwiener *et al.*, 2017); Campos species data came from SiBBr/ALA (https://bit.ly/2PqTd5X) with their coordinates cleaned using the 'CoordinateCleaner' R package (Zizka *et al.*, 2019). Following (Brown *et al.*, 2020), we thinned these occurrence records so that only one coordinate remained within every 20 km radius, using the R package 'spThin' (Aiello-Lammens *et al.*, 2015).

Environmental data

Environmental data are drawn from two sources: CHELSA-TraCE downscaled palaeoclimate data (10.16904/envidat.211) (Karger *et al.*, 2017; Yannic *et al.*, 2020; Karger, 2021) (both species- and ecosystem-level ENMs) and the ASTER Global Digital Elevation Model (v3) (NASA *et al.*, 2019) (ecosystem-level only). The 30 m ASTER data were aggregated to 100 m resolution, then used to produce two layers: a topographic position index (TPI) following Robinson *et al.* (2018), and a measure of exposure to peak insolation (following McCune and Keon, 2002; McCune, 2007; Ashcroft, Chisholm and French, 2008; Wilson *et al.*, 2019). Species-level ENMs used CHELSA-TraCE data at its native 30" (ca. 800 m) resolution; for ecosystem-level ENMs it was downscaled to 100 m resolution through bilinear interpolation. CHELSA-TraCE temperature data were debiased so that their present-day layers matched CHELSA's modern climatology (Karger *et al.*, 2017), and models were projected to 13 time slices at 500-year intervals from 6,000 BP to the present. From these data we calculated bioclimatic variables, then used variance inflation factors to select eight ecologically relevant variables describing our study area's general trends and extremes of rainfall and temperature: bio2 (annual mean diurnal temperature range), bio4 (temperature seasonality), bio5 (maximum temperature of the warmest month), bio8 (average temperature of the wettest quarter), bio9 (average temperature of the driest quarter), bio12 (annual precipitation), bio14 (precipitation of the driest month), and bio18 (precipitation of the warmest quarter). Further details on these steps are in S3.2.2.

Modelling

We used three modelling approaches. For ecosystem-level ENMs of Araucaria Forest and Campos, we employed random forest (RF) algorithms, one set with all-absence locality data and one using natural absences only (see above/S3.2.2), as well as the presence-background Maxent algorithm. Only Maxent was used for species-level modelling, since species-level absence data were not available.

For the RF models we used the R package 'biomod2' (Thuiller *et al.*, 2016), setting aside a randomly selected 25% of the occurrence data for evaluation of the models and using the remainder for training (75%) and cross-validation (25%). We ran 50 iterations of the RF algorithm and evaluated them using the AUC and TSS metrics (Allouche, Tsoar and Kadmon, 2006), selecting the model run which had the highest overall score across both metrics and cross-validation and set-aside evaluation data.

For the Maxent models we used the R package 'ENMeval' (Muscarella *et al.*, 2014; Kass *et al.*, 2021), tuning the model settings with an approach adapted from (Brown *et al.*, 2020). We set 10,000 random background points within the training area and split training presence and background data into four spatial blocks, which increases their independence and improves the transferability of model predictions (Fourcade, Besnard and Secondi, 2017). For each species we evaluated 50 candidate models, based on ten regularisation multiplier settings (at intervals of 0.5 between 0.5 and 5.0) and five feature class combinations (linear; linear and quadratic; hinge; linear, quadratic and hinge; linear, quadratic, hinge and product). We chose the model with the best combination of high AUC and low omission rate (which we assessed as the mean of AUC and 1-OR).

For both ecosystem- and species-level models, we evaluated the selected model runs using the Boyce Index (equivalent to the Spearman rank correlation coefficient) from the 'ecospat' package (Di Cola *et al.*, 2017), which varies from -1 to 1 with 0 representing a random prediction. The Boyce Index also converts model habitat-suitability outputs into predicted-to-expected ratios (i.e. F-ratios – see S3.2.3) (Hirzel *et al.*, 2006). To convert the outputs of species ENMs to floristically similar predicted assemblages, we performed k-means clustering (k=10) on each time slice in SAGA-GIS, then aggregated these using hierarchical clustering in the R package 'pvclust' (S3.2.3). This yielded four statistically significant floristic groups, one of which we subdivided into four to show further ecologically meaningful change. See S3.2.3 for information on the clusters' compositions and ecosystem affiliations, and S4.4 for additional ENM results.

Palaeo-vegetation proxy synthesis

We synthesised every available palaeo-vegetation proxy record from southern Brazil's highlands, subject to the following constraints: that the records included data from the last 6,000 years, that they had continuous sedimentation (i.e. discontinuous soil carbon isotope records were not included), that proxy diagrams (e.g. pollen percentages) and the depths of radiocarbon dates were available, and that the records had at least two dates. We made one exception to the two-date cut-off to include the record from Caçapava do Sul (Behling *et al.*, 2016), which has one date but covers only 500 years; in conjunction with a surface date, we considered its chronology to be adequately constrained. In total, we include 49 palaeo-vegetation proxy records in our synthesis, making it the most complete to date in the region (cf. Smith and Mayle, 2017; Wilson *et al.*, 2021). Raw data were available in the majority of cases, so we digitised relevant data from these records (S3.3). We constructed new age-depth models for all sites using the R package 'rbacon' (Blaauw and Christen, 2011; Blaauw *et al.*, 2020) and the SHCal20 (Hogg *et al.*, 2020) and Marine20 (Heaton *et al.*, 2020) calibration curves.

The impact of chronological uncertainty has been relatively little considered in studies attempting to link past vegetation, climate, and human changes, but its impact can be significant, severely weakening correlations between ecosystem changes and their potential drivers. We incorporate it here by using rbacon's 'proxy.ghost' function to plot proxy time series (S3.3, S4.2), and by plotting proxy values against multiple iterations of sites' age-depth models (fig. 3d-g). This approach helps to avoid the false impression of chronological precision that can arise when simply plotting proxy values against mean or median dates, providing a more accurate – if less precise – picture of the timings of vegetation changes and their potential causes.

New palaeoecological data

We present new multiproxy palaeoecological data from three sites: Amaral (site 29 in fig. 1d), Abreu e Garcia (site 26), and Pinhal da Serra (site 33) (additional details are in S3.4.2). Each is located within 1 km of previously studied southern Jê archaeological sites in the Canoas-Pelotas basin, which has more archaeological evidence for pre-colonial southern Jê occupation than anywhere else in southern Brazil's highlands (de Souza *et al.*, 2016). The region is also closer to (previously) contiguous areas of Araucaria Forest than most previously studied palaeoecological proxy sites, which are predominantly clustered around the plateau's south-eastern edge (Wilson *et al.*, 2021) (fig. 1d, S3.3).

The three new records were studied using pollen, macro- and microscopic charcoal, and stable carbon isotopes ($\delta^{13}C$) to reconstruct past vegetation and land use dynamics. For chronological control, seven samples from each site were submitted for radiocarbon dating to Beta Analytic, with age-depth models produced using 'rbacon' and the SHCal20 calibration curve (details in S3.4) (Blaauw and Christen, 2011; Blaauw *et al.*, 2020; Hogg *et al.*, 2020).

For pollen analysis, 1 cm^3 subsamples were processed using standard methods: deflocculation using 10% KOH, acetolysis and HF (Faegri and Iversen, 1989). Samples were further sieved to study large pollen grains, such as *Zea mays* and other cultigens, following (Whitney *et al.*, 2012). Fine and coarse pollen samples were mounted in silicone oil and counted at 400× and 1000× magnification using a Leica DME binocular microscope. Pollen identification used regional pollen atlases (Hooghiemstra, 1984; Roubik and Moreno, 1991; Behling, 1993; Colinvaux, Oliveira and Moreno Patiño, 1999; Bush and Weng, 2007) and the modern pollen reference collection at the University of Reading's Tropical Palaeoecology Research Group, assembled in part with specimens from the Museu Botânico Municipal of Curitiba, Brazil. Aquatic taxa and spores were counted but excluded from the terrestrial pollen sum. Due to poor preservation, especially in the Pinhal da Serra core, it was not possible to count all samples to the standard sum of 300 terrestrial pollen grains (Abreu e Garcia min. 285, mean 331; Amaral min. 247, mean 310; Pinhal da Serra min. 61, mean 111).

Macroscopic charcoal was examined for Abreu e Garcia and Amaral records. Subsamples of 1 cm^3 were extracted from the soil cores and soaked in 10% KOH for at least 24 hours, then washed through sieves at 100 and 180 µm mesh size. The remnant material in the sieves was placed in petri dishes and the charcoal particles were counted at 20x magnification following Long *et al.* (1998).

Stable carbon isotope analyses ($\delta^{13}C$) were performed on bulk sediment samples at the Laboratory of Geochemistry and Applied Stable Isotopes (LABASI) at the Departamento de Ecología, PUC, Santiago, Chile. Samples were analysed using a Thermo Delta V continuous flow Isotope Ratio Mass Spectrometer coupled to a Flash 2000 elemental analyser via a Conflo IV. Reported analytical sample precision is better than 0.2‰.

Archaeological data synthesis

We constructed sums of calibrated probability distributions (SCPDs) for the southern Jê and Guarani in southern Brazil to summarise the trends in archaeology-associated radiocarbon dates for both cultural groups. We used dates from de Souza, Mateos and Madella (2020), with dates originally designated as Taquara-Itararé used for the southern Jê and as Tupi-Guarani for the Guarani; in the latter case, only dates from locations south of 23°S were used, since areas further north are not relevant for Araucaria Forest expansion in southern Brazil. We excluded dates that had also been excluded by de Souza, Mateos and Madella (2020), those with no laboratory code, and dates with standard errors above 100 years (Robinson *et al.*, 2018). We then built SCPDs for each cultural group in the same way as Robinson *et al.* (2018), reducing the impact of oversampling by ordering dates within sites and, where sites had multiple dates within any given 100-year bin, merging these using OxCal's R_combine function (Ramsey and Lee, 2013). After these measures of chronometric hygiene and thinning, 195 radiocarbon dates remained for the southern Jê and 116 for the Guarani.

Author contributions

The overall aim of the study was conceived by FEM and OJW. The project design and methodological approach was devised by OJW. OJW undertook the ENM development, palaeoclimate analysis, and syntheses of palaeoecological and archaeological data. FEM collected the study's new sediment cores which were prepared and analysed for palaeo-proxies by MLC (pollen, charcoal) and CL ($\delta^{13}C$). OJW and FEM interpreted the results with MLC. OJW drafted the manuscript, which all authors reviewed before submission.

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Concluding discussion

1. Summary

Chapter 1 (Wilson *et al.*, 2019) demonstrated the challenges Brazil's Araucaria trees face in the immediate future. 21st-Century anthropogenic climate change is likely to degrade 85% or more of the species' most climatically suitable habitat, exacerbated by 20th-Century habitat loss which removed the natural vegetation cover from over a third of Araucaria's potential microrefugia. Campos areas are found to be extremely important for Araucaria's future, as they shelter a larger, less fragmented area of likely microrefugia than forest remnants (of which >95% of the most climatically suitable may become less than optimal in the coming decades).

Chapter 2 (Cárdenas *et al.*, 2019) found that, at least in contemporary contexts, pollen analysis can be quite insensitive to changes in Araucaria Forest – apparent structural differences (albeit ones which did not result in changes to floristic composition) were not reflected in modern pollen spectra. Pollen data registered only a subset of the taxa in the vegetation, with notable variability in their representation across space. 22 of the 27 genera evaluated were generally under-represented, and four of them were apparently palynologically silent. This has an important bearing on the interpretation of fossil pollen records: they may struggle to detect subtle shifts in structure or floristic composition, but, by extension, changes in fossil pollen composition probably reflect somewhat substantial changes in the past vegetation.

Chapter 3 (Wilson *et al.*, 2021) found that Ecological Niche Models (ENMs) predicted significant climate-driven changes in floristic composition across the southern Atlantic Forest biome from the LGM to the present and into the future. Under a pessimistic climate change scenario, the next few decades of the 21st Century could set in motion greater change to the biome's make-up than any three-millennia interval in the last 21,000 years – changes which may already be underway. The region's different ecosystems (and indeed their component species) are not all affected alike, however, which drives the past and future formation of no-analogue floristic assemblages. Many of the most notable past floristic changes came at times (such as the onset of the Holocene) and in locations (like the western plateau) which have previously had little attention from the region's modellers or palaeoecologists, but which represent priorities for future research. In locations where both forms of data could be compared, some evidence supported ENM predictions of ecological novelty, while many sites recorded less compositional change than expected. In part, this appears to be due to the significant shaping influence of non-climatic factors on southern Brazil's vegetation in the past – particularly, on these timescales, the promotion of grasslands by lowered past atmospheric CO_2 concentrations.

Chapter 4 demonstrated that two non-climatic factors – fire dynamics and human land use – have played very significant roles in shaping Araucaria Forests over the last 6,000 years. Contrary to some previous expectations, triangulating ENMs, palaeoclimate reconstruction and palaeoecological records shows that Araucaria Forest expansions in recent millennia do not require the invocation of a human cause – they occur at times and in places predicted by climate-driven models and an independent rainfall proxy. However, the magnitude of changes in ENM prediction and vegetation and climate proxy records are not closely related. This is because climate drove Araucaria Forest expansions at once remove – the immediate controlling factor was fire dynamics among the vegetation mosaic. (Campos grasslands are fire-adapted and require burning, whereas fires suppress Araucaria Forest expansions – though established forest rarely burns.) Increasing rainfall and temperatures slightly benefitted forest patches and suppressed fire, which drove positive feedback loops leading to runaway forest expansions when areas cross a critical threshold. Although Indigenous people do not appear to have driven these dynamics, Chapter 4 nonetheless reveals clear evidence that they shaped pre-colonial Araucaria Forests in important ways: intensely occupied areas had non-natural, positive relationships between fire and Araucaria trees, whose populations in the forest appeared in some records to become enriched – even, in one site, forming an anthropogenic Araucaria parkland with no analogue in any other palaeoecological proxy record. The dynamics of Araucaria Forests in the second half of the Holocene resulted from complex combinations of climate changes, fire dynamics, and Indigenous people – each of them important to consider for the ecosystem's conservation in the future.

2. Synthesis

The research in this thesis significantly advances our understanding of the vulnerability and resilience of Brazil's Araucaria Forests to climate changes over the last 21,000 years and further into the 21st Century. Though the ecosystem's immediate future appears grim, there are reasons to retain hope, some of which come from our understanding of the region's past.

Looking to the future, the principal conclusion is that anthropogenic climate change is likely to cause significant damage and disruption to Araucaria Forests, which are already under acute pressure from historic exploitation. Araucaria trees are likely to lose the great majority of their most climatically suitable habitat, and the Araucaria Forests we know today may have their ranges shrunk and shifted, replaced by more warm-adapted species, with their familiar composition effectively dismantled by the individualistic effects of climate change on their key component species (Chapters 1 and 3; Wilson *et al.*, 2019, 2021). These findings confirm expectations based on the climatic changes afflicting southern Brazil – warming temperatures and more variable rainfall are replacing the highlands' constant, cool and wet conditions (Beck *et al.*, 2018) – and, especially for Araucaria trees, they have been validated by subsequent studies.

One of the major uncertainties arising from Chapter 1 is Araucaria trees' potential response to the climatically suboptimal habitat which the ENMs and CHELSA data predict will dominate late in the 21st Century. Notably, most other research on similar questions – including Chapter 1's ENMs based on Worldclim, and the ENMs used in Chapter 3 – has produced less equivocal results, finding that climate conditions across much of southern Brazil will become so unsuitable as to be unavailable for Araucaria (Bergamin *et al.*, 2019; Castro *et al.*, 2020; Marchioro, Santos and Siminski, 2020; Trindade, Santos and Artoni, 2020; Saraiva *et al.*, 2021; Tagliari, Vieilledent, *et al.*, 2021; Lima *et al.*, 2022). There are several potential reasons for Chapter 1's prediction of such widespread mediocre habitat – the models' input locality or climate data, perhaps, or restricting the study to a subset of Araucaria's range – but the study's main conclusions have been arrived at independently on numerous subsequent occasions. Different analyses have produced a range of reductions in Araucaria's (or Araucaria Forests') climatically suitable habitat area, depending on climate scenario, timeframe, and dispersal scenario – 28-60% (Castro *et al.*, 2020), 43-64% (Saraiva *et al.*, 2021), 46-67% (Lima *et al.*, 2022), 45-77% (Marchioro, Santos and Siminski, 2020), 65-88% (Tagliari, Vieilledent, *et al.*, 2021) – but all show that anthropogenic climate change will present Araucaria with significant challenges in the coming decades. Analyses which have also considered remnant vegetation and/or protected area coverage (Castro *et al.*, 2020; Saraiva *et al.*, 2021; Tagliari, Vieilledent, *et al.*, 2021) further support Chapter 1's conclusions that the most important areas for Araucaria conservation in the future have lost much of their natural vegetation and are poorly protected, even relative to the wider ecosystem. To date, no other studies have examined potential microrefugia for Araucaria or Araucaria Forests, but coarse-scale refugia have been identified in broadly similar areas to those identified in Chapter 1 (Saraiva *et al.*, 2021).

Fewer studies have examined the impacts of floristic reassortment and compositional change in the southern Atlantic Forest under anthropogenic climate change scenarios. Chapter 3, examining a worst-case scenario for the most distant 21st-Century timeframe, found that such changes are likely to be considerable, in most places outstripping the natural floristic changes that have occurred over the last 21,000 years. Only two other studies have attempted similar work: Esser *et al*. (2019), which took in the entire Atlantic Forest biome, and (to a lesser extent) Trindade *et al.* (2020), focusing on the vegetation in Paraná. Esser *et al*., contrary to their own expectations (and a subsequent study including two of the three authors, Saraiva *et al.*, 2021), found that Araucaria Forest underwent the least range contraction of all the forest ecosystems in the biome (a maximum of 5% loss – at least 12 times less than other studies predict under similar scenarios). Trindade *et al*., aligning with the consensus view, projected that most of Paraná's Araucaria Forest would cede ground to Seasonally (semi-)Deciduous Forest (SDF) and/or Cerrado, with large areas failing to match any contemporary ecosystem. These areas may equate with the no-analogue assemblages Chapter 3 predicts for northern Araucaria Forest. There are hints of this in Esser *et al*., too – the area jointly suitable for Araucaria Forest, SDF and Atlantic Rainforest could double in the future, and Araucaria Forest areas' climatic uniqueness is likely to dwindle.

To date, Chapter 3 remains the only study to have examined past species- or community-level compositional change in the southern Atlantic Forest. Trindade *et al*. (2020) did extend their analysis of Paraná's ecosystems from the future into the past, but, as is common in such research, examined only the LGM and mid-Holocene. As in Chapter 3 and other previous studies (e.g. Costa *et al.*, 2017), their results demonstrate that using ENMs to distinguish between Araucaria Forest and Campos in a way that mirrors palaeoecological data is difficult: in the past, grasslands were consistently more extensive than predicted, and commonly occurred in areas modelled as forests – a phenomenon which obscured many of Chapter 3's predicted Araucaria Forest compositional shifts. This uncertainty, which limits our ability to understand Araucaria Forests' resilience to long-term climate changes, has three possible explanations.

The first is that Araucaria Forests were present in the catchments of these palaeoecological records but are simply not recorded. Chapter 2 demonstrates that many Araucaria Forest trees are under-represented in or absent in modern pollen spectra. Since Chapter 2 was published (Cárdenas *et al.*, 2019), two more studies have undertaken quantitative analyses of Araucaria Forest pollen-vegetation relationships (Guarinello de Oliveira Portes *et al.*, 2020; Piraquive Bermúdez, Theuerkauf and Giesecke, 2021). Taken together, the three studies demonstrate the complexities of relating pollen proportions to local land cover (cf. Whitney *et al.*, 2019), but lend no substantial support to the idea of extensive unrecorded Araucaria Forest patches around palaeoecological study sites. While the representation of different taxa and the formations they comprise does vary, Araucaria Forest is consistently identified in both modern and fossil pollen records.

The second possible explanation for the underprediction of Campos in the past is that Araucaria Forests are significant trespassers in the present, occupying expansive areas outside their climatic niche (cf. Robinson *et al.*, 2018). If this were the case, it would artificially inflate the range of conditions which Araucaria Forests appear to tolerate, hence their overprediction in comparison with palaeoecological data. However, Chapters 3 and 4 do not support this hypothesis. Large-scale expansions of Araucaria Forests in millennia past are the exception rather than the rule; there is no evidence of forests having drastically overtaken Campos across the region in the Holocene; and Indigenous people probably did not spread Araucaria Forests wholesale in the pre-colonial period to create widespread anthropogenic forest areas. As a result, the areas of continuous Araucaria Forest (which provide the greatest contribution to locality data for ENM studies) seem to be predominantly natural in origin. Chapter 3 demonstrates that there may be an ecologically relevant mismatch between present-day Araucaria Forest areas and the climatic conditions they prefer (since the climate is changing faster than the forest limits can adjust), but that its effects are reasonably minor. It is unlikely to explain the widespread discrepancy between predicted and observed occurrences of Campos and Araucaria Forest in the past.

The most likely explanation for the Campos-Araucaria Forest discrepancy in the past is that climate alone is insufficient to explain their distributions. Low atmospheric CO_2 concentrations almost certainly depressed Araucaria Forest in favour of Campos around the LGM, and explain much of the divergence between models and observations at that point in time (Gerhart and Ward, 2010; Svenning *et al.*, 2011; McElwain, 2018; Chapter 3 - Wilson *et al.*, 2021). By promoting grasslands prone to fires which suppressed Araucaria Forest regeneration (Chapter 4), these low-CO_2 legacies could last long after the atmospheric composition had become more favourable for woody formations. As Chapter 4 has demonstrated, the occurrence and timing of the non-linear, fire-mediated switches between Campos and Araucaria Forest are difficult to predict – the changes are (loosely) connected to the prevailing climate, but also depend on initial forest cover, and are likely to have a significant stochastic component too (van Nes *et al.*, 2018). For this reason, ENM studies which aim to discriminate between Araucaria Forest and Campos in the past or future should aim to incorporate these dynamics – at least in their discussions – or simply model the Araucaria Forest-Campos mosaic as a single entity.

So, what conclusions can be drawn from this thesis about the resilience of Brazil's Araucaria Forests to past and future climate change? The first is that there are major differences between those past and future climate changes. The Araucaria Forests we know today are likely to be significantly damaged – diminished and dismantled – by 21st-Century climate changes; they have experienced nothing similar in at least the last 21,000 years. Araucaria trees, which define the ecosystem, are likely to become disassociated from the forests' other key species in ways more extreme than have happened in past millennia. Under even optimistic climate change scenarios, Araucaria trees are likely to be lost entirely from most of their current area, much of which has already undergone conversion to anthropogenic land uses. No human has ever lived in a world without Brazil's Araucaria trees; sadly, the first to do so may already have been born. Microrefugia might shelter Araucaria Forest remnants for longer in places which are otherwise inhospitable, but the climate's one-way direction of travel in the foreseeable, ecologically relevant future offers little chance of widespread recovery without significant help.

But there is the possibility of that help. Chapter 4 sheds comprehensive light on relationships between Araucaria Forests and fire, climate changes and humans in the pre-colonial period. It shows that Araucaria Forests in areas occupied by the southern Jê fared very differently to others: under entirely inverted relationships between forest and fire, modest forest expansions occurred, and some areas saw apparent enrichment with Araucaria trees. Understanding how Indigenous land use produced these unexpected dynamics could be critical to the ecosystem's protection in the future. Chapter 3 shows that palaeoecological data record greater stability in southern Brazil's highland vegetation than ENMs predict, and climatic conditions control only a portion of Araucaria Forests' dynamics and extent. Chapter 1 highlights that small, resilient Araucaria holdouts will remain, even as the region becomes increasingly inhospitable. There is, therefore, a chance – a faint chance but real nonetheless – that Araucaria Forests could survive in the medium term: promoted by increasing rainfall and atmospheric CO_2, buffered by ambitious habitat restoration and conservation, and sheltered by microrefugia, in which long-lived populations are sustained by new forms of Indigenous-informed land use. If anthropogenic carbon emissions can be quickly reined in and aggressively reversed, this might possibly be enough to secure Araucaria Forests' survival still further into the future. The path towards these goals is narrow and uncertain, and they may ultimately be unattainable – but its existence is cause for hope, a demonstration of the past's value for the future, and a guide to the work that can bring the goals closer to reality.

3. Future directions and wider significance

This section does not focus on the practical (e.g. conservation) applications of specific research findings from different chapters in this thesis, which are generally covered in each study's conclusions. Rather, it discusses the novel directions in which my questions, methods and/or findings could be extended or further developed to help us understand the past and future of Brazil's Araucaria Forests, as well as analogous systems elsewhere. The following is loosely split into three sections, looking at past human-environment relationships, integrating palaeo-proxy data with ecological models, and the ways in which southern Brazil's ecosystems and ecological modelling could enhance each other.

3.1 New approaches to people and plants in the past

Possibly the biggest innovation in this thesis is the way in which Chapter 4 explores Araucaria Forests' vegetation histories and their responses to changing climates and human occupation. The analysis of archaeological and palaeoclimate data plays an important role in describing these potential drivers; this (reasonably common) step is necessary for the attribution of vegetation changes to one driver or the other, but, as Chapter 4 shows, it is not sufficient. Better is to complement these records with ENMs' explicit predictions of climate-driven ecosystem changes in space and time, which can be assessed using palaeo-data. Basing this assessment on as many relevant records as possible provides a full overview of what changes occurred where, which changes were more muted, and where expected changes were absent – a crucial step for generalising findings. Chapter 4's inclusion of available fire proxies also provided crucial insight into an additional ecologically and culturally important variable. Describing these synthesised records in light of their chronological uncertainty provided a more accurate – if occasionally less clear – picture of when the observed changes took place, allowing some to be correlated with relevant drivers and precluding that step with others. And including sites from across gradients of past human occupation – especially ones in which significant human influence was almost guaranteed (cf. Mayle and Iriarte, 2014) – allows the nature and spatiotemporal scale of anthropogenic vegetation changes to be elucidated. This enmeshing and triangulation of diverse methods allowed the study to move from correlating vegetation changes and their potential drivers to illustrating their underlying causal relationships – advancing from describing patterns to explaining the processes by which they occurred.

It is hard to see a technical reason why aspects this multifaceted approach could not be applied to similar questions elsewhere. ENMs can be built for almost any taxon, and several sources of gridded palaeoclimate data have global coverage (though inaccuracies and uncertainties will differ around the world). Southern Brazil, especially its highlands, is fortunate to have comparatively excellent palaeoclimate and palaeoecological proxy data, which considerably narrows the range of uncertainties arising from their synthesis, but many parts of the world have even more records available. Uncertainties and analytical assumptions cannot be entirely avoided when studying past human-environment relationships (or indeed in any scientific research), but using ENMs, making inclusive syntheses of existing palaeo-proxy data (both locations and proxies), and considering chronological imprecision all help to make these more explicit. Especially in tropical forests like Amazonia, where questions of ecosystems' responses to past climate changes and human actions are of critical importance, this approach could be extremely valuable (McMichael, 2021; Roberts, Hamilton and Piperno, 2021).

Chapter 4's approach yielded several important findings, among them patterns which might serve as markers of human land use in Araucaria Forests – a potential springboard for future research. Inverted fire-forest relationships, enriched *Araucaria* pollen contributions, and cultigen pollen were found in two distant regions, but it is not clear how widespread and/or consistent these patterns would be in other new fossil pollen records. It would, for example, be illuminating to examine sediment cores from the archaeologically rich Urubici region (Corteletti, 2012). Compared to Chapter 4's sites in the Campo Belo do Sul region, this area is at higher elevation, considerably further east, probably less accessible to Guarani groups, closer to the coastal Atlantic Rainforest and further from SDF – as a result, the vegetation, southern Jê occupation patterns, and their interactions could all have been markedly different. Additionally, Urubici is close to the Morro da Igreja site (Behling, 1995), which could help contrast vegetation dynamics with and without significant human influence.

The existence of anthropogenic modification (deliberate or incidental) to Araucaria Forests is well evidenced in Chapter 4; what remain unclear are the mechanisms which drove these changes. The ways in which Indigenous land use affects tropical forests are well understood in general terms (Levis *et al.*, 2018), but it is difficult to know exactly how the pre-colonial southern Jê brought about the observed transformations – nor is it obvious what existing archaeological or palaeoecological methods could shed light on this. One avenue, which has scarcely been explored in such studies anywhere in the world, could be to develop a kind of 'participatory palaeoecology' alongside Indigenous people – an idea suggested by Richer and Gearey (2017). At its foundation, this methodology acknowledges that a scientific ecological lens is only one way to understand the natural world, to which Indigenous or traditional ecological knowledge (TEK) is a complementary approach – in the same way, each could provide helpful (and in the latter case new) viewpoints on palaeoecological data.

Contemporary southern Jê groups have clear cultural continuities with their archaeologically-known ancestors (even after the damages inflicted by their colonial encounter), so there is the real possibility collaborative research with these communities could shed fascinating new light on past changes in the Araucaria socio-ecological system (cf. Tagliari, Levis, *et al.*, 2021) – insights which could be critical for conserving the Araucaria Forest-Campos mosaic into the future. This approach also has other benefits, quite apart from its potentially intriguing research findings: by making space to include Indigenous worldviews, it would fill the epistemological gap left by trying to understand (past) Indigenous activities using only 'western' scientific approaches; it would help avoid or rectify the inequity of doing research about Indigenous people without their input ('nothing about them without them'); and it would repatriate knowledge with potential cultural and/or political importance to the stakeholder communities it most concerns. At this point it is not clear how successfully this approach would inform our understanding of pre-colonial human-environment relationships, but there are few better places in the world to attempt it than with the southern Jê and Araucaria Forests.

However they were caused, the pre-colonial changes to Araucaria Forest structure and composition around archaeological sites appear, from the fossil pollen records, to have been substantial; a logical follow-up question is whether their floristic legacies can still be seen today (cf. McMichael, 2021). This is an intriguing question, related versions of which are commonly investigated in

Amazonia but largely untouched in southern Brazil. Pereira Cruz et al. (2020) made the first attempt to address it, using forest plot data from the IFFSC (Vibrans *et al.*, 2010, 2020), but by simply comparing areas of Guarani and southern Jê occupation against one another their methods obscured any signals resulting from the intensity of past human occupation. It would be interesting, then, to advance their approach by controlling for, *inter alia*, forest plots' climate conditions and disturbance histories to see whether modelled probability of archaeological evidence or proximity to known archaeological sites is associated with floristic changes that have persisted long-term. Alternatively, it might be possible to undertake new forest inventories along transects which span gradients of archaeological intensity, to see whether and how Araucaria Forests in areas which were more intensely occupied differ from those further afield (cf. Ferreira *et al.*, 2019). These lines of study could ultimately prove futile, however, as the deep and pervasive influence of colonial disturbances – felt in virtually all the region's remaining forests – may have eradicated all but the most substantial ecological legacies (Sevegnani *et al.*, 2019; Oliveira and Vibrans, 2020).

One tool which could greatly assist in developing our understanding of the Araucaria Forest-Campos mosaic's past dynamics – both human-driven and natural – is modelling land cover in site catchments from their fossil pollen records. Several methods for this exist (Sugita, 2007a, 2007b; Bunting and Middleton, 2009; Bunting *et al.*, 2018) and, compared to analysing pollen proportions alone, they more accurately reflect the land cover of different vegetation types, as well as their approximate distribution in space (e.g. Mariani *et al.*, 2017). The results of Chapter 2 – and, particularly, Piraquive Bermúdez et al. (2021) – are a notable step in this direction, providing essential data on which such analyses can be founded. There are significant challenges in accurately reconstructing forest and grassland cover in mixed landscapes like the Araucaria Forest-Campos mosaic (Whitney *et al.*, 2019), but the binary system can also simplify the analysis. If pollen-derived maps of land cover could be produced, they would be a valuable communication tool for participatory palaeoecology with Indigenous communities, as well as helping with comparisons against model predictions or in synthesising findings across space (Bunting and Middleton, 2009; Bunting *et al.*, 2018).

3.2 Palaeo-data and models

Comparing model predictions and palaeo-vegetation proxy data was foundational for Chapters 3 and 4, and it is a process which leverages each method's complementary strengths to reveal new and important ecological insights. One such insight in Chapter 3 is that compositional change in fossil pollen records is often more muted than ENMs would predict. It is possible to explain this pattern with ecological arguments, but it is important to note that it could be reflecting an artifact from the modelling process itself – comparing the last 6,000 years of modelled compositional change between Chapters 3 and 4, for instance, finds that the former predicted more marked shifts than the latter. A range of methodological choices could be responsible: although the climate data has the same ultimate foundation, it was downscaled differently in each study; additionally, the species modelled, their locality data, the modelling algorithms, and the clustering approaches used to build assemblages all differ between the two. Any of these could result in material differences in the predictions, but the most important source of inferentially significant variation would be the underpinning palaeoclimate data. Spatial palaeoclimate data necessarily incorporate various uncertainties and assumptions, so making predictions based on a range of data sources is preferable as it increases the likelihood that the true past climatic conditions are encompassed (and therefore modelled against) (Varela, Lima-Ribeiro and Terribile, 2015). This is becoming more possible as new sources of spatial palaeoclimate data become available at increasing spatial and temporal resolutions (e.g. Osman *et al.*, 2021). Testing different permutations of data sources, model approaches and analytical choices will clarify the range and sources of uncertainty in predictions of ecological change, thereby narrowing the gap between predictions and observations – and ultimately helping explain the ecological underpinnings of any remaining divergence.

In addition to combining existing palaeoecological records with ENM predictions, an important future research step would be to develop new palaeo-vegetation proxy data. Chapter 3 highlights how the most variable areas in the centre and west of southern Brazil's highland plateau have historically been neglected in palaeoecological research, and suggests that investigations in the region might yield interesting results – potentially quite different from those found in existing proxy records. Chapter 4's Pinhal da Serra record is a candidate for just such investigations, lying some way west of the plateau's 'centre of palaeoecological gravity' along its southern and eastern edges. Its poor pollen preservation may preclude this, but the studied core covers more than 30,000 years (one of the longest terrestrial records in southern Brazil), with exploratory pollen analyses providing tantalising hints of no-analogue SDF-like forests in a grassland matrix (not presented in this thesis due to low pollen sums). This would be an additional approach to confirm (or clarify, or refute) Chapter 3's findings: permutation testing the modelling would narrow the range of our uncertainty around the ENM predictions, whereas filling in gaps in the palaeoecological record would shore up our understanding of actual past vegetation dynamics – together, these approaches would tighten the gap between predictions and observations, improving our ability to explain the ecological phenomena underlying the approaches' remaining differences.

It would also be possible to use past-projected ENMs to provide a 'first impression' of unstudied areas – an even more explicit form of hypothesis generation than in Chapter 3. One of the most intriguing targets for this in the Neotropics is Paraguay. The landlocked country is a crossroads of biodiversity at the heart of South America, containing parts of two global biodiversity hotspots (Atlantic Forest SDF formations, and Cerrado), a corner of the world's largest tropical wetland (the Pantanal), and, in the Chaco, one of the continent's most idiosyncratic ecosystems (Myers *et al.*, 2000; Oliveira-Filho and Fontes, 2000; Olson *et al.*, 2001). As far as can be told, Paraguay has not a single fossil pollen, phytolith, $\delta^{13}C$ or charcoal record from within its borders – the only country in South America for which this is true (e.g. Flantua *et al.*, 2015; Smith and Mayle, 2017). It is a rare blank on the palaeoecological map – its Quaternary vegetation dynamics have never really been studied at all.

Yet Paraguay's vegetation history could be key to many questions of Neotropical biogeography. Paraguay occupies a crucial area within South America's 'dry diagonal', so could help unlock the histories of the Chaco, Cerrado and SDF ecosystems/biomes (Dryflor, 2016; Mayle, 2019; Luebert, 2021). Historical forest connections between Amazonia and the Atlantic Forest likely passed close to Paraguay, driving up the two regions' biodiversity – but when, where, how, and in what form these connections existed is almost entirely unknown (Ledo and Colli, 2017). The Chaco Low, found above Paraguay, is one of the continent's most important climatic features – palaeoecology could shed light on its past fluctuations and their impacts (see Literature Review fig. 4-1; Smith and Mayle, 2017). The Guarani migration from Amazonia to southern Brazil probably also passed through Paraguay late in the Holocene, but what environments these people encountered, how they changed them, and the impacts of European colonisation on their landscape management must currently be guessed at. Ultimately, palaeoecological proxy data will need to resolve these questions, but ENMs can help to direct these studies by highlighting areas which appear to have been stable, dynamic or novel at different points in time. Combining these approaches in this way could significantly assist in prioritising research efforts, as well as providing hypotheses for new palaeoecological records to test.

These concerns are closely connected to the research in this thesis. Palaeoclimate data suggest that the hills and mountains in eastern Paraguay and Brazil's Mato Grosso do Sul state – including the Serra de Maracaju and Serra da Bodoquena – would have been suitable for Araucaria Forest taxa for millennia until early in the Holocene. Apart from a tantalising hint in Bergamin *et al*. (2019), this has never previously been suggested (their figure 3 shows modelled Araucaria Forest in this area at the LGM; it is not discussed). Previous evaluations of *Araucaria angustifolia*'s population migrations in response to Late Quaternary climate changes have focused exclusively on movements north and south within Brazil (e.g. De Oliveira *et al.*, 2020), but east-west movements very likely occurred as well (cf. Williams *et al.*, 2004). *Araucaria* pollen is scarce in all existing palaeo-vegetation records at the LGM and in almost all until late in the Holocene (Chapters 3 and 4), but the earliest evidence for large populations appears to come from the west of Araucaria Forests' contemporary limits – the nearest available records to Paraguay (Fernandes, 2009; Bertoldo, Paisani and Oliveira, 2014; Ladchuk, Parolin and Bauermann, 2016). Using ENMs and new palaeo-data to understand the extent to which Araucaria Forests and their component taxa previously occupied Paraguayan territory could provide crucial, novel insights into the ecosystem's past, potentially revealing currently vacant facets of its environmental niche, highlighting alternate sources of ancestral or refugial populations (and associated genetic diversity), and developing new scenarios for its climate-driven population history.

3.3 New ways to model the future

This thesis used several simple innovations in its modelling of Araucaria Forests and their future resilience to climate change. Chapter 1 used a high-resolution global digital elevation model (GDEM) to explore the potential mitigating impact of topography on climate change, identifying possible microrefugia for Araucaria trees (NASA *et al.*, 2019). The same study also used fine-scale maps of natural vegetation remnants to highlight the ways past habitat loss are compounding Araucaria's vulnerability to future climate changes (Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais - INPE, 2015). Chapter 3 used a 'predict-then-assemble' approach to studying compositional change, allowing floristic assemblages to be built up from species-level and facilitating investigations of compositional novelty (Nieto-Lugilde *et al.*, 2018). Aspects of these approaches are becoming more common in ENM studies (e.g. Esser, Neves and Jarenkow, 2019; Tagliari, Vieilledent, *et al.*, 2021), but there is no reason why they could not be a routine part of such research – GDEMs, by definition, have global coverage, global datasets on forest cover and/or quality exist (e.g. Grantham *et al.*, 2020), and it is hardly more difficult to combine modelled distributions of many species than to model on or an ecosystem unit. Together, these approaches can provide closer-to-realistic insights into the fates of threatened plants around the world.

A source of uncertainty in the ENMs in this thesis – and indeed all applications of these methods to trees or ecosystems – is in the temporal overlap between locality and climate data (Roubicek *et al.*, 2010; Baker *et al.*, 2016). This can be illustrated using Araucaria trees as an example. The research in Chapters 1, 3 and 4 used ENMs to correlate Araucaria tree locations and climate data, generating an overview of Araucaria's climatic niche and thence its changes in space and time. The overwhelming majority of those locality records come from adult individuals, as is almost certainly the case for all tree species. However, the locations of those trees are not the result of the climate today, or over the last decade, or even (in some cases) in the last century: Araucaria seedlings have a mortality rate of around 80%, with vastly more individuals dying before reaching 50 cm height than at any other life stage, so conditions experienced at the sapling stage probably play the larger role in determining where the trees are found (Paludo, Mantovani and Reis, 2011; Paludo *et al.*, 2016). Indeed, established Araucaria stands suffering recruitment failure can still persist for centuries, implying that adult Araucaria trees do not necessarily reflect favourable contemporary climatic conditions (Paludo *et al.*, 2016). Atmospheric conditions are also changing rapidly – since the late 20th Century, parts of Brazil have been warming by 1°C per decade (de Barros Soares *et al.*, 2017) – so there is a real possibility that the mismatch between current and biologically relevant climates could have a meaningful impact on model outputs. This factor may play a role in the discrepancy between modelled and officially mapped ecosystem limits in Chapter 3, and may also be relevant in the many other studies which use ENMs to predict changes in long-lived trees or ecosystems (Nogués-Bravo *et al.*, 2016).

It would be possible to investigate the impact of this mismatch with Araucaria in at least two ways. Firstly, combining forest plot surveys (e.g. Vibrans *et al.*, 2010, 2020) and data on the species' growth rates (e.g. Paludo *et al.*, 2016) could yield estimates of the time since individual trees were seedlings, and therefore vulnerable to climate change. For a majority of living individuals, this period is probably covered by climate data derived from instrumental records, which could be used to examine whether adjusting the climate reference period affects our understanding of Araucaria's niche. (Independent confirmation could come from the spatial age structure of Araucaria stands or the distribution of seedlings, since senescing populations in regeneration failure may be a sign of greater climate stress.) This approach could also be applied further back in time, using Araucaria pollen in palaeoecological records and long-term palaeoclimate data to extend our understanding of Araucaria's environmental niche to a wider-than-contemporary range of climates (cf. Williams and Jackson, 2007; Nogués-Bravo *et al.*, 2016). Araucaria trees are an ideal focus for approaches like these – its range has been the subject of extensive forest surveys in the last decade, its growth rates are reasonably well studied (a side-effect of the 20th-Century timber trade which devastated its populations), and its pollen can be effectively identified in palaeoecological records over long timeframes – but the applications for such research are relevant far more widely than southern Brazil.

Southern Brazil's highlands could be a fertile test bed for other modelling innovations. This thesis has made effective use of distribution modelling, but predicting species' abundance provides even more useful outputs for a range of purposes (Pagel *et al.*, 2014; Hill *et al.*, 2017). Abundance modelling continues to be less common than distribution modelling because it requires significant amounts of data, but Araucaria trees – perhaps uniquely among tropical and subtropical species – could meet these exacting demands. As well as global datasets on canopy cover, Brazil has excellent data on land cover and land use (Souza *et al.*, 2020), forest surveys provide unbiased information on Araucaria abundance across the landscape (e.g. Vibrans *et al.*, 2010, 2020), and historical censuses of southern Brazil's Araucaria timber 'resource' (298 million trees in 1949/50) allow for model predictions to be independently verified (Nodari, 2016). This combination of rich data is extremely rare, even in temperate regions, and the abundance modelling it could facilitate would shed important light on Araucaria's population losses since the onset of the colonial period, the locations of its most important remaining populations, how land use and climate changes are likely to affect it in the future, and ways of targeting conservation and restoration to mitigate their negative effects. This level of insight would be unprecedented for a culturally important, conservation critical tropical tree species.

The plateau could also pioneer new approaches to understanding grasslands' vulnerability to global changes. Campos grasslands are probably Brazil's most climate-change-exposed ecosystems, since they occupy a colder subset of Araucaria Forest's niche, itself found in the coldest parts of the country (Neves *et al.*, 2017). Nonetheless, their longstanding status as 'Brazil's neglected biome' has meant that their responses to climate change have not yet been examined – a clear priority for future work along the lines of Chapter 1 (Overbeck *et al.*, 2007, 2015). Extending the models developed in Chapter 4 would allow Campos and Araucaria Forest distributions to be projected to future climate scenarios, examining their independent responses as well as their interactions. As Chapters 1, 3 and (especially) 4 have demonstrated, however, the distinction between Campos and Araucaria Forest is not simply climatic – the mosaic's boundaries are instead maintained by the actions of fire and land use (including grazing) and their interactions with woody vegetation cover. To incorporate these into predictions of the mosaic's dynamics, climate-driven distribution models could be combined with data on fire frequency, woody canopy cover, and land use; this should help refine the models' ability to predict Campos's actual distributions and their changes into the future. Such an approach would be relevant to grasslands and forest-grassland mosaics the world over. It could feasibly even be extended into the past, since Araucaria Forest-Campos δ^{13}C signatures can be related to the basal area of woody vegetation (Silva and Anand, 2011). These ideas, as throughout this thesis, would build on insights from the past to understand how land use and climate changes could combine to reshape the Araucaria Forest-Campos mosaic into the future.

4. Concluding coda

About 28 million years of independent evolution separate Brazil's Araucaria trees and their Andean sister species (Forest *et al.*, 2018). If this period were compressed to 24 hours, the early hours of the morning would see the evolution of the first cat but North and South America would only meet at 9.30 pm, and the first evidence for *Homo sapiens* would emerge two and a quarter hours later at 11.45pm. The research in this thesis has taken a long view of this ancient species and its eponymous forests, but even the 21 millennia of floristic changes covered in Chapter 3 span only the last minute before midnight on our timeline. Six seconds ago, Late-Holocene climate changes and the southern Jê began radically reshaping the highland landscape with fire and cultivation, until the Indigenous communities were driven from their land. *Araucaria angustifolia* was then felled from hyperdominance to Critically Endangered in a third of a second, laid low in a literal blink of an eye (de Carvalho and Nodari, 2010; Thomas, 2013). Now, the immediate future holds such challenges that it will be immensely difficult for this iconic species to survive even the next quarter-second to the end of the 21st Century.

If Brazil's iconic Araucaria Forests are to survive another second, minute, or even hour longer, we need to learn from their past – from the day just ended. Understanding how climate changes reorganised the region's flora, how Indigenous people enriched Araucaria Forests, how microrefugia might shelter populations, and how the last century's habitat damage must be mitigated – all these steps are critical. *Araucaria angustifolia* will not survive the Anthropocene and its aftershocks, but learning these lessons from its story might allow us to change the new day's trajectory – for the good of its fellow species, their ecosystems, and us all.

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Appendices

Supplementary Information for Chapter 1: Cold spot microrefugia hold the key to survival for Brazil’s Critically Endangered Araucaria tree

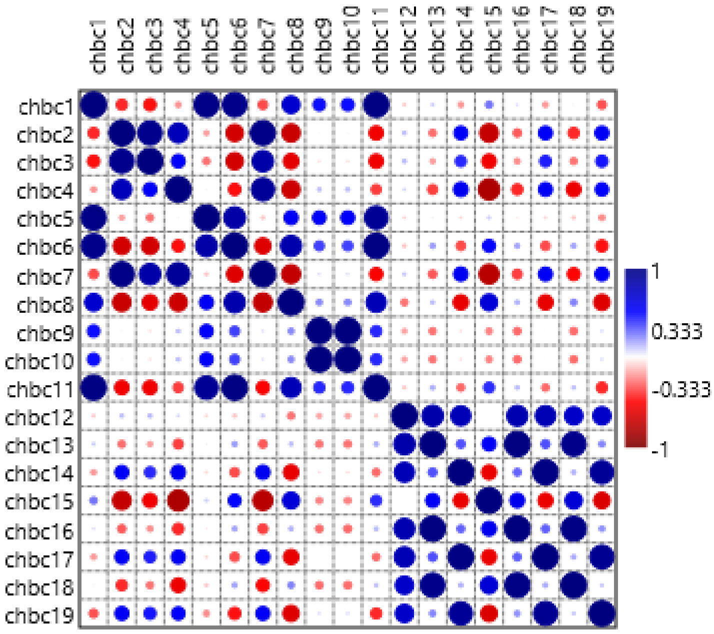
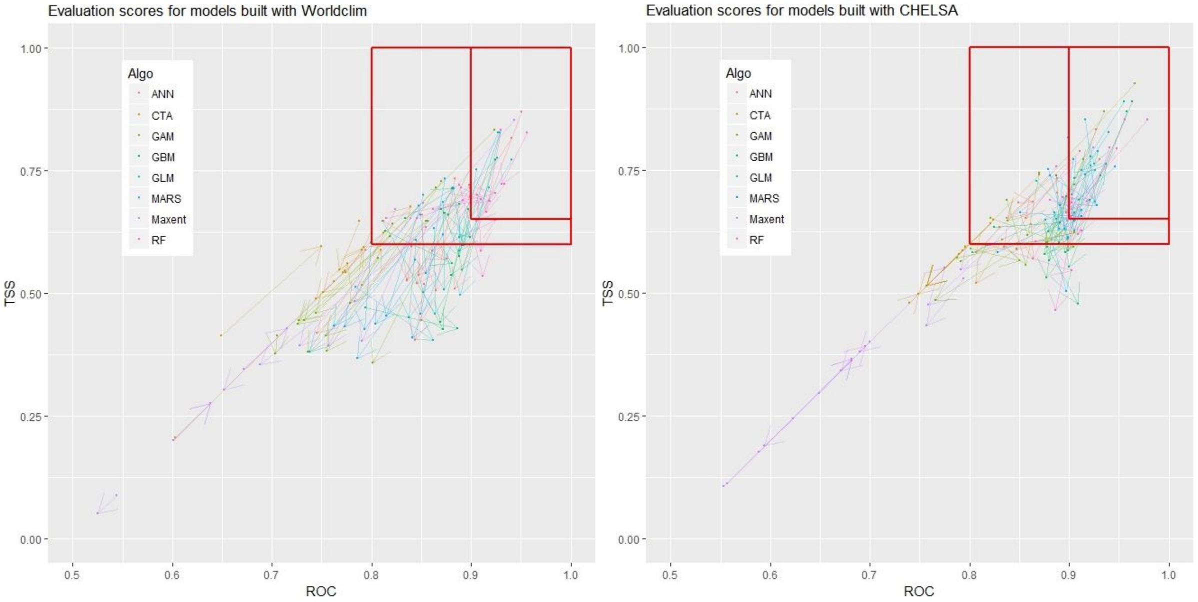


Figure S1: Correlation statistics (Pearson linear r) for CHELSA bioclimatic variables.



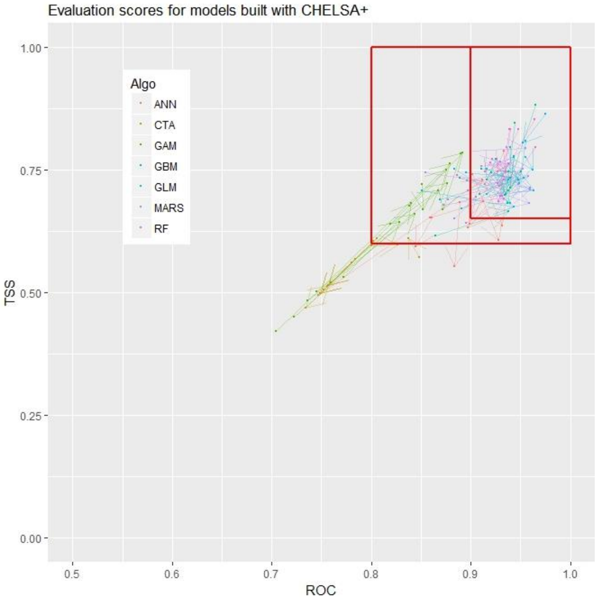


Figure S2: Evaluation scores (area under receiver operating curve, ROC, and true skill statistic, TSS) for all model runs for Worldclim, CHELSA and CHELSA+. Colours denote the algorithm used (note the absence of Maxent and different colour for RF for CHELSA+). Arrows' starting points are scores from internal cross-validation and end points are scores from the set-aside evaluation data. Models whose arrows start and end within the larger red box met the 'lobar' standard; those starting and ending within the smaller box met the 'hibar' standard.

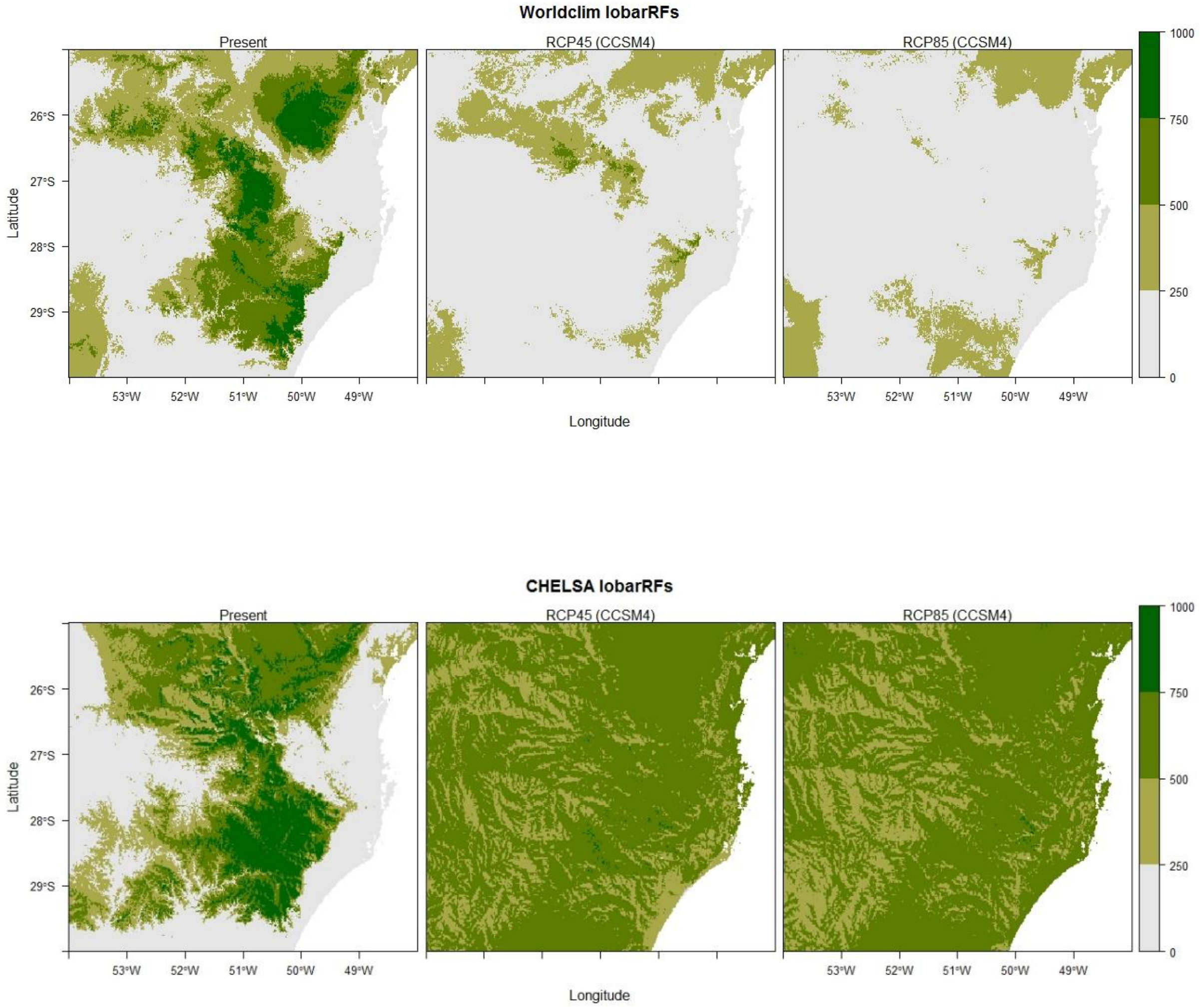


Figure S3: predictions of Araucaria's distribution made using the same algorithm (random forests) and GCM (CCSM4).

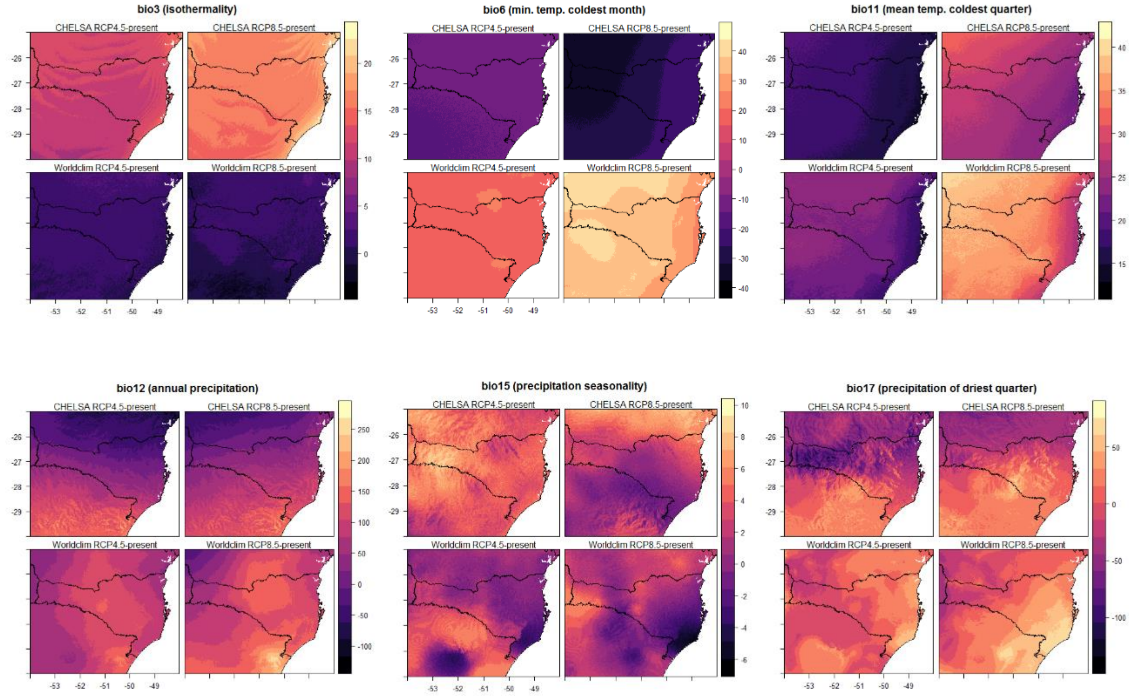


Figure S4: figure to show the differences between future projections (RCP4.5 at left, RCP8.5 at right, both from CCSM4 GCM) and present for CHELSA (top) and Worldclim (bottom)

Area (km^2)	Araucaria's p_{occ}	Worldclim	CHELSA	CHELSA+
Present	0-25%	111,844	94,714	70,799
	25-50%	69,227	53,109	62,925
	50-75%	69,833	51,035	63,156
	75-100%	32,811	8,5794	87,771
2070 RCP4.5	0-25%	247,518	1,399	182
	25-50%	31,604	102,873	108,359
	50-75%	4,593	180,314	163,233
	75-100%	0	66	12,877
2070 RCP8.5	0-25%	258,214	0	2
	25-50%	24,886	90,390	98,483
	50-75%	615	194,217	180,193
	75-100%	0	44	5,973

Table S1: areas predicted for each p_{occ} class for each ensemble model under the included climate scenarios

Supplementary Information for Chapter 3: Floristic change in Brazil's southern Atlantic Forest biodiversity hotspot: From the Last Glacial Maximum to the late 21st Century

Contents

Supplementary Methods

Downscaling palaeoclimate data

The delta change method is a widely used (e.g. Hijmans *et al.*, 2005; Hamann *et al.*, 2013; Lorenz *et al.*, 2016; Wang *et al.*, 2016; Brown *et al.*, 2018) three-step process: data is debiased by generating anomalies (past minus present) for each variable at the GCM's coarse native resolution, interpolated to finer resolution, then summed to an accurate, high-resolution modern-day climatology (here, CHELSA) which permits the inclusion of fine-scale landscape features, variables and complexity that are absent in GCM data. The 'current' time period used for calculating anomaly layers was 1979-1989, for which both PaleoView and CHELSA provide data and for which PaleoView data has been debiased (using the ERA-Interim climate data which underpins CHELSA) (Fordham *et al.*, 2017; Karger *et al.*, 2017).

We followed the methods of PaleoClim (Brown *et al.*, 2018) for downscaling precipitation: PaleoView anomaly layers (2.5° resolution) were computed for each month by subtracting the precipitation of past timeslices from the calibration period; the resulting anomaly layers were then interpolated to 30" resolution using tensioned splines, and summed to CHELSA precipitation grids for the calibration period. Since CHELSA precipitation layers only cover Earth's land surface, and sea-level changes through the studied period require data on currently-submerged land, we extended the data using an Inverse-Distance Weighting algorithm with an elliptical search area (following Lorenz *et al.*, 2016).

Our downscaling of mean, maximum and minimum temperature uses a modified version of the delta change method, following CHELSA's PMIP approach (Karger and Zimmermann, 2019). At kilometre scales, temperature is more closely linked to elevation than is precipitation, and changes to sea level heights since the LGM have led to changes in locations' elevation and, consequently, their temperatures (which decrease with altitude). Using local topographic lapse rates (e.g. Hamann *et al.*, 2013; Wang *et al.*, 2016; Karger *et al.*, 2017) allows these changes to be taken into account, preserving each dataset's original relationship between elevation and temperature and reducing the impact of interpolation artefacts over areas of sharp temperature change (such as southern Brazil's escarpment).

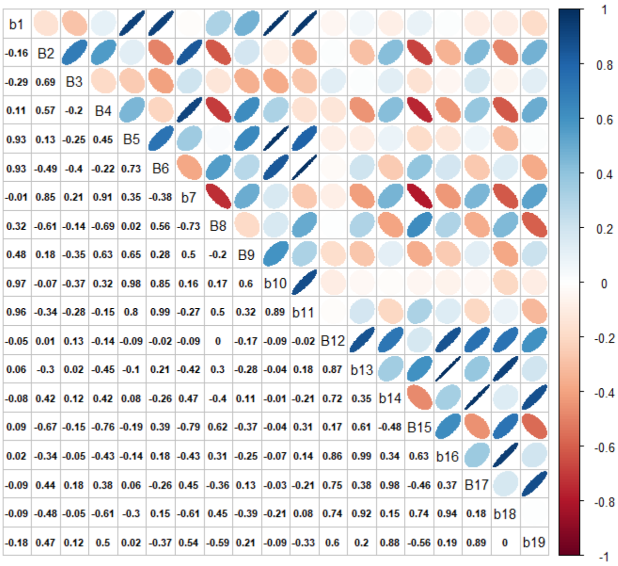
To do this, we generated anomaly layers from PaleoView data at 2.5° resolution then used B-splines to interpolate these to 0.5° resolution. We aggregated CHELSA temperature data for the calibration period to this resolution and summed the anomaly files to these grids to create 0.5°-resolution palaeoclimate files. We then aggregated sea-level-adjusted GEBCO elevation to this coarse resolution and used geographically weighted regression to determine each 0.5° grid cell's lapse rate (temperature increase with elevation, i.e. slope) and sea-level temperature (i.e. intercept). These values for slope and intercept were then used to predict high-resolution temperatures from the 30"-resolution sea-level-adjusted elevation data:

$$t = LR \ \times elev + SLT$$

where *t* = temperature at a given 30" grid cell, *LR* = lapse rate (slope from GWR), *elev* = elevation from 30" GEBCO data, and *SLT* = sea-level temperature (intercept from GWR).

Species distribution modelling

We assessed the correlation of bioclimatic variables based on a random sample of 500 points from within our study area; the mean positive correlation for our chosen variables was 0.35 (0.0 - 0.75), and for negative correlations it was -0.33 (-0.02 - -0.76).



b1																		
-0.16	B2																	
-0.29	0.69	B3																
0.11	0.57	-0.2	B4															
0.93	0.13	-0.25	0.45	B5														
0.93	-0.49	-0.4	-0.22	0.73	B6													
-0.01	0.85	0.21	0.91	0.35	-0.38	b7												
0.32	-0.61	-0.14	-0.69	0.02	0.56	-0.73	B8											
0.48	0.18	-0.35	0.63	0.65	0.28	0.5	-0.2	B9										
0.97	-0.07	-0.37	0.32	0.98	0.85	0.16	0.17	0.6	b10									
0.96	-0.34	-0.28	-0.15	0.8	0.99	-0.27	0.5	0.32	0.89	b11								
-0.05	0.01	0.13	-0.14	-0.09	-0.02	-0.09	0	-0.17	-0.09	-0.02	B12							
0.06	-0.3	0.02	-0.45	-0.1	0.21	-0.42	0.3	-0.28	-0.04	0.18	0.87	b13						
-0.08	0.42	0.12	0.42	0.08	-0.26	0.47	-0.4	0.11	-0.01	-0.21	0.72	0.35	b14					
0.09	-0.67	-0.15	-0.76	-0.19	0.39	-0.79	0.62	-0.37	-0.04	0.31	0.17	0.61	-0.48	B15				
0.02	-0.34	-0.05	-0.43	-0.14	0.18	-0.43	0.31	-0.25	-0.07	0.14	0.86	0.99	0.34	0.63	b16			
-0.09	0.44	0.18	0.38	0.06	-0.26	0.45	-0.36	0.13	-0.03	-0.21	0.75	0.38	0.98	-0.46	0.37	B17		
-0.09	-0.48	-0.05	-0.61	-0.3	0.15	-0.61	0.45	-0.39	-0.21	0.08	0.74	0.92	0.15	0.74	0.94	0.18	b18	
-0.18	0.47	0.12	0.5	0.02	-0.37	0.54	-0.59	0.21	-0.09	-0.33	0.6	0.2	0.88	-0.56	0.19	0.89	0	b19

Figure S1: Correlation plot and coefficients of bioclimatic variables sampled across our study area. Bioclimatic variables with a capital 'B' were included, and ones with a lower-case 'b' excluded.

Two other drivers of vegetation distribution commonly cited in the literature but excluded here are elevation and frost frequency. Elevation is a static variable known to correlate closely with other climatic variables (e.g. minimum temperatures), but whose relationship with these variables is not necessarily constant through time; it should not therefore be used as a predictor in modelling studies (Stanton *et al.*, 2012). Frost frequency is known to control the distribution of MOF and Campos on Brazil's southern highlands but correlates very closely with Bio6, so was excluded.

Species	Pres.	TSS	AUC	GLM	GAM	ANN	GBM	RF	CTA	MARS
Alctri	435	0.620	0.907				2	7		1
Apulei	136	0.552	0.903	1	1		3	4		1
Araang	197	0.519	0.887		1		3	6		
Calbra	165	0.753	0.963	2	2		4	3		
Cecgla	170	0.807	0.955		1		4	5		
Cedfis	455	0.479	0.807		2	1	3	4		
Clesca	476	0.723	0.925	2	1		3	1		3
Cupver	495	0.490	0.817		2		2	5		1
Dansec	18	0.974	1.000				4	2	1	3
Dicsel	225	0.653	0.908		1		4	5		
Dribra	283	0.770	0.948		1		1	4	1	3
Erapol	45	0.574	0.905	4		3	2			1
Eutedu	197	0.755	0.933		1		4	5		
Hyplut	33	0.794	0.934	2				3		5
Ilemic	100	0.458	0.878		2		3	5		
Litbra	115	0.784	0.957		1		5	3		1
Luediv	407	0.629	0.891			1	5	5		
Matela	344	0.559	0.876				4	6		
Mikdec	24	0.700	0.950	2		1	1	5		1
Mimsca	154	0.663	0.896		3		4	2		1
Myrfro	150	0.558	0.857	1			3	6		
Ococat	147	0.715	0.945	1			4	5		
Ocopub	482	0.594	0.867		2		3	5		
Podlam	91	0.807	0.965		2		3	4		1
Podsel	72	0.688	0.916		3		2	2		3
Schten	94	0.579	0.853	2	2		1	2		3
Slogui	178	0.688	0.942		1		5	3		1
Tririo	14	0.468	0.964	1		1	3	6		
Weihum	36	0.658	0.936	3				3		4
Weipau	73	0.611	0.926	2			5	1		2

Table S1: Modelled species (for interpretation of abbreviations, see table 1 in main text), the number of available presence records, the TSS and AUC scores for the ensemble models evaluated against held-back occurrence data, and the number of runs of each algorithm included. Algorithm abbreviations: generalized linear models (GLMs), generalized additive models (GAMs), artificial neural networks (ANNs), generalized boosting models (GBMs), random forests (RFs), classification tree analysis (CTA) and multiple adaptive regression splines (MARS).

Assemblage analysis

We projected binary SDMs for each of our 30 species to nine different time slices, which, when 'stacked', produced over 42,000 unique combinations of species presence and absence. To facilitate the analysis of floristic change, it was important to reduce these presence-absence combinations. We converted a data frame of all 42,023 presence-absence combinations to a dissimilarity matrix using the Bray-Curtis method and the R package 'vegan' (Oksanen *et al.*, 2019), and complete-linkage hierarchical clustering produced 34 maximally distinct clusters (i.e. predicted floristic assemblages). For each of these 34 assemblages we calculated the prevalence of the modelled species, averaged across all time slices; this ranges from 0 (absent from all the assemblage's pixels) to 1 (present in all pixels of the assemblage). We then repeated the clustering process on these aggregated assemblages to establish their relationships, which divides the 34 assemblages into three broad clusters *a*, *b* and *c* (figs. 4, S2). Fig. S2 shows the frequency with which each assemblage occurs through time, as well as their relationships; fig. 4 shows the main assemblages' relationships, distributions and compositions.

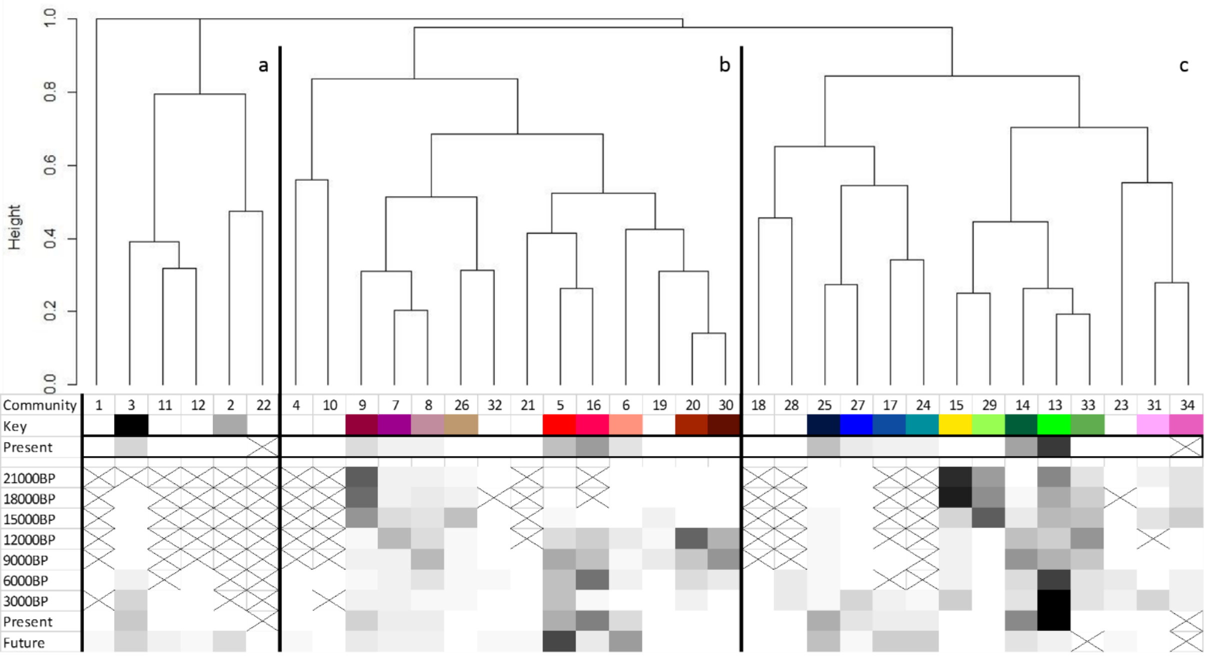


Figure S2: Complete-linkage cluster dendrogram of the 34 maximally distinct potential assemblages. Colours in the 'key' row refer to colours used in figs. 4-6 in the main text; assemblages without an assigned colour never reach 5% coverage in any timeslice. Shading indicates the prevalence of assemblages in different timeslices, and 'X' in a cell denotes absence.

Palaeo-proxy comparison

We aimed to include every pollen, carbon isotope ($\delta^{13}C$) and/or phytolith site within our study area, as well as a selection of sites from the surrounding region to constrain their interpretation and provide context for broader environmental changes. Sites were excluded if they did not cover at least one studied timeslice, if a full description of the results could not be found (i.e. conference abstracts are not included, but unpublished theses are), or if they did not have at least two dates. This low barrier for chronological control reflects the fact that many palaeoecological sites in tropical South America are relatively poorly dated (Smith and Mayle, 2017); seven sites did not meet this criterion, and had the barrier been raised to three dates fourteen more would have been excluded.

Fig. 3 no.	Site name	Publication	Proxies	ylat	xlong	Oldest time slice
1	Serra dos Orgãos	(Behling and Safford, 2010)	Pollen	-22.4583	-43.0281	12000
2	Serra da Bocaina	(Behling *et al.*, 2007)	Pollen	-22.7139	-44.5667	9000
3	Morro de	(Behling, 1997a)	Pollen	-22.7833	-45.5333	21000

	Itapeva					
4	Serra de Botucatu	(Bissa and de Toledo, 2015)	Pollen	-23.0119	-48.3778	21000
5	Terraço Ivaí	(Alcantara dos Santos, 2013)	Phytoliths	-23.2492	-53.2508	21000
6	Trincheira Reserva	(Alcantara dos Santos, 2013)	$\delta^{13}C$, phytoliths	-23.2773	-53.248	9000
7	Colônia	(Ledru *et al.*, 2005; Ledru, Mourguiart and Riccomini, 2009; Rodríguez-Zorro *et al.*, 2020)	Pollen, temperature biomarkers	-23.8667	-46.7056	21000
8	Curucutu	(Pessenda *et al.*, 2009)	Pollen, $\delta^{13}C$	-23.9834	-46.7458	21000
9	Água dos Papagaios	(Ladchuk, Parolin and Bauermann, 2016; Luz *et al.*, 2019)	Pollen, $\delta^{13}C$, phytoliths	-24.0978	-52.3956	6000
10	SAN-76	(Toledo *et al.*, 2007)	Foram $\delta^{18}O$	-24.4333	-42.2833	21000
11	Santana St8	(Cruz *et al.*, 2006)	Speleothem $\delta^{18}O$	-24.5308	-48.7267	21000
12	Serra Campos Gerais	(Behling, 1997b)	Pollen	-24.6194	-50.2396	12000
13	Iapó River	(Kalinovski, Parolin and de Souza Filho, 2016)	$\delta^{13}C$, phytoliths	-24.7525	-50.0883	18000
14	NAP 63-1	(Dauner *et al.*, 2019)	Temperature biomarkers	-24.8384	-44.3187	21000
15	Turvo	(Rasbold, Parolin and Caxambu, 2016)	$\delta^{13}C$, phytoliths	-25.0494	-51.5561	15000
16	Ponta Grossa	(Silva, 2018)	$\delta^{13}C$, phytoliths	-25.1519	-50.0853	21000
17	Aroeiras	(Silva, 2018)	$\delta^{13}C$, phytoliths	-25.2347	-51.2236	12000
18	Caratuva Peak 2	(Scheer *et al.*, 2014)	Pollen, $\delta^{13}C$	-25.2413	-48.8288	6000
19	Guarapuava	(Calegari, 2008)	$\delta^{13}C$, phytoliths	-25.3525	-51.4669	6000
20	Reserva do Iguaçu	(Biffi, 2019)	$\delta^{13}C$	-25.7895	-51.9191	21000
21	LaPAS-KF02	(Pivel *et al.*, 2013)	Foram $\delta^{18}O$	-25.84	-45.2	12000
22	Serra do Araçatuba	(Behling, 2006)	Pollen	-25.9082	-49.0018	12000
23	Tijucas do Sul	(Chiapini *et al.*, 2018)	$\delta^{13}C$, phytoliths	-25.9281	-49.1989	12000

24	Volta Velha	(Behling and Negrelle, 2001)	Pollen	-26.0955	-48.6832	21000
25	Buriti	(Bertoldo, Paisani and Oliveira, 2014)	Pollen	-26.1854	-52.7638	18000
26	Cerro do Touro Watershed	(de Oliveira *et al.*, 2008; de Oliveira, Behling and Pessenda, 2008)	$\delta^{13}C$	-26.232	-49.2245	21000
27	Campo Erê	(Cecchet, 2015)	$\delta^{13}C$, phytoliths	-26.4112	-53.1886	21000
28	Mata Preta	(Calegari *et al.*, 2015)	$\delta^{13}C$, phytoliths	-26.4654	-52.2139	6000
29	Coxilhão	(Silva, 2018)	$\delta^{13}C$, phytoliths	-26.5781	-51.6953	3000
30	Hs1	(Paisani *et al.*, 2013, 2014, 2019; Calegari *et al.*, 2015)	$\delta^{13}C$, phytoliths	-26.5883	-51.5618	15000
31	Hs17	(Paisani *et al.*, 2019)	$\delta^{13}C$, phytoliths	-26.5901	-51.7864	21000
32	Hs13	(Paisani *et al.*, 2014, 2016, 2019; Calegari *et al.*, 2015)	$\delta^{13}C$, phytoliths	-26.6027	-51.7541	6000
33	Xanxerê	(Calegari, 2008)	$\delta^{13}C$	-26.8789	-52.9406	6000
34	Canoas Ponte Alta do Norte	(Pagotto, 2018)	$\delta^{13}C$	-27.1322	-50.4144	21000
35	GeoB2107-3	(Gu *et al.*, 2017)	Pollen	-27.18	-46.45	21000
36	Botuverá Bt2	(Cruz *et al.*, 2005, 2007)	Speleothem $\delta^{18}O$, trace elements	-27.2233	-49.1583	21000
37	Obera	(Zech *et al.*, 2009)	$\delta^{13}C$	-27.3931	-55.5311	21000
38	36GGC	(Carlson *et al.*, 2008)	Foram $\delta^{18}O$, trace elements	-27.5267	-45.5333	21000
39	Serra da Boa Vista	(Behling, 1993, 1995)	Pollen	-27.6999	-49.1536	15000
40	Tabuleiro Summit	(Behling and de Oliveira, 2018)	Pollen	-27.7539	-48.8444	9000
41	Ciama 2	(Jeske-Pieruschka *et al.*, 2013)	Pollen	-27.8968	-48.8681	21000
42	Garopaba	(Kuhn *et al.*, 2017)	Pollen	-28.0367	-48.6283	3000
43	Morro da Igreja	(Behling, 1993, 1995)	Pollen	-28.1267	-49.4806	9000
44	Serra do Rio Rastro	(Behling, 1993, 1995)	Pollen	-28.3868	-49.5478	12000
45	Riachinho Valley	(Carvalho do Amaral *et al.*,	$\delta^{13}C$	-28.6438	-48.9967	3000

		2012)				
46	Sangão	(Carvalho do Amaral *et al.*, 2012)	$\delta^{13}C$	-28.6472	-49.0716	3000
47	Figueirinha Lake	(Carvalho do Amaral *et al.*, 2012)	Pollen, $\delta^{13}C$	-28.6612	-48.9944	3000 (pollen) 21000 ($\delta^{13}C$)
48	São José dos Ausentes	(Pereira, 2017)	$\delta^{13}C$	-28.7085	-50.171	21000
49	Campo Mãe Luzia	(Val-Peón *et al.*, 2019)	Pollen	-28.8815	-49.3592	6000
50	Cambará do Sul	(Behling *et al.*, 2004)	Pollen	-29.0549	-50.0681	21000
51	Santa Rosa do Sul	(Cancelli, 2012)	Pollen	-29.1783	-49.7494	6000
52	São João do Sul	(Cancelli, 2012)	Pollen	-29.2242	-49.8017	6000
53	Banhado Amarelo	(Scherer and Lorscheitter, 2014)	Pollen	-29.3133	-50.1369	3000
54	Fazenda do Pinto	(Behling, Bauermann and Neves, 2001)	Pollen	-29.3848	-50.5332	6000
55	São Martinho da Serra	(Bauermann *et al.*, 2008)	Pollen	-29.4558	-53.6978	3000
56	Alpes de São Francisco 1	(Scherer and Lorscheitter, 2014)	Pollen	-29.4572	-50.6158	15000
57	Rincão das Cabritas	(Jeske-Pieruschka and Behling, 2012)	Pollen	-29.4764	-50.5728	15000
58	CPCN Pro Mata	(Dümig *et al.*, 2008; Silva and Anand, 2011)	$\delta^{13}C$	-29.4805	-50.1716	9000
59	Alpes de São Francisco 2	(Leonhardt and Lorscheitter, 2010)	Pollen	-29.4931	-50.6217	21000
60	São Francisco de Assis	(Behling, Pillar and Bauermann, 2005)	Pollen	-29.5867	-55.2172	18000
61	Serra Velha	(Leal and Lorscheitter, 2007)	Pollen	-29.6061	-51.6486	9000
62	Santo Antônio da Patrulha	(Macedo *et al.*, 2010)	Pollen	-29.7458	-50.5489	3000
63	Tramandaí Lagoon	(Lorscheitter and Dillenburg, 1998)	Pollen	-29.962	-50.1769	6000
64	Passinhos	(Macedo *et al.*, 2007)	Pollen	-30.0342	-50.3864	12000

65	Barrocadas	(Bauermann, 2003)	Pollen	-30.0449	-50.6144	21000
66	Águas Claras	(Bauermann, 2003)	Pollen	-30.0984	-50.8514	12000
67	GeoB6211-2	(Chiessi *et al.*, 2014, 2015; Gu *et al.*, 2018)	Pollen, foram $\delta^{18}O$, trace elements, temperature biomarkers	-32.5	-50.24	18000

Table S2: Palaeo-proxy sites used in this analysis. Coordinates were taken from descriptions and/or maps in original publications; some are approximate.

We generated new age-depth models for all pollen sites using Bacon in R (Blaauw and Christen, 2011; R Core Team, 2018), calibrating radiocarbon dates using the SHCal13 curve (Hogg *et al.*, 2013; following Marsh *et al.*, 2018) for terrestrial sites and the Marine13 curve (Reimer *et al.*, 2013) for marine sites. Because age-depth relationships in soil profiles are frequently more complex and variable than in lake or peat sediments, we used a cautious approach to interpreting these sites' chronologies, only using proxy information for dated sections, avoiding extrapolation of dates and assuming discontinuous sedimentation between horizons distant in time (so avoiding interpolation of proxy values). Exceptions to these rules were sites with minimal signs of changed sedimentation with depth, whose original authors had interpolated ages with depth, or which had explicit age-depth models in their original publications (e.g. the soil profiles from CPCN Pro Mata - Dümig *et al.*, 2008; Silva and Anand, 2011).

Supplementary results

Palaeoclimate proxies and downscaled data

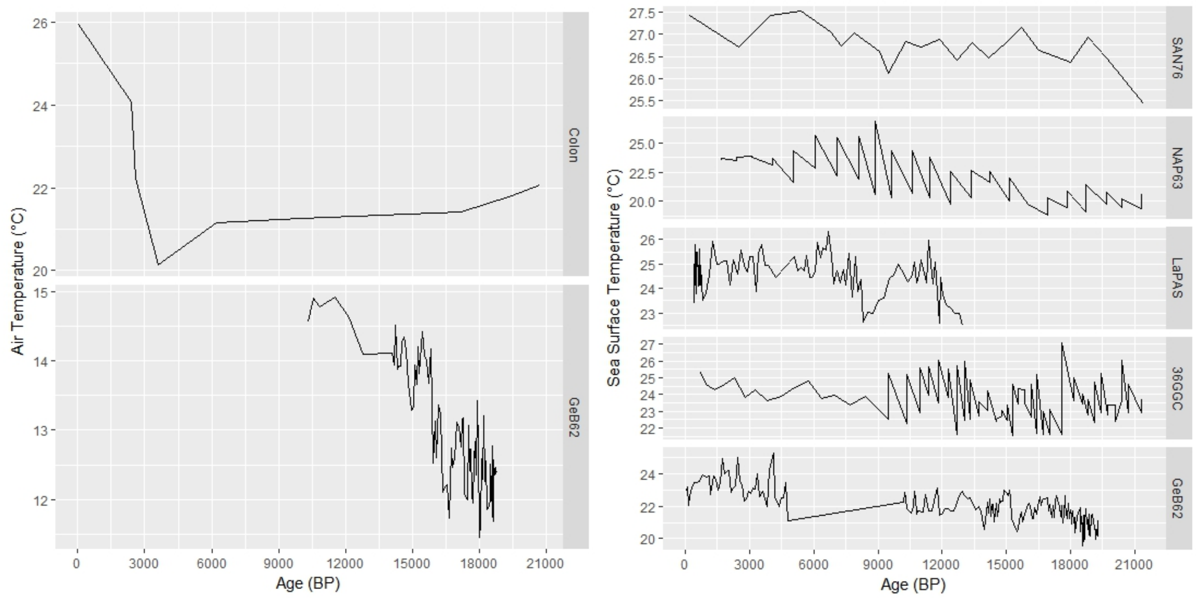


Figure S3: Air temperature (left) and sea surface temperature (right) records from palaeo-proxy sites in southern and south-eastern Brazil. Site codes are abbreviations of site names (table S2).

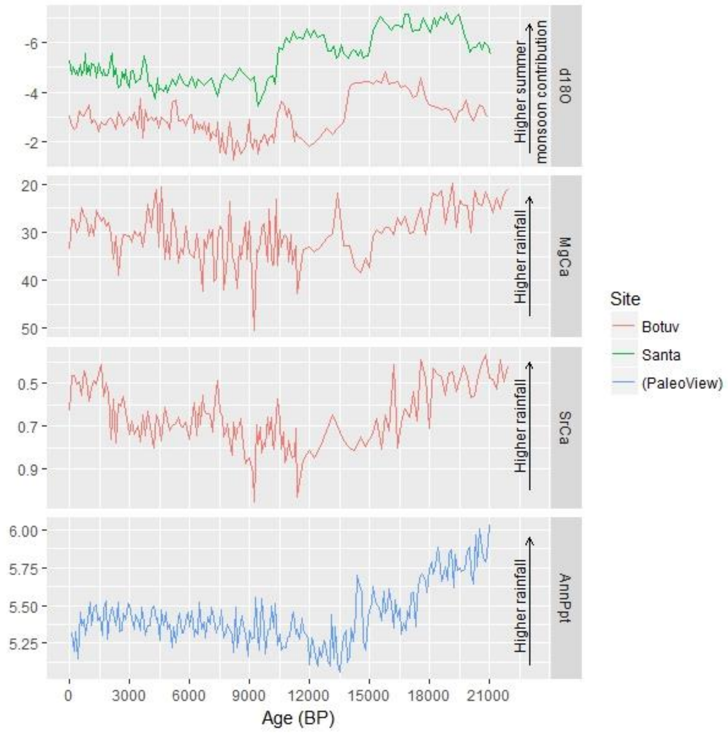


Figure S4: Proxies of past precipitation from Botuverá (Bt2) and Santana (St8) speleothems (Cruz et al., 2005, 2006, 2007), with PaleoView's average annual precipitation (mm/day, median of the four 2.5° pixels around Botuverá).

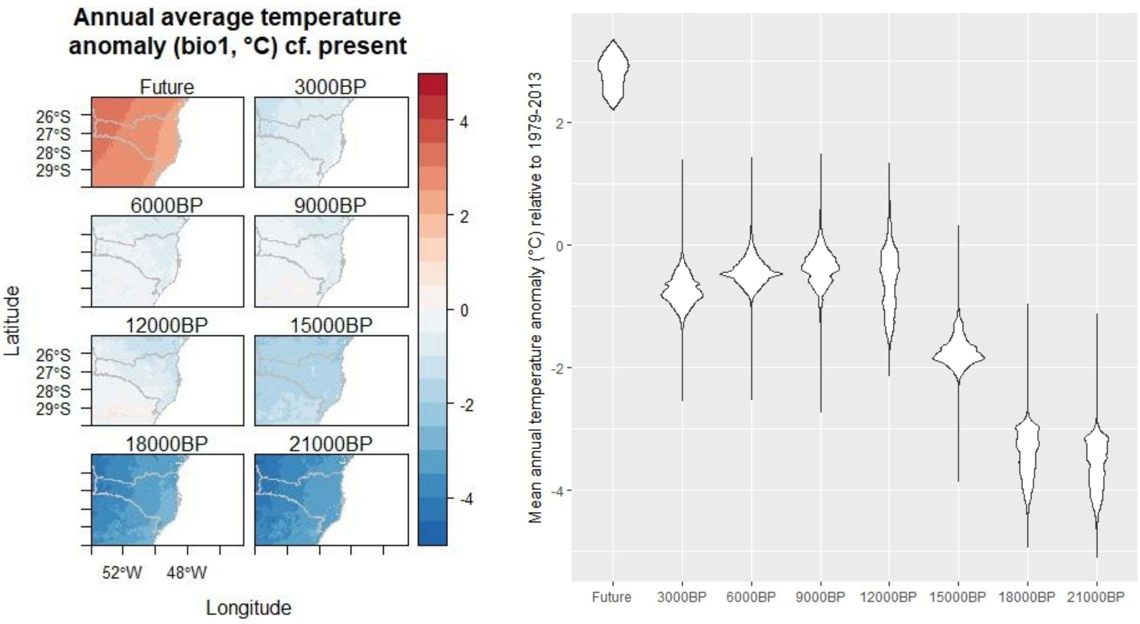


Figure S5: Mean annual temperature differences between the present and past/future time slices.

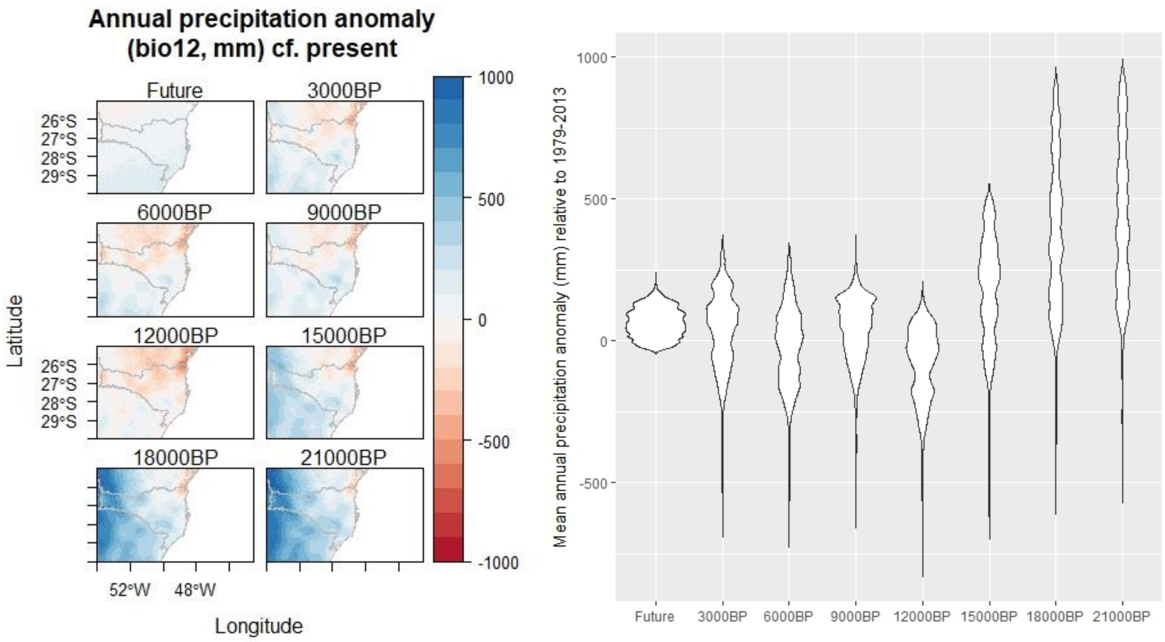
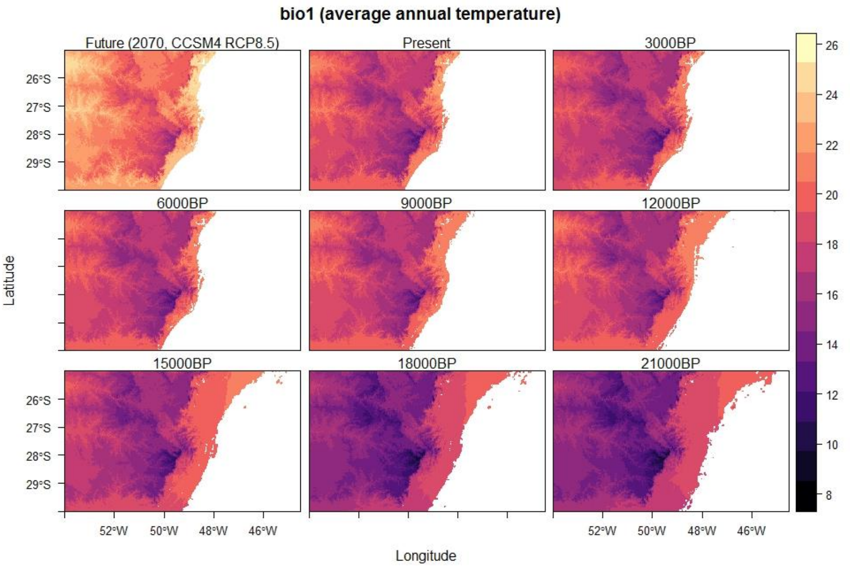
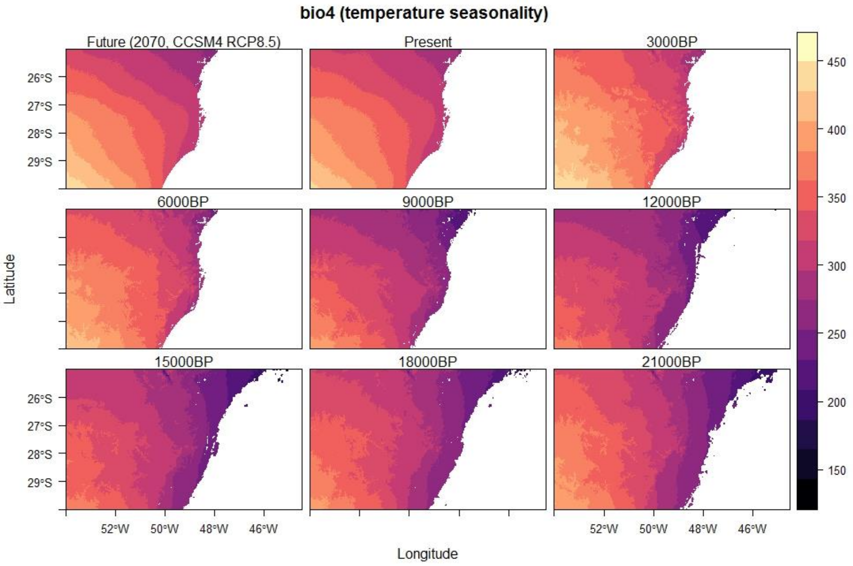


Figure S6: Mean annual precipitation differences between the present and past/future time slices.


bio1 (average annual temperature)


bio4 (temperature seasonality)

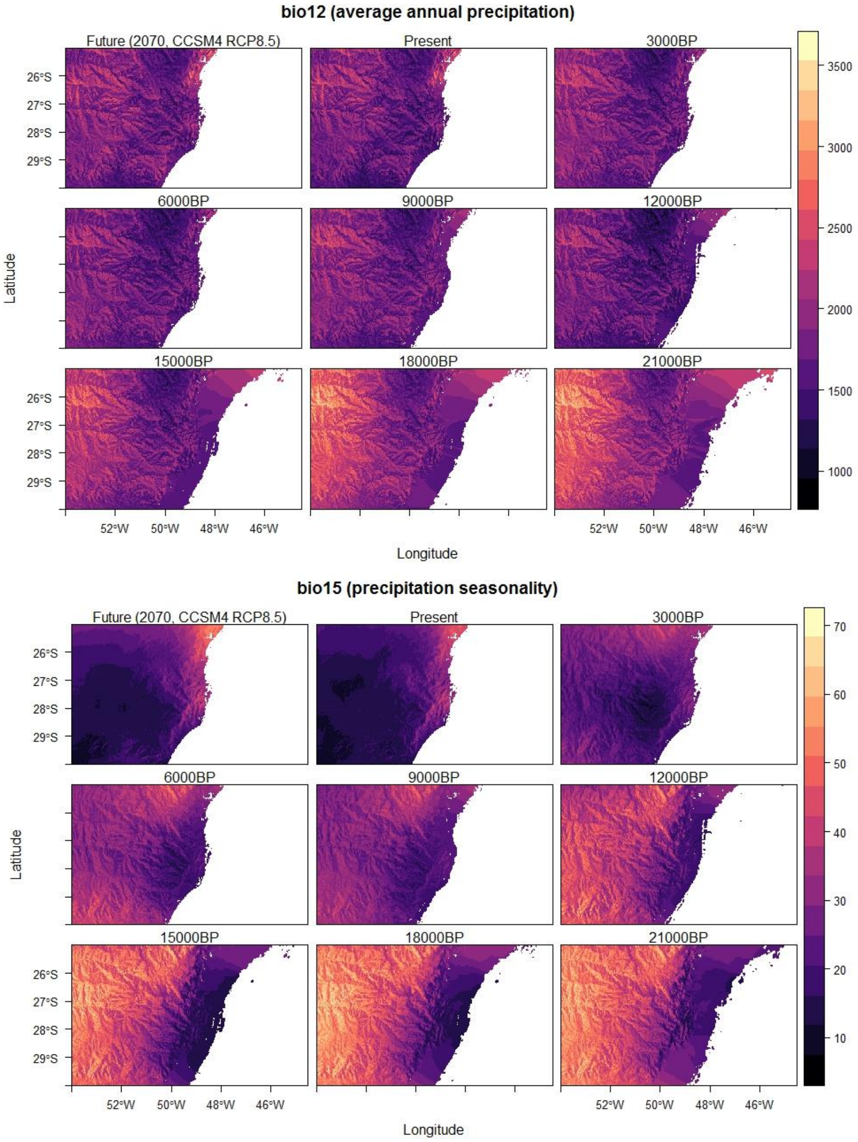


Figure S7: Reconstructed temperature and precipitation variables (annual mean and seasonality) from downscaled Paleoview data.

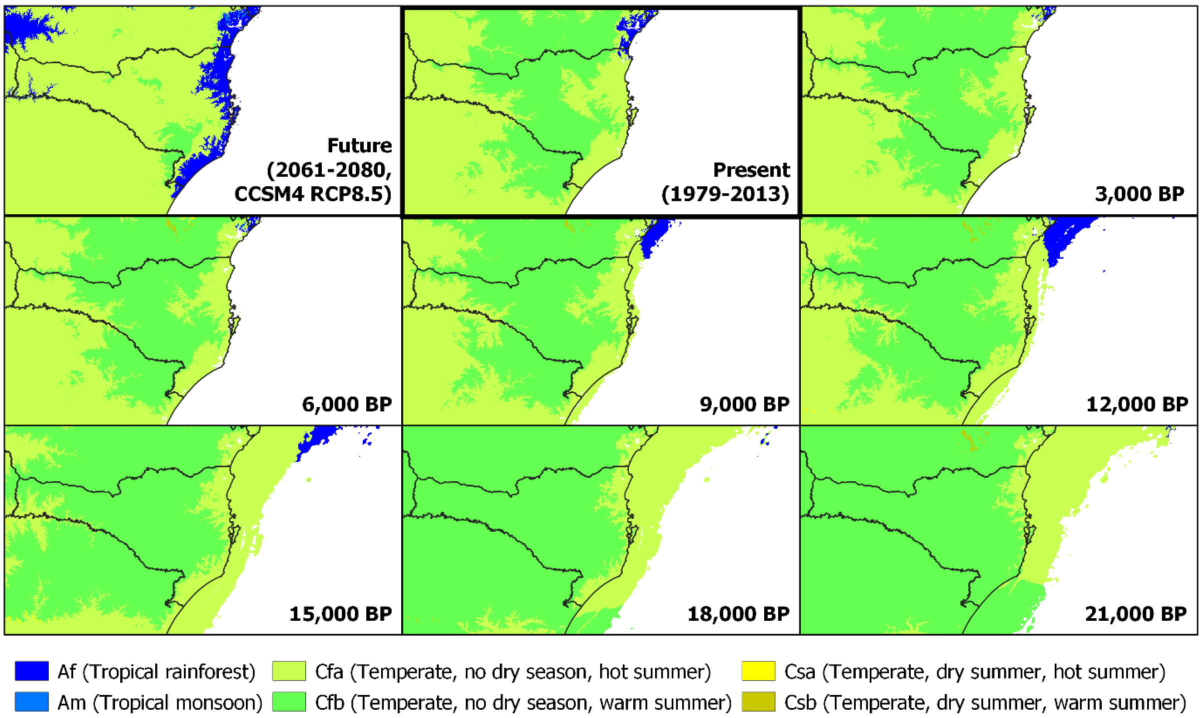
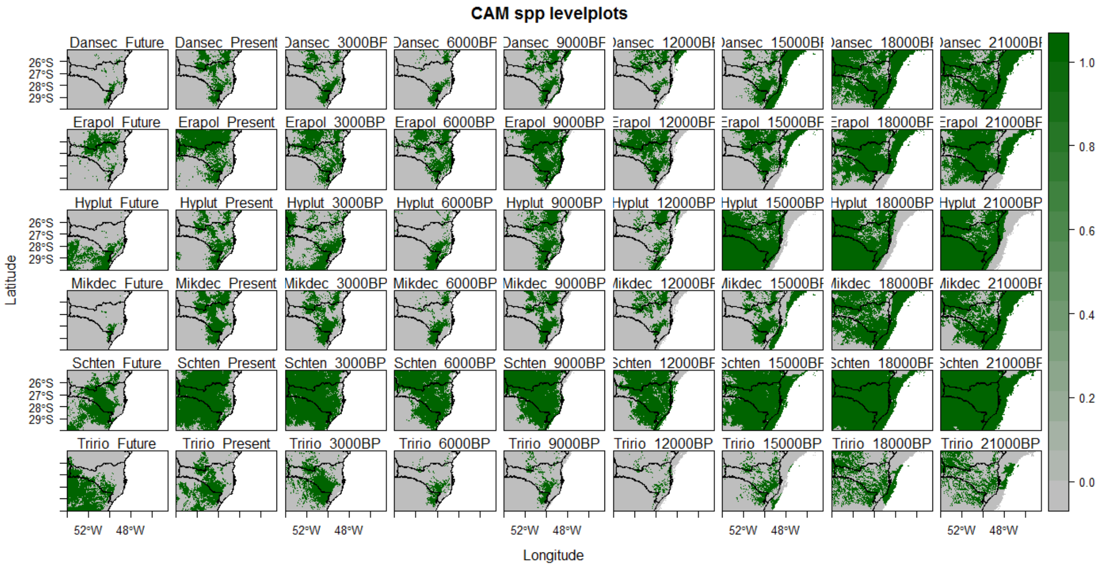
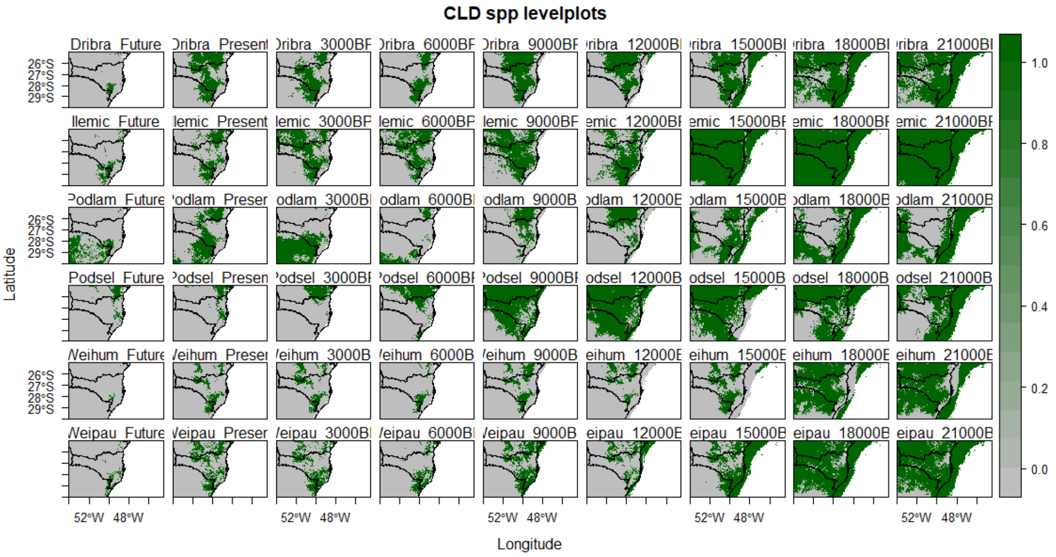
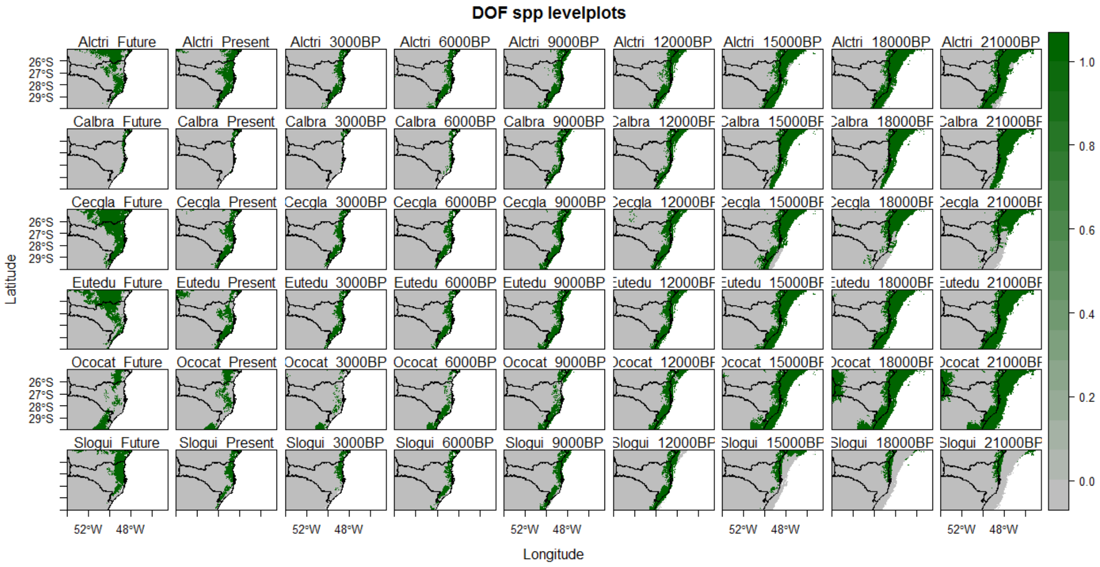


Figure S8: Köppen-Geiger climate classifications (following Peel, Finlayson and McMahon, 2007; Beck et al., 2018) for our study area through time.

Modelled species distributions through time







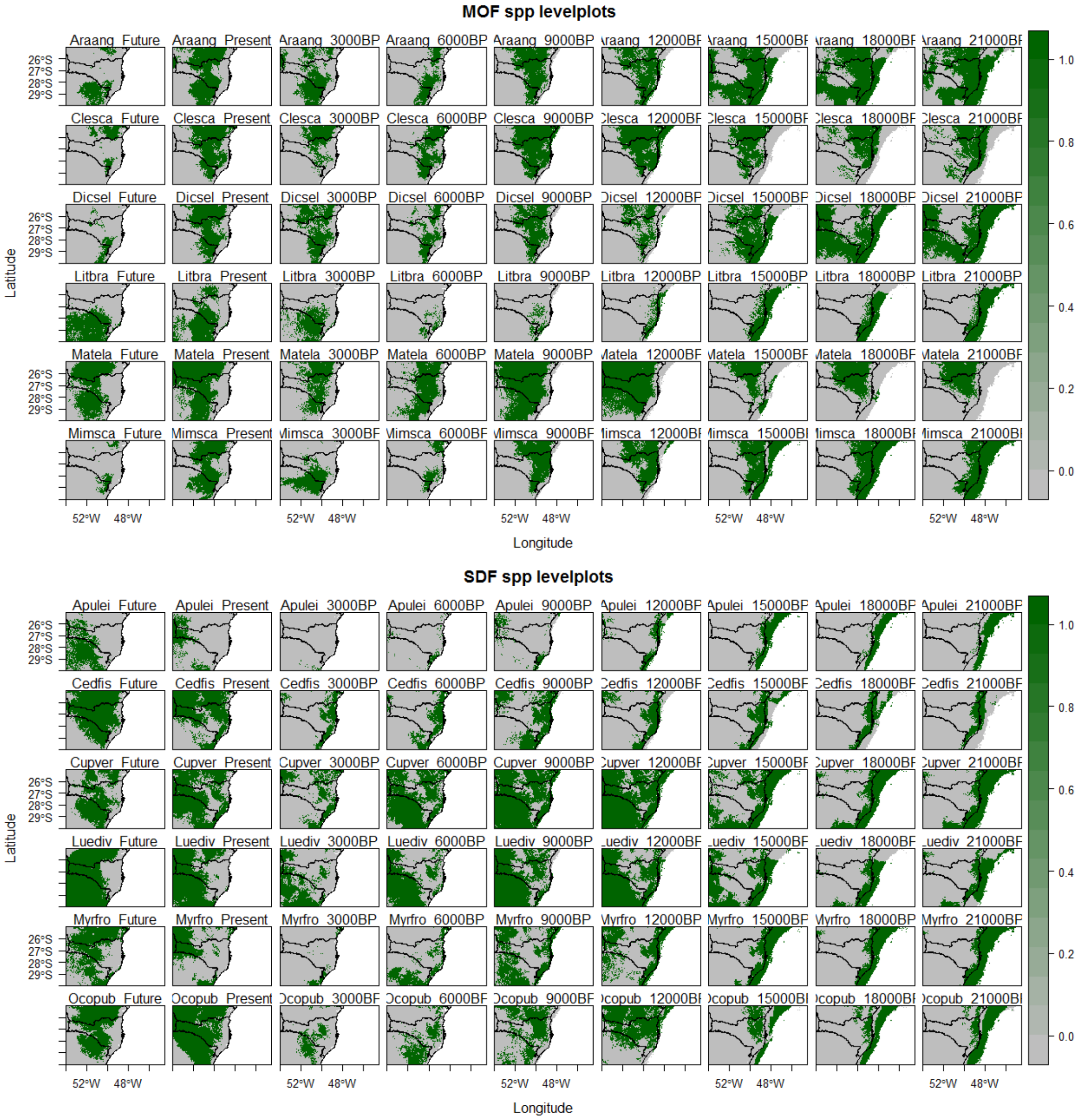


Figure S9: Distributions of modelled species grouped by their most representative ecosystem: Cloud Forest (ALT), Campos (CAM), Dense Ombrophilous Forest (DOF), Mixed Ombrophilous Forest (MOF) and Seasonally Deciduous Forest (SDF).

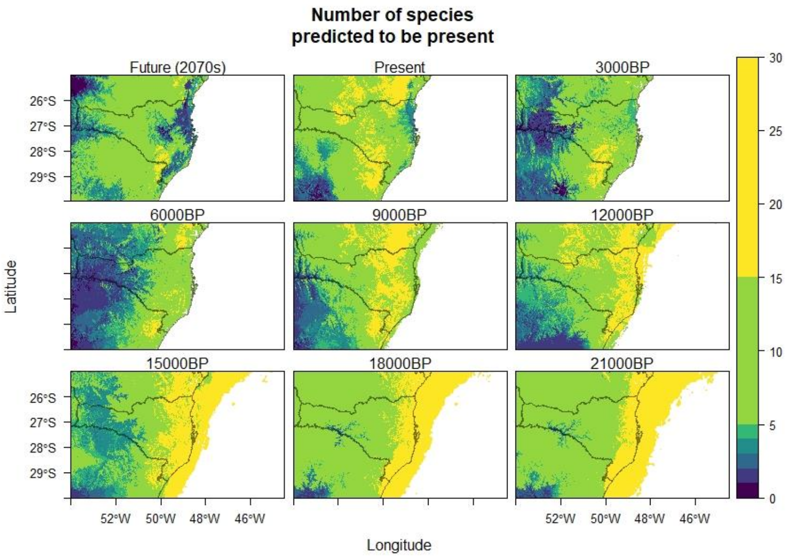
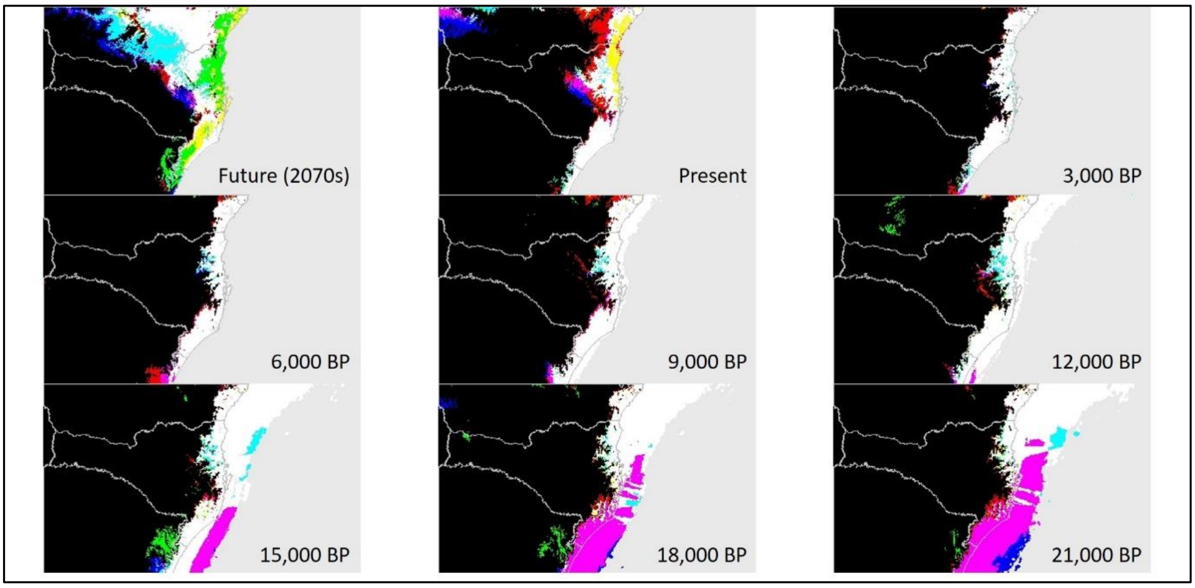


Figure S10: Number of species predicted to occur in each pixel of our study area through time.



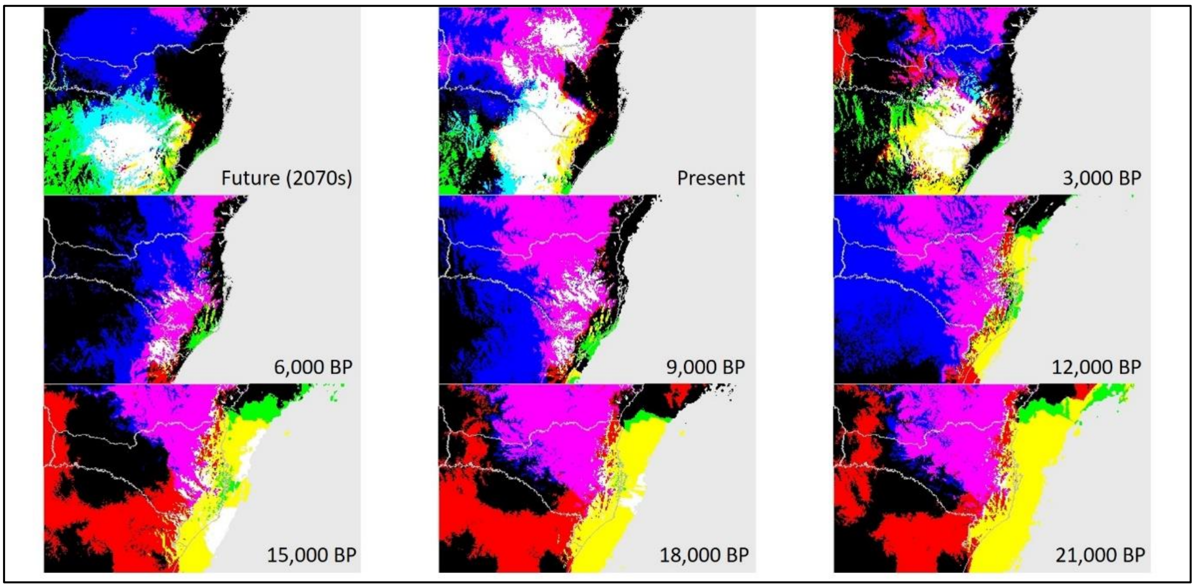


Figure S11: Changing floristic associations in Atlantic Rainforest (top) and Araucaria Mixed Forest (bottom). For each plot, a representative species has been assigned to red, green and blue (ARF: Alchornea triplinervia, Cecropia glaziovii, Euterpe edulis; AMF: Araucaria angustifolia, Lithraea brasiliensis, Matayba elaeagnoides), with their overlaps represented by combinations of those colours. White areas indicate all three species co-occurring, black areas indicate none of the selected species occurring.

Modelled species and modern-day ecosystems

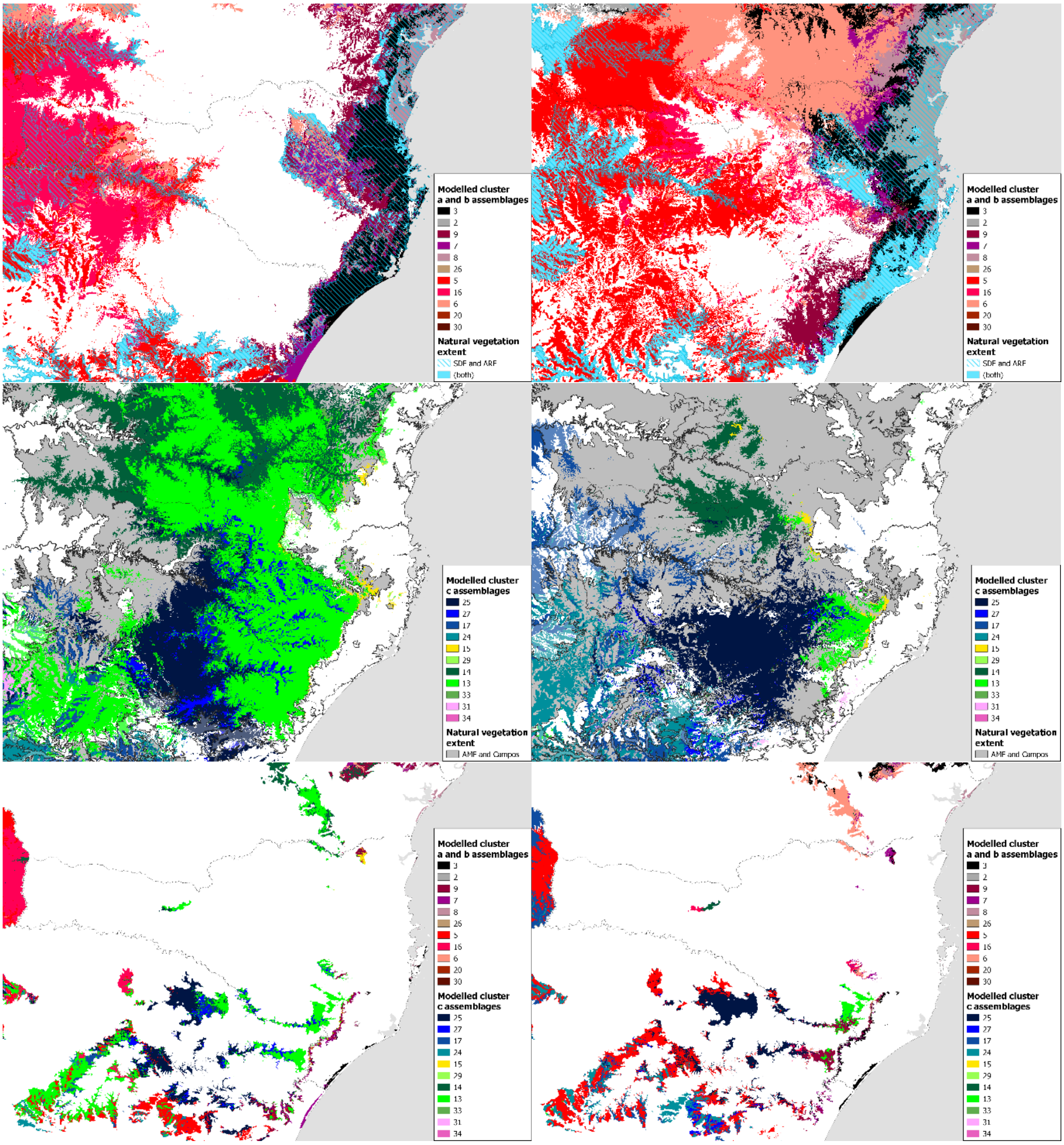


Figure S12: Present (left) and future (right) assemblages overlaid with Brazil's official vegetation: SDF and DOF with assemblages from clusters a and b (top), MOF and Campos with cluster c assemblages (middle) and ecotones plus Misiones province, Argentina with all assemblages (bottom).

Maximum floristic change

This is calculated by comparing, for each modelled pixel of present-day land in our study area, the Bray-Curtis dissimilarity scores between floristic assemblages in pairs of consecutive time slices.

Area experiencing maximum change (km²)

Time slice interval	Including future time slice	Past time slices only
Present-2070s	102,823.70	NA
3ka-Present	30,399.39	63,534.42
6ka-3ka	28,192.37	46,202.13
9ka-6ka	10,914.98	22,644.27
12ka-9ka	6,363.84	13,150.57
15ka-12ka	89,911.33	105,632.37
18ka-15ka	12,846.77	24,971.74
21ka-18ka	1,462.70	6,779.59

Table S3: Area experiencing maximum floristic change at each interval.

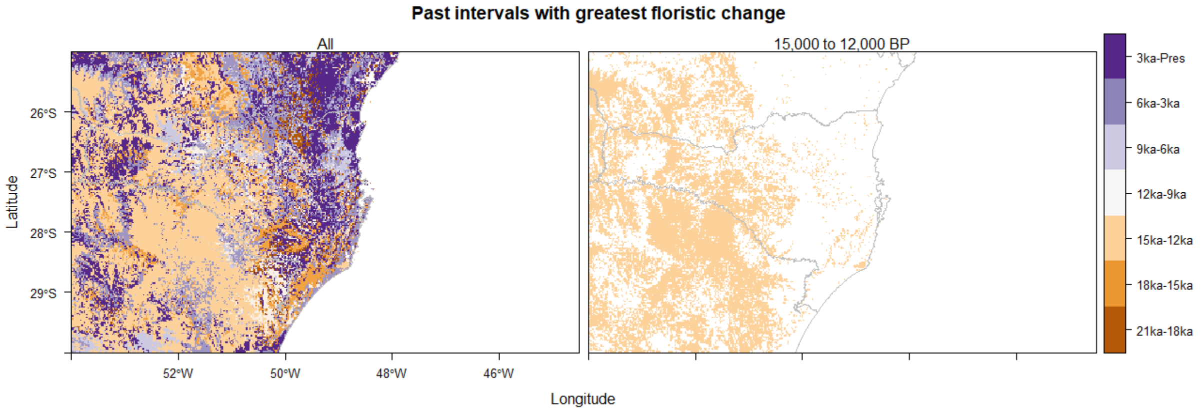


Figure S13: Map showing the past time slice (i.e. excluding the future scenario) which brought the greatest floristic change to different parts of the study area.

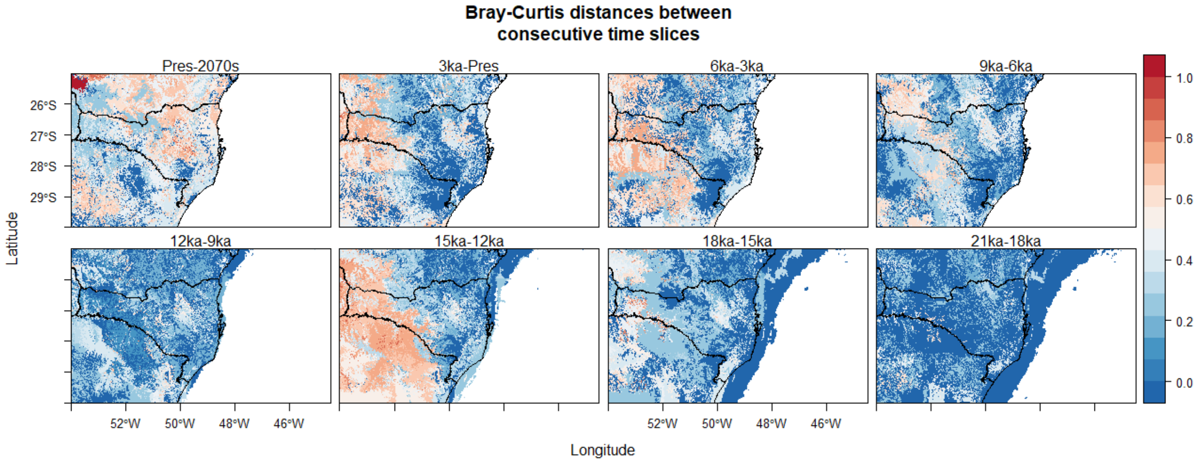


Figure S14: The (dis)similarity of floristic assemblages between consecutive time slices – red denotes assemblages which are more dissimilar and blue those which are more similar.

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Supplementary Information for Chapter 4: How climate, Indigenous people and fire shaped Brazil's Araucaria Forests through the Late Holocene

Supplementary information

Contents

S1. Endemicity in the Atlantic Forest biome

Our claim that one in every 50 species of Earth's seed plants is endemic to the Atlantic Forest – also made, and extended to non-fish vertebrates, in Wilson *et al.* (2021) – echoes the findings of Myers *et al.* (2000) in their original designation of global biodiversity hotspots. Myers *et al.* defined the Atlantic Forest biome in its strictest sense, i.e. solely as the coastal rainforests, whereas its more accurate modern definition includes Araucaria Forests, Campos, Seasonally Deciduous Forests and more (Oliveira-Filho and Fontes, 2000). This change in spatial extent alters the sizes of the biome's total and endemic species pools, as do advances in taxonomic research (table S1.1). However, although the definitions and data used by Myers *et al.* have been superseded in the last two decades, this particular summary statistic continues to hold broadly true: 2% of the world's seed plant species and 3% of its non-fish vertebrate species are found in the Atlantic Forest biome and nowhere else (table S1.1).

Taxon	**Source**	**Atlantic Forest endemic species**	**Atlantic Forest total species**	**Atlantic Forest % endemicity**	**Global species total**	**Atlantic Forest endemics as % of global total**
Vascular plants	Myers *et al.* (2000)	8,000	20,000	40%	300,000	2.7%
Seed plants	Atlantic Forest: Zappi *et al.* (2015). Global: Nic Lughadha *et al.* (2016).	7,432	15,004	49.5%	370,492	2.0%
Terrestrial vertebrates (amphibians, reptiles, mammals, birds)	Myers *et al.* (2000)	567	1,361	41.7%	27,298	2.1%
	Atlantic Forest: Lima Figueiredo *et al.* (2021). Global: Lima Figueiredo *et al.* (2021), Scheffers *et al.* (2019)	954	2,645	36%	31,500 – 34,500	2.8 – 3.0%

Table S1.1: Original and updated species richness and endemicity estimates in the seed plants and non-fish vertebrates (amphibians, reptiles, mammals and birds) of the Atlantic Forest biodiversity hotspot.

S2. Reviewing the evidence for pre-colonial influence on Brazil's Araucaria Forests

The description of Araucaria Forests as cultural landscapes, heavily shaped by beneficial human actions, especially in the past, has grown in popularity over recent years. There are good reasons to think that Araucaria Forests could have been domesticated by Indigenous people, but as yet there has been little firm evidence to show that they were. The same small set of studies ultimately underpins claims of major anthropogenic influence, and for various reasons they cannot effectively support the contention of Indigenous domestication of Araucaria Forest, Araucaria trees, or the wider landscape.

In this section we highlight a number of recent claims around the domestication or anthropogenic expansion of Araucaria Forest or two of its key species, *Araucaria angustifolia* and *Acca sellowiana* (feijoa). We highlight the narrow evidence base upon which these claims stand and critically evaluate the studies which constitute it. In particular, we draw attention to the erroneous conflations of hypothesis with proof, correlation with causation, and modern (post-)colonial dynamics with those from before European arrival – confusions which occur frequently in discussions of past human-environment relationships in Araucaria Forest and their legacies.

Key illustrative quotes are presented below in reverse chronological order, with the most recently published appearing first; this has a bearing on which studies were available for citation by the authors.

1. Clement (2021, p. 14): *"Although Araucaria angustifolia remains have been associated with more recent human occupations (~1.5 k BP) in southern Brazilian [coastal shell mound] sites (Scheel-Ybert, 2013), the expansion of Araucaria forests began by ~4 k BP, associated with human landscape management (dos Reis, Ladio and Peroni, 2014; Scheel-Ybert and Boyadjian, 2020)."*
2. Clement (2021, p. 19): *"Starting ~4 k BP, araucaria (Araucaria angustifolia) expanded through the gallery forests in the interior of the southern Atlantic Forest (Scheel-Ybert and Boyadjian, 2020). Between ~1.4 and 1 k BP, this was mainly driven by human dispersal (Pereira Cruz et al., 2020)."*
3. Sühs *et al.* (2021, p. 1): *"Although the distribution of forests and grasslands remained under dynamic stability for the past 70,000 years, an expansion of forests over grasslands has initiated ~5000 years BP, highly influenced by pre-Columbian people (Bitencourt and Krauspenhar, 2006; dos Reis, Ladio and Peroni, 2014) and reducing the area occupied by grasslands (Behling, 1995; Behling and Pillar, 2007)."*
4. Sühs *et al.* (2021, p. 5): *"In southern Brazil, highland vegetation mosaics are part of a cultural landscape that has been shaped by pre-Columbian people (Bitencourt and Krauspenhar, 2006; dos Reis, Ladio and Peroni, 2014; Robinson et al., 2018). Pre-Columbian people fostered the expansion of Araucaria forests and, especially in the last 1.5 ka BP, likely increased fire frequency in such landscapes (Kern, 1998; Behling et al., 2004; Bitencourt and Krauspenhar, 2006; Lauterjung et al., 2018; Robinson et al., 2018)."*
5. Bogoni *et al*. (2020, p. 2): *"Starting from small refuges located in South America, the FOM [Araucaria Forest] has been managed by pre-Columbian native people since Late Pleistocene and its distribution has widely increased (Bitencourt and Krauspenhar, 2006; dos Reis, Ladio and Peroni, 2014). This human-made expansion led to the domination of the upper forest stratum by araucaria trees, whereas Myrtaceae and Lauraceae are the main plant families forming the middle and lower vertical strata of subtropical forests [...] Feijoa has also been historically influenced by humans, resulting in a certain level of domestication in situ that has favored more varieties of productive trees with large fruits (dos Santos et al., 2009)."*
6. Bogoni *et al*. (2020, p. 7): *"Empirical evidences so far, indicates which this aforementioned dynamics in the FOM is derived from historical terms spread since the Late Pleistocene—due to forest expansion via Amerindian people (Bitencourt and Krauspenhar, 2006; dos Reis, Ladio and Peroni, 2014; Robinson et al., 2018)"*

7. Bogoni *et al.* (2020, p. 8): *"Both araucaria and feijoa underwent domestication and human-made expansion process (Bogoni, Graipel and Peroni, 2018; Robinson et al., 2018)."*

8. Pereira Cruz *et al*. (2020, p. 3): *"Recent research has shown that human action was essential for these [Araucaria] forests to reach their maximum distribution (Lauterjung et al., 2018; Robinson et al., 2018)."*

9. Pereira Cruz *et al.* (2020, p. 10): *"In the State of Santa Catarina palynological evidence indicates that the opening of clearings for cultivation started between 3760 and 2430 B.P (Fig 1) (Robinson et al., 2018). [...] The Southern-Jê were probably responsible for Araucaria forest expansion over grasslands (dos Reis, Ladio and Peroni, 2014; Lauterjung et al., 2018; Robinson et al., 2018)."*

10. Pereira Cruz *et al.* (2020, p. 12): *"Our analysis explained only 7% of data variation; however, given the wide spectrum of environmental characteristics that may influence vegetation patterns at the landscape scale, past Amerindian cultures may be an important factor to consider. Our results indicate past Southern-Jê and Guarani distributions are another factor driving differences in present-day forest species composition."*

11. Bogoni *et al.* (2020, p. 7): *"The massive modern retraction of Araucaria forests reversed their pre-historical expansion induced by past paleoindian populations through human seed dispersal (dos Reis, Ladio and Peroni, 2014; dos Reis et al., 2018; Robinson et al., 2018)."*

12. Bogoni *et al*. (2018, p. 3), in a paper entitled *"The ecological footprint of Acca sellowiana domestication maintains the residual vertebrate diversity in threatened highlands of Atlantic Forest": "Like Araucaria in local landscapes, Feijoa has been subjected to historical anthropogenic influence promoting a certain level of domestication of some populations in situ, which has resulted in increased fruit size and productivity by human selection (Bitencourt and Krauspenhar, 2006; dos Santos et al., 2009; dos Reis, Ladio and Peroni, 2014; Mello and Peroni, 2015). [...] the expansion of FOM [Araucaria Forest] by pre-Columbian people (i.e., indigenous Xokleng and Kaingang) favored the expansion of Feijoa and other associated Myrtaceae (dos Santos et al., 2009; dos Reis, Ladio and Peroni, 2014)."*

13. Lauterjung *et al.* (2018, abstract): *"In particular, it was hypothesized that Araucaria angustifolia, an endangered South American conifer, was dispersed from its Pleistocene glacial refugium to its maximum occurrence distribution (MOD), mainly by pre-Columbian human groups (ca 2000 years ago). [...] The estimated dispersal time required for the species to reach its MOD from its putative refugium without human help is not consistent with the rapid and recent expansion of the species. Hence, we argue that humans played an important role in expanding the distribution of the currently endangered species, and it needs to be accounted for when analyzing landscape genetics or in the development of conservation strategies."*

14. Lauterjung *et al.* (2018, p. 9): *"To reinforce the idea of the anthropogenic dispersal, our simplified model found that it would take more than 14,000 years for the species to reach its maximum occurrence distribution when involving only non-human dispersal. This time interval is higher than the actual period of 4000–1500 years reported by palynology, demonstrating the need of external, i.e. anthropogenic help for dispersal of this species."*

15. Robinson *et al.* (2018, abstract): *"Here, we develop and test a model of natural ecosystem distribution against vegetation histories, paleoclimate proxies, and the archaeological record to distinguish human from temperature and precipitation impacts on the distribution and*

expansion of Araucaria forests during the late Holocene. Carbon isotopes from soil profiles confirm that in spite of climatic fluctuations, vegetation was stable and forests were spatially limited to south-facing slopes in the absence of human inputs. In contrast, forest management strategies for the past 1400 years expanded this economically important forest beyond its natural geographic boundaries in areas of dense pre-Columbian occupation, suggesting that landscape modifications were linked to demographic changes, the effects of which are still visible today."

16. Suhs *et al*. (2018, abstract): "*In the southern Brazilian highlands, pre-Columbian societies created domesticated landscapes through the use and management of forests, including nurse Araucaria angustifolia trees, a common conifer in these regions."*
17. Suhs *et al.* (2018, p. 3): "*Previous studies have shown that as a consequence, domesticated landscapes were created through forest use and management (Zeder, 2016), including the management of araucaria trees, whose seeds constituted part of the diet of these peoples (Bitencourt and Krauspenhar, 2006; dos Reis, Ladio and Peroni, 2014)."*
18. Dos Reis *et al.* (2014, abstract): "*We also studied the role of human groups in the construction of Araucaria forests. [...] The ecological characteristics of both species [A. araucana and A. angustifolia] have favored their rapid territorial expansion since the Holocene; however, palynological, archaeological, and ethnobotanical evidence reinforces the hypothesis that the human groups involved played a key role in this process."*
19. Dos Reis *et al*. (2014, p. 5): "*Aspects related to the regeneration of A. angustifolia are similar to those described for A. araucana, and their recruitment is also dependent on large clearings [...] adult trees can also tolerate fire, particularly in grassland environments [...] Although forest fires are currently uncommon in areas where A. angustifolia occur, palynological studies show that there was a time when fire was more frequent, mainly during the A. angustifolia forest expansion period (Behling and Pillar, 2007; Bauermann et al., 2008). The same authors associate the existence of grasslands with the management practices of fire used by human groups in the Holocene. [...] Once again, human practices appear to have played an important role in the expansion and formation of Araucaria forests, increasing opportunities for regeneration of the species and, thereby, increasing the availability of part of their food supply."*
20. Dos Reis *et al*. (2014, p. 9): "*The evidence supports the idea that the different cultures that have interacted with these forests could have favored their expansion and their abundance in the past. Local communities possibly recognized the ecological characteristics of both species, particularly their resilience and great capacity for adaptation and regeneration, and so have been able to learn to manage or manipulate the forests according to their cultural and symbolic criteria. [...] The communities that currently maintain traditional in situ and ex situ management practices, by means of tolerance, enhancement, and protection in the occurrence area, and by cultivation of seeds and/or transplanting trees outside the range, could have been more able to preserve them."*

This non-exhaustive set of quotations demonstrates how progressively more strident, assertive and/or certain claims have been building up on an evidence base that has remained relatively narrow and, in our view, somewhat unsupportive of the more confident declarations included above. In the following section we critically evaluate the studies cited above as evidence for the domestication or human-driven/-aided expansion of Araucaria Forest landscapes or species, and assess the support they lend to the authors' claims.

- Scheel-Ybert and Boyadjian (2020) (cited in quotes 1 and 2). This paper provides a wide-ranging overview of the archaeology and (in particular) plant use of the sambaqui (shell mound)-building people, who lived along southern Brazil's coast for much of the Holocene and are described as 'fisher-gardeners' with a mixed economy. However, the paper does not directly deal with *Araucaria angustifolia* or Araucaria Forest, except to note that *Araucaria* phytoliths and starch grains were observed in two sites around 500-1200 cal BP, probably from cultural exchange with highland groups (citing the findings of Wesolowski *et al.*, 2010). It makes no mention of the timings of or explanations for past Araucaria Forest expansions.

- Pereira Cruz *et al*. (2020) (cited in quote 2, excerpts in quotes 9 and 10). This study set out to evaluate floristic legacies of past southern Jê and Guarani land use in Santa Catarina state. The authors modelled the potential distributions of archaeological sites from each tradition, then compared these predictions against floristic data from the Santa Catarina Forest Floristic Inventory (IFFSC; Vibrans *et al.*, 2010, 2020). Unfortunately, the study compares floristic patterns between the archaeological groups, rather than between climate- or disturbance-matched areas of high and low predicted occupation for each group. As a result, the results do not evaluate whether particular species are more or less abundant in areas with more intense human occupation – instead they simply reflect the overlapping distributions of the studied groups with different vegetation types.

  High elevations (and, secondarily, proximity to rivers) were found to explain the distribution of southern Jê archaeological sites; these areas were associated mainly with species from high-elevation Araucaria Forest (and, to a lesser extent, the Seasonally Deciduous Forests that follow the Uruguay river). Proximity to rivers and the coast were the most important factors for the distribution of Guarani archaeological sites; these sites were associated with species of the Uruguay river's Seasonally Deciduous Forests and coastal Atlantic Rainforest. In fact, the gradient of species associated with southern Jê and Guarani archaeological sites (Pereira Cruz *et al.*, 2020, fig. 7) almost perfectly mirrors the IFFSC's lists of the most important species in Araucaria Forest (southern Jê), Seasonally Deciduous Forest (shared) and Atlantic Rainforest (Guarani) (Schorn *et al.*, 2012). The first two axes of the redundancy analysis used to produce this gradient together explain only 7% of the total variation in the data, indicating that other factors, such as climate, play a far more significant role than broad-scale southern Jê/Guarani archaeology in explaining floristic patterns.

  In summary, this study shows which forest ecosystems the southern Jê and Guarani were most likely to live among, but it does not – and by design cannot – show any lasting floristic legacies associated with their occupations.

- Robinson *et al.* (2018) (cited in quotes 4-9 and 11, excerpt in quote 15). This study provides, by far, the strongest direct evidence to date for pre-colonial Indigenous expansion of/influence on Araucaria Forests. It is, accordingly, one of the studies most frequently cited to support claims of Araucaria Forest landscape domestication.

  The authors focus on two areas (shown in fig. S1.1 and main text fig. 1d), one (Lages) with little archaeological evidence of human occupation, and one (Campo Belo do Sul) where past southern Jê occupation was intense; these are the first palaeoecological records from the Campo Belo do Sul area. They first model Araucaria Forest distribution with topography, based on its configuration in Lages (along valley bottoms and on shaded slopes); forests outside this predicted niche make up 6% of the Lages area. By contrast, 33% of the Campo Belo do Sul area consists of forests outside the predicted niche. The authors then examine stable carbon isotopes ($\delta^{13}C$) from transects of soil pits across plateaus and valleys in both areas. In Lages there is little change from the beginning of the record at about 7,500 cal BP – the shaded slope and riparian area are dominated by C3 vegetation (most likely forest) and the exposed slope and plateau by C4 plants (grassland). In Campo Belo do Sul, transitions from C4-dominated to C3-dominated vegetation occur, in all parts of the transects, starting (where dates are available) around 1,000-1,200 cal BP (our S4.2). Noting that an independent rainfall proxy record (Bernal *et al.*, 2016) shows this period saw no major change (certainly no increase) in precipitation (our fig. 3a), but that it did coincide with increases in archaeological evidence (our fig. 3c), the authors attribute these expansions – and the differences between Lages and Campo Belo do Sul – to the southern Jê.

The key assumption on which these conclusions rest is that the patterns at Lages and Campo Belo do Sul should be the same in the absence of pre-colonial human influence. This assumption may not be valid. The Campo Belo do Sul sites are approximately 60 km west-north-west of Lages and at significantly lower elevation (approximately 750-980 m compared to ca. 1100 m; fig. S1.1). Additionally, whereas Lages sits well within modern Campos vegetation, Campo Belo do Sul is closer to or within areas of (formerly/naturally) continuous Araucaria Forest (fig. S1.1). The Campo Belo do Sul sites are also the first palaeoecological proxy records in this part of the plateau, so it is unclear whether they should be expected to exhibit the same changes through time as Lages and better-studied areas along the south-eastern plateau edge. Altogether, these observations suggest that different vegetation patterns between the two regions could potentially have been caused by natural (e.g. climatic) differences between the sites.

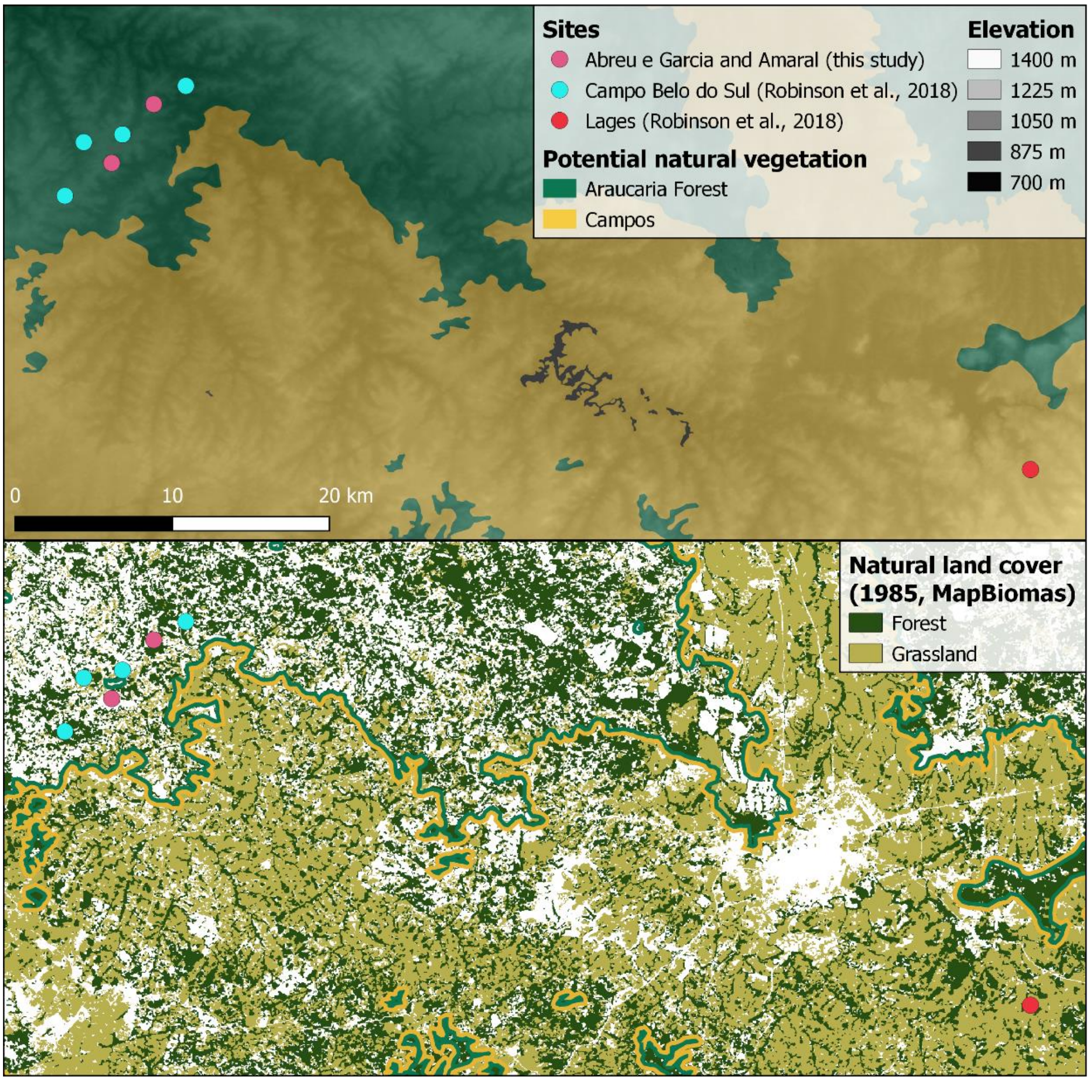


Figure S1.1: The environmental context for the Campo Belo do Sul and Lages study areas: their elevation and potential natural vegetation (top) and the distribution of modern vegetation remnants (below, using natural grassland and forest in 1985 from MapBiomas (Souza *et al.*, 2020)*).*

There is some evidence within the study that suggests this could be the case. The Lages valley has a clear pattern of forest in riparian areas and shaded slopes, and grassland on exposed slopes and plateau, which is constant throughout the record. By contrast, all parts of the Mata Queimada and Heraldo valleys in Campo Belo do Sul (including riparian areas and shaded slopes) start off as grassland and become more C3-dominated through time – no studied part of the Campo Belo do Sul valleys is forested in the earliest (undated) parts of the records. This may mean that the expansion of Araucaria Forest onto the plateau tops in Campo Belo do Sul – interpreted by the authors as a clear signal of human landscape transformation – was instead part of a general trend for all parts of this region's landscape to move from grassland to forest. Such a trend, and its difference from Lages, could potentially have natural causes.

The transferability of the vegetation distribution model between the two areas can also be queried. As outlined above, the model was derived from the distributions of Araucaria Forest in the Lages area (high elevation, core Campos). Continuous Araucaria Forest covers (or covered, before 20th-Century deforestation) much of the highlands, especially at lower elevations than those occupied by Campos (our fig. 1a). Logically, then, it follows that a distribution model which predicts forest only in valley bottoms and on shaded slopes will make incorrect predictions for the large parts of the region where Araucaria Forest covers/covered all parts of the landscape and Campos is naturally absent. The key question is whether the model's predictions can be legitimately transferred between Lages and Campo Belo do Sul. Given how much closer the latter area is to continuous Araucaria Forest, and in light of the between-region differences in vegetation histories revealed by the study's soil carbon records, attributing spatial differences solely to pre-colonial Indigenous societies may not be warranted. (It is also worth noting that differences in the intensity and/or spatial patterns of 20th-Century deforestation between Lages and Campo Belo do Sul (fig. S1.1) could also affect the model's representation of ecological truth and its transferability between regions.)

These caveats do not necessarily invalidate the study, its findings or the implications they have for pre-colonial impacts on Araucaria Forests by southern Jê people. They do, however, mean that the study should not be interpreted as delivering the definitive evidence that fully resolves the issue of southern Jê alteration of Araucaria Forests. An important next step would be to account for potential natural differences between Lages and Campo Belo do Sul – both in their spatial distribution of Araucaria Forest and in their vegetation histories – to help clarify the extent to which the observed patterns can be confidently attributed to human actions.

- Bogoni *et al*. (2018) (cited in quote 7, excerpt in quote 12). This study starts from a position of *Acca sellowiana* (feijoa) having been (at least incipiently) domesticated in the past, then evaluates the trophic relationships between feijoa and vertebrates and the influence on those relationships of several variables, one of which is evidence of feijoa domestication activities. The references cited to support the presumption of feijoa domestication predominantly deal with *A. angustifolia*/wider Araucaria Forest (Bitencourt and Krauspenhar, 2006; dos Reis, Ladio and Peroni, 2014; Mello and Peroni, 2015), with dos Santos *et al* (2009) the only one to explicitly deal with feijoa domestication. All these studies are evaluated in more detail below.

  This study does not set out to provide independent evidence of feijoa domestication, but nonetheless finds it in three of the four examined sites: some feijoa trees close to abandoned rural properties showed evidence of having been pruned in the past, for example, and trees with larger fruits tended to be closer to the property foundations, both of which indicate use and management of – and care for – individual trees. Furthermore, these apparently more domesticated feijoa trees produced four times more fruit than 'under-domesticated' ones and experienced more frugivory from more species; evidence for domestication accounted for a small (6%) but statistically significant part of the observed variability in mammal-feijoa fruit interactions.

  However, this study looks only at evidence of modern incipient domestication: the people who appear to have managed the studied feijoa trees were cattle breeders, loggers and pinhão extractors, and their properties could have been abandoned as recently as 10 years before the study. The study does not provide evidence on any pre-colonial and/or Indigenous domestication of feijoa. It could be assumed that Indigenous people may also have incipiently domesticated feijoa because feijoa's characteristics are inherently desirable to people – its fruits are 2-12 times larger than those of other Araucaria Forest Myrtaceae species and attract/support a range of potential prey animals (Bogoni, Graipel and Peroni, 2018; Bogoni, Batista, *et al.*, 2020) – and because Indigenous knowledge can become incorporated into colonial societies' human-environment relationships (see Moura, 2021, for some examples from southern Brazil's highlands). However, this study (and that of dos Santos *et al.*, 2009, discussed below) does not provide direct evidence that this took place.

- Lauterjung *et al*. (2018) (cited in quotes 4, 8 and 9, excerpts in quotes 13 and 14). This study has two main components: a phylogeographic evaluation of *Araucaria angustifolia*'s chloroplast genome (cpDNA), and an evaluation of the time required for the species to reach its maximum extent from a putative single glacial refugium, based on modelling, demographic and palaeoecological data.

  The results of the phylogeographic analysis can be summarised as follows: the cpDNA haplotype network exhibits a star-like shape, one haplotype dominates in all sampled populations, genetic variability is much higher within populations than between them, and there is no evidence of spatial structure or isolation by distance. These findings are interpreted as supporting recent, rapid expansion from a single refugial population. We lack the specific expertise to comment in detail on these findings, but note three brief observations.

  Firstly, palaeoecological research has shown that species do not always retreat to a single large refugium during unfavourable periods, then sweep out from them in a wave as conditions improve. Instead, small areas preserving favourable conditions can form microrefugia, helping species persist in patches across a landscape before expanding into newly suitable surroundings from multiple sites (Rull, 2009; Dobrowski, 2011). This phenomenon has previously been inferred for the southern Atlantic Forest (Costa *et al.*, 2017; Wilson *et al.*, 2021), and a more wide-ranging phylogeographic study suggests *A. angustifolia* probably had several refugia (Stefenon *et al.*, 2019). Secondly, and perhaps relatedly, in plant species where cpDNA is paternally inherited (as in conifers) and pollen dispersal contributes more to gene flow than seed dispersal (as is the case for *A. angustifolia*), cpDNA is less sensitive to spatial genetic structuring than genomic DNA: long-distance dispersal of pollen can homogenise populations' cpDNA (Myers, Chung and Chung, 2007; Medina-Macedo *et al.*, 2015). A number of other studies have investigated *A. angustifolia*'s phylogeography using a range of methods and populations (some of them more extensive than in Lauterjung et al.), and can provide a wider view on the genetic evidence for the species' post-refugial expansions (Auler *et al.*, 2002; Stefenon, Gailing and Finkeldey, 2007; Stefenon *et al.*, 2008, 2019; Medina-Macedo *et al.*, 2015; de Sousa *et al.*, 2020). Thirdly, we note that human influences need not necessarily be invoked to explain rapid post-refugial population expansions – conceivably, changes to more suitable climatic conditions could have the same effect.

  The second part of this study is designed to demonstrate that human involvement is a necessary explanation for *Araucaria*'s apparently rapid post-refugial expansions. The authors use a previously identified refugial area for *A. angustifolia* (from Barros *et al.*, 2015), estimate the time it would have taken an *A. angustifolia* population to migrate from there to its furthest modern extent (300 km, 14,000 years), and note that, without human help, the species could not have covered the observed distances in the 4,000 years that have elapsed since *Araucaria* pollen began expanding in six highland pollen cores (Behling, 1995, 1997b; Behling, Bauermann and Neves, 2001; Behling *et al.*, 2004). There are a number of problems with this approach.

Firstly, the refugium identified by Barros et al. (2015) may be irrelevant for this study. The authors only examined areas above 900 m elevation, which would automatically rule out the identification of refugial areas in the lower-elevation western areas of the plateau. The refugium was also delimited on the basis of being suitable for *A. angustifolia* at the Last Glacial Maximum – but Araucaria trees are adapted to cool, moist conditions, and the cold, wet LGM probably presented the species with a less stressful climate than the warmer, drier and more seasonal start of the Holocene (Cruz *et al.*, 2007; discussed in Wilson *et al.*, 2021). At some of the most stressful times in the late Quaternary, therefore, *A. angustifolia* populations may well have sheltered somewhere else entirely, completely changing the estimates of required dispersal distance and time.

Crucially, there is published palaeoecological evidence that shows that, from early in the Holocene, *A. angustifolia* populations were well established much closer to the western extreme of the species' modern extent than the sites and putative refugium used by Lauterjung *et al*. (2018). The Buriti/Pato Branco site (Bertoldo, Paisani and Oliveira, 2014) has some of the region's highest *Araucaria* pollen percentages – and possibly therefore some of the largest *A. angustifolia* populations – through much of the Holocene, and is located in south-western Paraná (S3.3, S4.2). The Buriti site is of particular interest because it is the only long pollen record in the centre-west of the plateau (see Wilson *et al.*, 2021), but it cannot be assumed that other unstudied areas of the highlands would not also show established, expanding or retreating *A. angustifolia* populations at times or in places not covered by the half-dozen well-known pollen records used here (S4.2).

In summary, contrary to the conclusions of Lauterjung *et al.* (2018), there is no need to invoke human dispersal to explain the modern extent of *A. angustifolia* populations – climatic causes and unacknowledged past populations provide the better explanation.

- Dos Reis *et al*. (2018) (cited in quote 11). This study looks at modern managed/cultural landscapes in modified Araucaria Forest, characterising the human-environment interactions focused on three useful species, Araucaria, erva mate (*Ilex paraguariensis*) and caraguatá (*Bromelia antiacantha*). Genetic analyses of the three species are also conducted. All the interviewed smallholders see Araucaria trees as the landscape's defining feature, connected with a sense of regional identity, but not commercially important on their own. The species are protected, promoted, managed and used to different extents, and there are traces of incipient domestication activities for all three species, though these are strongest and most evident in the selection and growth of caraguatá hedges. With the species' genetic diversity effectively conserved in these manged landscapes, the authors suggest they represent a functional 'conservation-by-use' system (a finding echoed by Zechini *et al.*, 2018). However, these activities are all contemporary and undertaken by smallholders; the study does not consider pre-colonial or Indigenous relationships with the land (and, in examining systems in which cattle have a central role, the extent to which comparisons can be extended is somewhat limited).
- de Oliveira Portes *et al*. (2018) (not cited above). Unlike the other studies discussed here, de Oliveira Portes *et al*. (2018) appears never to have been cited in support of claims that pre-colonial Indigenous people shaped Araucaria Forests. This is somewhat surprising, because it provides very clear evidence that Indigenous people used fire to maintain the Araucaria Forest-Campos mosaic in south-eastern Brazil's Serra da Bocaina. High fire frequencies about 700 years ago are associated with low forest pollen percentages, despite conditions

favourable for forest expansion (S4.2). Forest areas (especially with *Podocarpus*) were able to expand after European arrival decimated Indigenous populations, reducing the incidence of fires. When colonial settlement reached the Serra da Bocaina, fires returned to higher levels (though still lower than previously), which in turn resulted in increased Campos pollen. The study shows neither anthropogenic forest expansion, however, nor notable impacts of humans on forest composition, and *Araucaria* pollen is rare throughout, reaching a maximum contribution of just 0.7%.

- Mello & Peroni (2015) (cited in quote 12). This study examines the modern cultural landscapes of caívas, a traditional managed landscape of natural forest canopy with extensive (cattle) grazing on native or naturalised pastures in the understorey. Caívas, and the related faxinais landscapes, arose during the 19th Century as ways of producing erva mate (*Ilex paraguariensis*) and rearing cattle. Landowners undertake a range of management actions, most commonly collecting firewood, raising cattle, trimming or mowing herbs, and pruning, collecting and planting erva mate. As with the landscapes examined by dos Reis *et al*. (2018, see above), the caívas in this study are undoubtedly the product of deep human-environment relationships in the Araucaria Forest region, but they are not directly related to pre-colonial use or domestication of the forest by Indigenous people, and any attempts to link the two by analogy would require careful consideration.

- Dos Reis *et al*. (2014) (cited in quotes 1, 3, 4, 5, 6, 9, 11, 12 and 17, excerpts in quotes 18-20). In our non-exhaustive survey of studies describing Araucaria Forest as domesticated, no paper is used as supporting evidence more frequently than this. After Robinson *et al*. (2018), it provides the most compelling suite of evidence for Indigenous people having shaped Araucaria Forests in pre-colonial times. Jointly examining Brazil's *Araucaria angustifolia* and its Patagonian/Andean sister species *A. araucana*, the authors synthesise existing ecological, archaeological, palaeoecological, and ethnobotanical knowledge (no new data is included) to conclude that Araucaria forests on both sides of South America are culturally important with long histories of having been shaped by people – including, in their view, having been expanded by human actions.

  The authors highlight a range of reasons why high cultural value of Araucaria forests should be expected: millennia-long coexistence between Indigenous societies and the forest ecosystems; Araucaria forests' evident cultural importance to historical and contemporary Indigenous and non-Indigenous groups; and ecological traits which favour human use of the Araucaria trees – high seed productivity for food, sufficient adaptability to share a range of environments with people, the ability to regenerate in open or disturbed environments, and gravity-mediated seed dispersal that makes their collection easier.

  This study demonstrates why it is reasonable – even sensible – to suppose that southern Jê (and possibly Guarani) groups significantly manipulated Brazil's Araucaria Forests; in this way, it builds on the more focused observations of Bitencourt and Krauspenhar (2006), discussed below. What the study does not specifically show, however, is supportive palaeoecological evidence attesting to this manipulation. The authors cite Bauermann *et al*. (2008) and Behling and Pillar (2007) in support of their description of (probably anthropogenic) fires increasing at the same time as Araucaria Forest's expansion, but although both papers discuss fire and the highland ecosystem, they do not actually support this interpretation. Behling and Pillar's (2007) discussion of past fire dynamics in the late Holocene highlands draws heavily on the Cambará do Sul record (Behling *et al.*, 2004), which in fact shows that Araucaria Forest increases were most clearly associated with decreases in burning (fig. 3e, S4.2, fig. S4.2.6). The São Martinho da Serra record (Bauermann *et al.*, 2008) is located slightly south of the plateau in Seasonally Deciduous Forest, has low forest pollen throughout (making responses to changes in fire hard to see) with *Araucaria* pollen extremely low or absent (S4.2). No other primary palaeoecological research is cited. (Evidence for co-occurring increases in fire, Indigenous occupation, and Araucaria pollen has recently emerged for *A. araucana* in Patagonia; Nanavati *et al.*, 2020.)

In light of this, we suggest that dos Reis *et al*. (2014) can and should be interpreted as demonstrating why significant pre-colonial Indigenous influence on Araucaria Forests was likely, but not as providing direct evidence of its occurrence, or of past Araucaria Forest expansions having been caused or mediated by Indigenous people.

- Dos Santos *et al*. (2009) (cited in quotes 5 and 12). The authors conduct ethnobotanical research to investigate the traditional ecological knowledge (TEK) held by agricultural householders about feijoa (*Acca sellowiana*). They find evidence of feijoa's ongoing incipient domestication in southern Brazil, with various groups of respondents maintaining, managing, commercially cultivating or using feijoa trees and fruit. In a way, activities promoting the domestication of feijoa should not be a surprise – it is a widely appreciated, commercially important crop, cultivated on farms and in orchards, in Colombia, New Zealand and Australia (Evans, 2020).

  This paper is also the foundation for claims that feijoa – and occasionally, by extension, Araucaria Forest – was domesticated by Indigenous people in pre-colonial times. However, the study offers no direct support to this idea: the authors focus solely on modern TEK among non-Indigenous informants, with the more distant past, Indigenous land use, and their intersections all going unmentioned. For instance, Bogoni *et al*. (2018) attribute their assertion that "the expansion of FOM [Araucaria Forest] by pre-Columbian people (i.e., indigenous Xokleng and Kaingang) favored the expansion of Feijoa and other associated Myrtaceae" (p. 3, quote 10 above) to both dos Reis *et al*. (2014) and dos Santos *et al*. (2009), but dos Reis *et al*. (2014) do not mention past changes in Myrtaceae populations and dos Santos *et al*. (2009) do not mention palaeoecology or Indigenous people at all. In addition, because of the morphological similarity of *Acca* pollen to grains of other Myrtaceae trees (especially in degraded fossil records), it might not even be possible to observe the past expansion of feijoa specifically.

- Bauermann *et al*. (2008) (cited in quote 19). See discussion of dos Reis *et al*. (2014).

- Behling & Pillar (2007) (cited in quote 19). See discussion of dos Reis *et al*. (2014).

- Bitencourt and Krauspenhar (2006) (cited in quotes 3, 4, 5, 6, 12 and 17). A synthesis of then-established and -emerging ecological, archaeological and palaeoecological research, similar to but smaller in scope than dos Reis *et al*. (2014), this study was among the first to highlight the accumulating evidence indicating a potential human cause for Araucaria Forest expansions in the Common Era. As the authors recognise, such a relationship had been hypothesised decades before by Aubreville (1948) in an attempt to explain how Araucaria Forests had canopies overtopped by abundant, large, mature Araucaria trees yet also very limited recruitment. Aubreville's suggestion was that Indigenous fire use had previously encouraged *A. angustifolia* regeneration by keeping the forest understorey open; the dense, angiosperm-dominated lower and middle forest strata depressing *A. angustifolia* regeneration would therefore have developed as a consequence of Indigenous depopulation in recent centuries.

Similar to dos Reis *et al*. (2014), this study demonstrates why it is reasonable to suggest that Indigenous communities played an important role in shaping pre-colonial Araucaria Forests – it is one of the earliest studies to suggest the hypothesis. The authors, however, are far more cautious in their interpretations of the correlations between archaeological and palaeoecological evidence than are many of the statements which cite them. They speak of "the **possible** contribution of man" to Araucaria Forest expansions, and how the peak of those expansions "**might** also reflect the influence of human action"; indeed, even the paper's title is qualified as "**Possible** prehistoric anthropogenic effect on *Araucaria angustifolia* […] expansion during the late Holocene" (Bitencourt and Krauspenhar, 2006, p. 109 and 114, emphasis added). The value of such circumspection in interpreting correlations like this is illustrated by Iriarte and Behling (2007), who, contrary to the original authors and most of the studies quoted in this review, instead draw a plausible causal relationship from forests to people, suggesting that expanded Araucaria Forests provided the resources which fuelled the cultural flourishing of the southern Jê.

- Behling *et al*. (2004) (cited in quote 4). See discussion of dos Reis *et al*. (2014).
- Kern (1998) (cited in quote 4). This paper reviews then-current ethnographic and archaeological evidence on human occupations in the southern Atlantic Forest, but appears not to discuss any direct evidence of pre-colonial ecosystem transformation by humans.

Since Bitencourt and Krauspenhar (2006) published their hypothesised link between the southern Jê's growth and Araucaria Forest expansions in the late Holocene, significant archaeological and palaeoecological advances have been made; we now have more and better data on the Araucaria Forests' past and the development of the southern Jê culture (see Corteletti and Iriarte, 2018, for archaeology; and this study or Wilson *et al.*, 2021, for palaeoecology). However, few studies have tried to combine both by design (cf. Mayle and Iriarte, 2014) – Robinson *et al.* (2018) is the standout exception – with the result that the separate lines of evidence are still more often brought together using broad correlations than definitive causal links. Recent attempts to use other methods to address the question have had (occasionally significant) flaws. Evidence of modern human-environment relationships in Araucaria Forest could, with nuance and caveats, help us understand how past land use may have shaped the ecosystem, but too often these findings have been interpreted directly and uncritically as being representative of different Indigenous societies in a very different pre-colonial temporal context.

As a result, although the view of modern Araucaria Forests as pre-colonial Indigenous cultural landscapes is widespread, it remains a position supported by little direct evidence. Believing that such evidence will emerge remains a fundamentally well-reasoned stance: the multiple strands of favourable ecological, cultural, archaeological and palaeoecological research put forward by dos Reis *et al.* (2014) and Bitencourt and Krauspenhar (2006) cannot be rejected wholesale, and suggest that major past human impacts on Araucaria Forest are plausible, perhaps even probable. But our review of the current evidence undoubtedly shows that such connections have yet to be proven beyond doubt. The findings of Robinson *et al*. (2018) come closest to settling the debate, but the uncertainties we highlight around the study's core assumption emphasise how further research can help better account for potential natural drivers of the observed changes, integrate a wider array of the existing data, and provide clarity on when, where, how, and to what extent the southern Jê shaped Brazil's Araucaria Forests over recent millennia. The research we present in our present study aims to do just this.

S3. Supplementary methods

S3.1. Palaeoclimate data

Median Absolute Deviation (MAD) is a robust measure of climate (here, precipitation) variability, identifying sudden or large-amplitude deviations from a moving normal. Sub-annual trace element ratio data from Botuverá (Bernal *et al.*, 2016; https://www.ncdc.noaa.gov/paleo-search/study/21060) was first aggregated to decadal resolution, since MAD is sensitive to the number of observations in a time window. (The record's relatively coarse, multi-decadal stable isotope ratios were therefore not used.) Observations that were at least three times above or below the 100-year moving median proxy value were treated as outliers, which Riris and Arroyo-Kalin (2019) identify as a conservative threshold for extreme outliers. The anomaly count in 100-year bins was summed across the three trace element proxies, and this anomaly count was compared to the standard deviation of the dataset mean. Riris and Arroyo-Kalin (2019) suggest time bins with an anomaly count more than two standard deviations above the mean represent periods with significantly more variable rainfall than normal.

S3.2. Ecological niche modelling

S3.2.1. Locality data

For ecosystem-level models, a regular grid of points spaced 0.1° apart was set within the training data extent, and this was compared with data on remnant natural vegetation areas. For this, we used data from MapBiomas collection 4 (Souza *et al.*, 2020) (actual vegetation) and Macrocaracterização dos Recursos Naturais do Brasil (MRNB; IBGE - Instituto Brasileiro de Geografia e Estatística, 2019) (potential natural vegetation). The MapBiomas project is a multi-institutional initiative to generate annual land use land cover maps based on automatic classification processes applied to satellite images (the complete project description can be found at http://mapbiomas.org). We used MapBiomas data from 1985, since it includes greater areas of natural vegetation than more recent data points (though still much reduced from pre-colonial baselines), aggregated from 30m to 100m resolution. Grid points were considered 'present' if they: a) occurred in the Atlantic Forest biome; b) were classed as 'natural forest' (for Araucaria Forest) or 'natural grassland' (for Campos) in the MapBiomas data; and c) occurred in relevant areas (including ecotones) under the MRNB classification – E/EM/EN/M for Campos and E/EM/M/NM/OM/SM for Araucaria forest, where 'E' is 'estepe' (Campos), 'M' is 'floresta ombrófila mista' (Araucaria Forest), and letter pairs are ecotones with other vegetation types. Araucaria Forest's natural distribution extends into north-eastern Argentina, which is not covered by either MRNB or MapBiomas for 1985; here we considered points within the Araucaria Moist Forests WWF ecoregion (Olson *et al.*, 2001) with medium or high forest landscape integrity (Forest Landscape Integrity Index >6) (Grantham *et al.*, 2020) as presences.

We used two different approaches of translating non-presence grid points to absences for the modelling algorithms that required them (fig. S3.2.1.1, S3.2.3). The 'all absences' approach interpreted any point that did not qualify as a presence as a true absence. This included points that lack natural vegetation because of recent human-caused habitat change, rather than topoclimatic unsuitability, so could introduce inaccuracies. We therefore also employed a 'natural absences' approach, where the only non-presence points interpreted as absences were those that fell outside the relevant MRNB vegetation region or occurred in areas of other natural vegetation in the MapBiomas data. In contrast to the all-absence approach, the natural-absence approach is less affected by anthropogenic habitat loss, but does omit points where the absence of Campos or Araucaria Forest is the result of real (and informative) topoclimatic preference. We include both strict and permissive (respectively) approaches, acknowledging that each likely captures a different subset of 'true' absences and that the 'correct' answer, if it could be found, likely lies somewhere between the two.

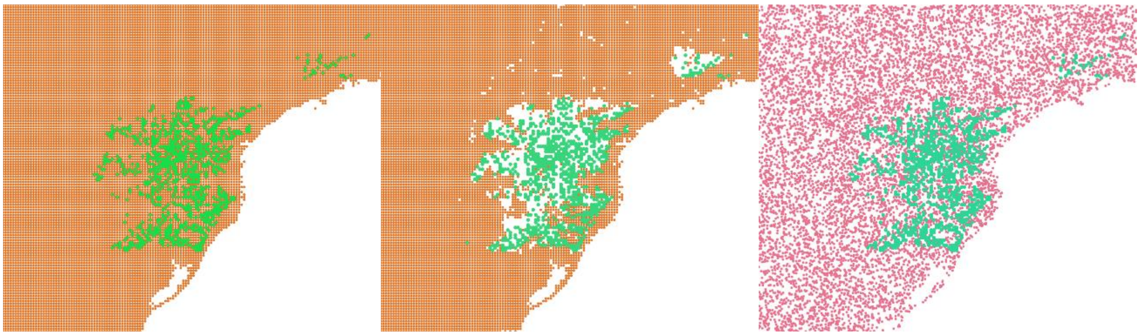


Figure S3.2.1.1: Maps showing the approaches to presence (green), absence (orange) and background (purple) data points, illustrated using Araucaria Forest: all absences (left), natural absences (centre), and random background (right). The presence-absence approaches (left and centre) were used to train ecosystem-level Random Forest models, and the presence-background approach (right) was used for the Maxent algorithm in both ecosystem- and species-level models (but note that ecosystem- and species-level Maxent models used different sources of presence points).

For the modelling of key species, we identified 10 important Campos species (Andrade *et al.*, 2019) and 20 tree species with high importance in different parts of Araucaria Forest's range (Klein, 1975; Universidade Federal de Santa Maria, 2001; Roderjan *et al.*, 2002; Schorn *et al.*, 2012; Oliveira-Filho *et al.*, 2014) (table S3.2.1.1). Additionally, we elected to model five further highly important species important from each of Atlantic Rainforest and Seasonally Deciduous Forest (Schorn *et al.*, 2012) since, in the present day, these forests sit on a floristic continuum rather than being sharply divided and their compositions (and therefore distinctions between them) may have differed significantly in the past (Wilson *et al.*, 2021). Analysing this suite of species allows us to discern changes both within and between Campos, Araucaria Forest, and other formations, including the development of forest communities that may not fit well with modern forest classifications. Pre-processed locality data for tree species was taken from Zweiner *et al.* (2017), derived in turn from the Neotropical Tree Communities database (de Lima *et al.*, 2015). Locality data for Campos species was downloaded from SiBBr/ALA (https://bit.ly/2PqTd5X) and coordinates were cleaned using the 'CoordinateCleaner' R package (Zizka *et al.*, 2019). Following Brown *et al.* (2020), we thinned these occurrence records so that only one coordinate remained within every 20 km radius, using the R package 'spThin' (Aiello-Lammens *et al.*, 2015).

Species	**Pres. Pts.**	**AUC**	**Boyce Index (Spearman correlation)**	**Seasonally Deciduous Forest**	**Araucaria Forest**	**Campos**	**Atlantic Rainforest**
Alchornea triplinervia	184	0.807	0.986				Y
Alsophila setosa	74	0.827	0.945				Y
Andropogon lateralis	86	0.854	0.891			Y	
Araucaria angustifolia	79	0.851	0.980		Y		
Baccharis crispa	234	0.821	0.949			Y	
Blepharocalyx salicifolius	173	0.805	0.969		Y		
Casearia sylvestris	370	0.754	0.949	Y			
Cedrela fissilis	211	0.758	0.954	Y			
Chaetogastra gracilis	66	0.734	0.807			Y	
Cinnamodendron dinisii	35	0.874	0.831		Y		
Clethra scabra	166	0.837	0.985		Y		
Cupania vernalis	238	0.770	0.949	Y	Y		
Cyathea phalerata	98	0.889	0.871				Y
Dicksonia sellowiana	104	0.880	0.962		Y		
Gamochaeta americana	50	0.833	0.855			Y	
Hieronyma alchorneoides	57	0.906	0.922				Y
Ilex paraguariensis	180	0.831	0.974		Y		
Lithrea brasiliensis	79	0.819	0.909		Y		
Luehea divaricata	241	0.756	0.975	Y	Y		
Machaerium stipitatum	156	0.766	0.904	Y			
Matayba elaeagnoides	194	0.719	0.994		Y		
Mimosa scabrella	120	0.837	0.919		Y		
Nectandra lanceolata	191	0.811	0.938	Y			
Nectandra megapotamica	279	0.798	0.993	Y	Y		
Ocotea porosa	103	0.901	0.907		Y		
Ocotea puberula	226	0.773	0.959	Y	Y		
Ocotea pulchella	269	0.765	0.970		Y		
Parapiptadenia rigida	166	0.788	0.965	Y			
Paspalum notatum	128	0.569	0.879			Y	
Paspalum	98	0.685	0.801			Y	

plicatulum							
Paspalum pumilum	50	0.894	0.952			Y	
Piptochaetium montevidense	64	0.905	0.565			Y	
Podocarpus lambertii	84	0.795	0.879		Y		
Psychotria vellosiana	180	0.867	0.877				Y
Schizachyrium microstachyum	88	0.787	0.897			Y	
Schizachyrium tenerum	50	0.887	0.851			Y	
Sebastiania commersoniana	142	0.793	0.963		Y		
Sloanea lasiocoma	73	0.836	0.924		Y		
Syagrus romanzoffiana	100	0.815	0.812	Y			
Vernonanthura discolor	83	0.894	0.976		Y		

Table S3.2.1.1: The 40 modelled species, the number of presence points used for training the Maxent models, their model evaluation scores, and the ecosystems in which each species has the most phytosociological importance.

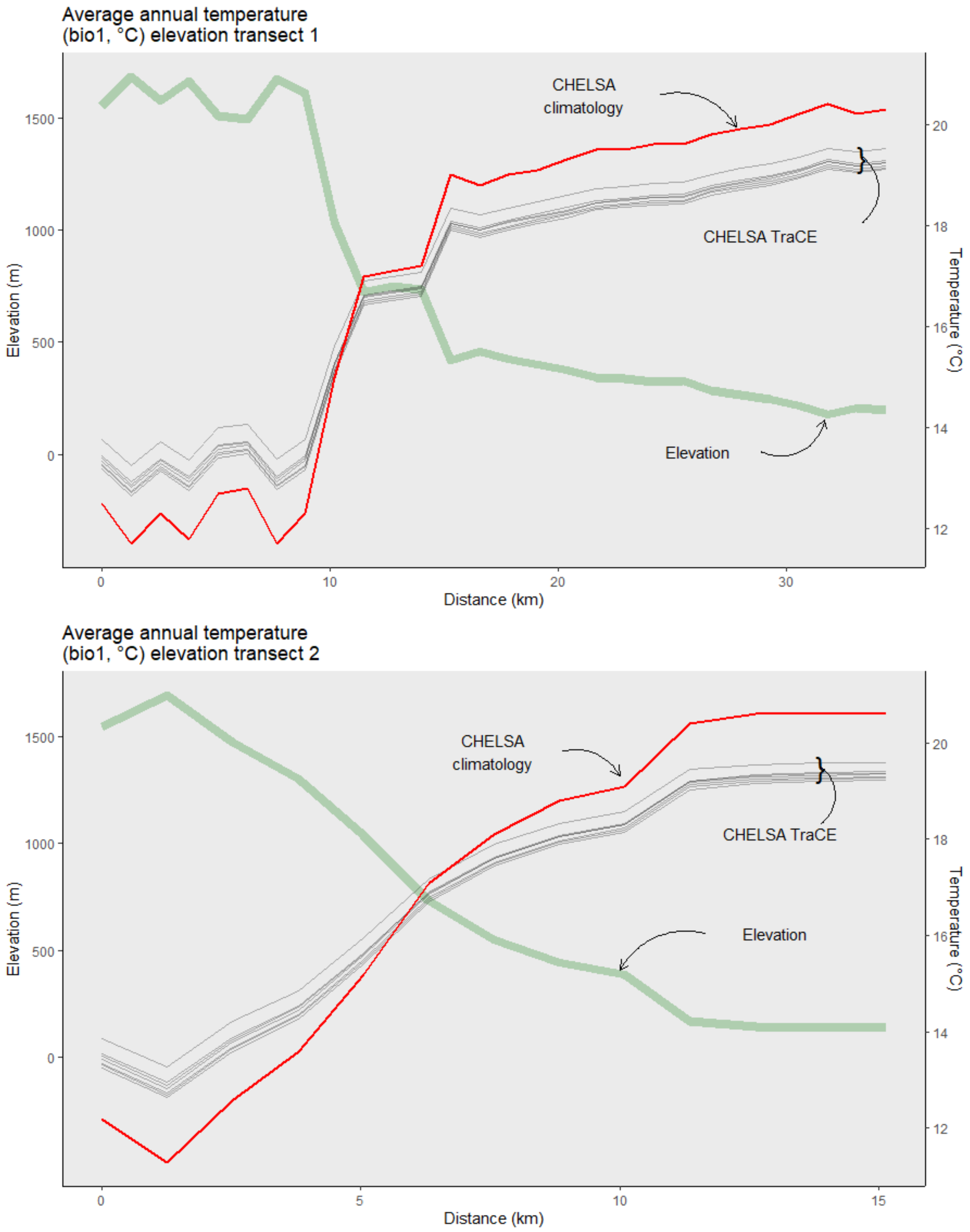
Ecosystem	**Model**	**AUC cross-validation**	**AUC set-aside evaluation**	**TSS cross-validation**	**TSS set-aside evaluation**	**Boyce Index (Spearman correlation)**
Araucaria Forest	Maxent	0.910	0.897	-	-	0.969
	RF all absences	0.947	0.946	0.818	0.814	0.994
	RF natural absences	0.954	0.977	0.845	0.881	0.999
Campos	Maxent	0.988	0.987	-	-	0.986
	RF all absences	0.993	0.978	0.970	0.924	0.975
	RF natural absences	0.997	0.990	0.986	0.903	0.982

Table S3.2.1.2: Evaluation metrics for ecosystem-level ENMs.

S3.2.2. Environmental data

Environmental data is drawn from two sources: CHELSA-TraCE downscaled palaeoclimate data (10.16904/envidat.211) (Karger *et al.*, 2017; Yannic *et al.*, 2020; Karger, 2021) (both species- and ecosystem-level modelling) and the ASTER Global Digital Elevation Model (v3) (NASA *et al.*, 2019) (ecosystem-level modelling only). The 30m ASTER data was aggregated to 100m resolution, then used to produce two layers, a topographic position index (TPI) and a measure of exposure to peak insolation. The topographic position index was calculated following Robinson *et al.* (2018), taking the difference between a cell's elevation and the average of its neighbours in a five-cell (500m) radius then standardising the output so it had a mean of 0 and standard deviation of 1. Positive TPI values indicate relatively high topographic position (e.g. ridges and plateaus) and negative values indicate depressions and valleys. Exposure to peak insolation (McCune and Keon, 2002; azimuth of 315°; McCune, 2007) was calculated as in Ashcroft *et al.* (2008) and Wilson *et al.* (2019).

For ecosystem-level modelling of Araucaria Forest and Campos, CHELSA-TraCE data was downscaled to 100m resolution through bilinear interpolation. Species-level modelling used CHELSA-TraCE data at its native 30” (ca. 800m) resolution. The CHELSA-TraCE palaeoclimate dataset consists of palaeoclimate data downscaled using the CHELSA algorithm (Karger *et al.*, 2017; Karger and Zimmermann, 2019) from 2.5° resolution to 30” (ca. 800m) (Karger, 2021). We projected models to 13 time slices covering 500-year intervals from 6,000 BP to the present; each period is averaged over 100 years. Compared to the CHELSA climatology (1979-2013), the CHELSA-TraCE data underestimates some sharp, ecologically important temperature gradients in our study area (such as across the highlands’ eastern escarpment) by up to 2°C, with these deviations remaining consistent through the last 6,000 years (fig. S3.2.2.1). We used a change factor approach to correct for these discrepancies, generating a correction layer (calculated as climatology/TraCE) for each monthly modern-day temperature layer and multiplying this with past CHELSA-TraCE temperature layers. Because they are less directly linked to elevation, precipitation layers were not corrected.


Average annual temperature (bio1, °C) elevation transect 1

Average annual temperature (bio1, °C) elevation transect 2

Figure S3.2.2.1: CHELSA-TraCE systematically underestimates temperature differences across steep elevation gradients (green) at two locations on the highlands' eastern escarpment. Average annual temperatures from CHELSA-TraCE from 6,000 BP to present (black) are compared to those from CHELSA's 1979-2013 climatology (red).

Bioclimatic variables were then generated from monthly precipitation and corrected temperature layers using the 'dismo' R package. Best practice in species distribution modelling requires that variables are biologically relevant and not closely correlated (Fourcade, Besnard and Secondi, 2017). We evaluated the 19 bioclimatic variables' multicollinearity using variance inflation factors, using the ‘vifcor’ function from the ‘usdm’ R package (Naimi *et al.*, 2014) and a correlation threshold of 0.75. This yielded eight ecologically relevant variables which describe the general trends and extremes of rainfall and temperature in our study area: bio2 (annual mean diurnal temperature range), bio4 (temperature seasonality), bio5 (maximum temperature of the warmest month), bio8 (average temperature of the wettest quarter), bio9 (average temperature of the driest quarter), bio12 (annual precipitation), bio14 (precipitation of the driest month), and bio18 (precipitation of the warmest quarter).

S3.2.3. Modelling

The F-ratios from the Boyce Index evaluation describe the predicted-to-expected ratios of different habitat suitability classes in model outputs. An F-ratio of 0.5 indicates there are half as many presence points in a predicted habitat suitability class as would be expected by chance (i.e. low-suitability habitat), an F-ratio of 1 suggests there are as many presences as would be expected (marginal habitat), an F-ratio of 2 indicates there are twice as many as would be expected (good habitat), etc. To compare our modelled predictions of Araucaria Forest and Campos, we converted habitat suitability values to F-ratios, reclassified areas with F-ratios <1 to zero (i.e. sub-marginal habitat to absences), incremented all values by 1 and log10 transformed them. We then subtracted the Campos values from those of Araucaria Forest to show changes in their relative suitability through time and space; this approach has particular value because large parts of our study area (including most palaeoecological proxy sites) show little change in their predictions of the presence or absence of either ecosystem over the last 6,000 years.

To analyse the changing compositions of southern Brazil’s ecosystems through the last 6,000 years, we clustered the outputs of our individual species models into a smaller number of predicted assemblages (cf. Wilson *et al.*, 2021). We first used k-means clustering in SAGA-GIS (k=10) on each time slice’s 40 species-level habitat suitability maps, which resulted in 130 predicted assemblages (13 time slices with 10 clusters each). Because each time slice was clustered independently, floristically similar clusters are likely to have been identified at different times. To combine these similar clusters/assemblages, we used the R package ‘pvclust’ to perform hierarchical clustering with p-values calculated over 10,000 bootstrap replications.

Four statistically significant clusters were identified (96-100% support), one of which encompassed most of the range of Araucaria Forest and Seasonally Deciduous Forest; this we split into four further subgroups (assemblages 1, 2, 4 and 6; 70-100% support) to better analyse ecologically meaningful compositional changes. The modelled assemblages relate to: Atlantic Rainforest (assemblage 3); Seasonally Deciduous Forest (assemblage 2); Araucaria-Seasonally Deciduous Forest ecotones (assemblage 4); Araucaria Forest with some Campos (assemblage 1); Campos with (higher-elevation) Araucaria Forest (assemblage 5); and high-elevation Araucaria Forest and Campos, with some more cold-adapted Atlantic Rainforest species (assemblage 7). Assemblage 6 is mostly representative of Araucaria Forest, containing elements of Araucaria Forest, Campos and Seasonally Deciduous Forest, but it is the cluster least well represented by our modelled species – in the modern day much of its distribution lies outside the Atlantic Forest biome our study focuses on. The assemblages, their modern distributions and their species compositions are illustrated in fig. S3.2.3.1.

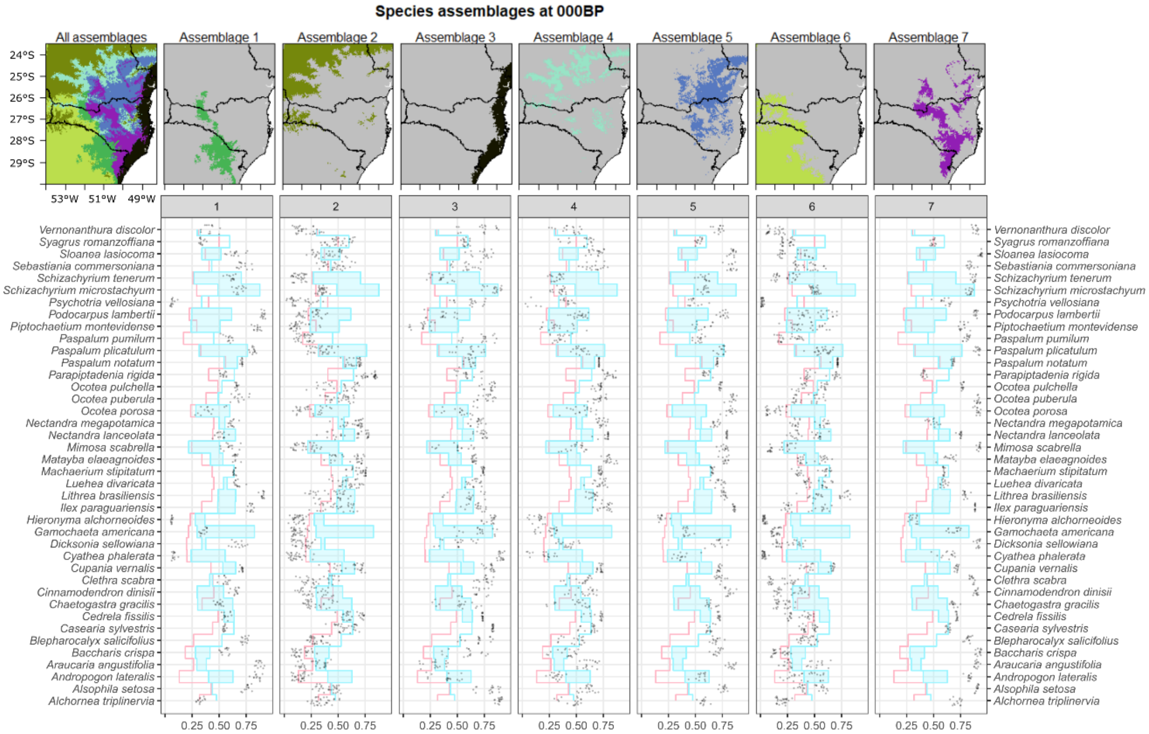
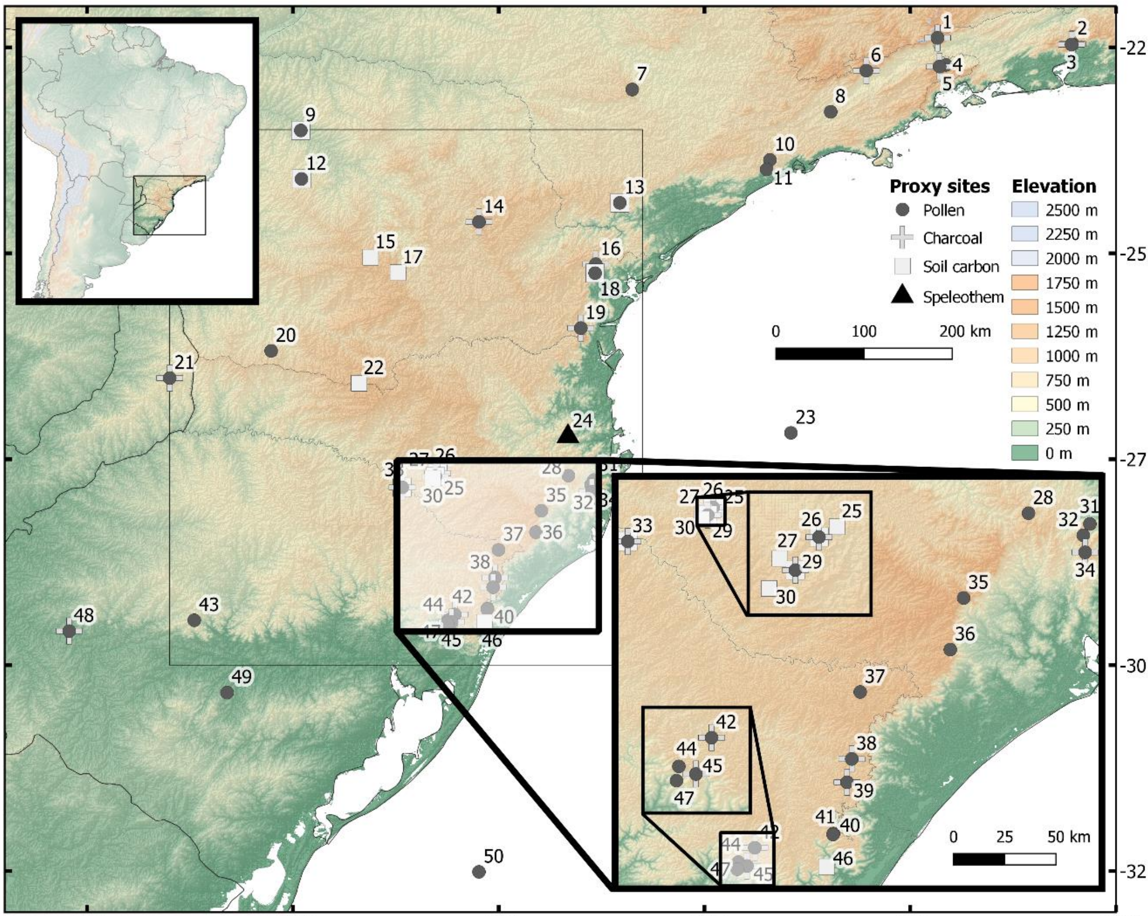


Figure 3.2.3.1: The predicted assemblages produced by the clustering analysis, their distributions in the present day, and their species-level compositions. In the lower part of the plot, dots show the modelled habitat suitability values (from low to high, left to right) for each species (rows) within each assemblage; red lines show the values above which 90% of species presence locations were found; and blue lines/zones indicate marginal habitat (the lowest and highest values with an F-ratio of 1). Species with more dots further to the right (left) of the red and blue lines/zones are more likely to be present in (absent from) a given assemblage.

S3.3. Palaeo-vegetation proxy synthesis

Where possible, we used raw data on proxy values – either included in original publications (Saia, 2006; Dümig *et al.*, 2008; Fernandes, 2009; Pessenda *et al.*, 2009; Scheer *et al.*, 2014; Fischer, 2015; Rasbold, Parolin and Caxambu, 2016b; Luz *et al.*, 2019) or in data repositories (Behling, 1995, 1997a, 1997b; Behling *et al.*, 2004; Ledru, Mourguiart and Riccomini, 2009; Gu *et al.*, 2017, 2018) (https://doi.pangaea.de/10.1594/PANGAEA.872561, https://doi.pangaea.de/10.1594/PANGAEA.872851, https://doi.pangaea.de/10.1594/PANGAEA.872855, https://doi.pangaea.de/10.1594/PANGAEA.888010, https://doi.org/10.17632/7gxn9g87cf.1, https://doi.org/10.21233/n39h81, https://doi.org/10.21233/n3jm87, https://doi.org/10.21233/n33q4q, https://doi.org/10.21233/n34924, https://doi.org/10.21233/n3848x) – but raw data are not available for the great majority of proxy records in the region. We therefore digitised proxy diagrams from the remaining studies, using Fiji/ImageJ (Schindelin *et al.*, 2012) to extract: the percentages of *Araucaria* pollen and the (most) relevant forest pollen group; counts or percentages of any potential cultigen pollen (e.g. *Zea mays*); δ^{13}C isotope values; and counts or concentrations of charcoal or charred particles. We constructed new age-depth models for all records using the 'rbacon' package (Blaauw and Christen, 2011; Blaauw *et al.*, 2020) and the SHCal20 (Hogg *et al.*, 2020) and Marine20 (Heaton *et al.*, 2020) calibration curves for terrestrial and marine sites, respectively. Where sites had no date within the last 1,000 years, we followed Wilson *et al.* (2021) and added a surface date of -54 ± 15 cal years BP (i.e. 1991-2019 AD), a period which encompasses the extraction dates of almost every core in our synthesis.

The requirement for included records to have two dates represents a comparatively low bar for chronological quality (Flantua, Blaauw and Hooghiemstra, 2016; Smith and Mayle, 2017; Wilson *et al.*, 2021), but even so several records (mainly $\delta^{13}C$ isotope records or sites from older studies) failed to meet it. Raising the requirement to three dates would have excluded 10 more sites, including some with the most significant and relevant findings in the region. The resulting temporal uncertainty in many records of past Araucaria Forest-Campos dynamics has been little considered in the past, yet has a major bearing on our ability to interpret the timings of vegetation changes and their links with potential human and climatic drivers. We sought to address this by plotting records' proxy values in a way that incorporates the uncertainty in their age-depth models, adapting the 'rbacon' package's 'proxy.ghost' function (S4.2). Where a subsample falls in a well-constrained part of a core's age-depth model, it is plotted with a darker and more tightly focused line; where its age is more uncertain this appears fainter and more blurred. This approach helps to avoid the false impression of chronological precision that can arise when simply plotting proxy values against mean or median dates, and provides a more accurate – if less precise – picture of the timings of vegetation changes.



1: Agulhas Negras; 2: Serra dos Órgãos; 3: Vale das Antas; 4: Serra da Bocaina 2; 5: Serra da Bocaina; 6: Morro de Itapeva; 7: Serra de Botucatu; 8: Jacarei; 9: Lagoa Fazenda; 10: Colônia; 11: Curucutu; 12: Água dos Papagaios; 13: Lagoa Vermelha; 14: Serra Campos Gerais; 15: Turvo; 16: Morro Capivari Mirim; 17: Aroeiras; 18: Caratuva Peak PCII; 19: Serra do Araçatuba; 20: Buriti; 21: PP Cruce Caballero; 22: Coxilhao; 23: GeoB2107-3; 24: Botuverá BTV21a; 25: Heraldo; 26: Abreu e Garcia; 27: Baggio; 28: Serra da Boa Vista; 29: Amaral; 30: Luis Carlos; 31: Tabuleiro Summit; 32: Moor Mirante; 33: Pinhal da Serra; 34: Ciama 2; 35: Morro da Igreja; 36: Serra do Rio Rastro; 37: Cachoeira do Puma; 38: São José dos Ausentes; 39: Cambará do Sul; 40: Banhado Amarelo; 41: Serra das Pedras Brancas; 42: Fazenda do Pinto; 43: São Martinho da Serra; 44: Alpes de São Francisco 1; 45: Rincão das Cabritas; 46: CPCN Pro-Mata; 47: Alpes de São Francisco 2; 48: São Francisco de Assis; 49: Caçapava do Sul; 50: GeoB6211-2

Figure S3.3.1: Map of the synthesised palaeoecological sites and the proxies they record.

Site no.	Site name	Site code	Source(s)	Latitude	Longitude
1	Agulhas Negras	AguNe	(Behling, Jantz and Safford, 2020)	-22.385	-44.670
2	Serra dos Órgãos	SdOrg	(Behling and Safford, 2010)	-22.458	-43.028
3	Vale das Antas	ValAn	(de Oliveira Portes *et al.*, 2020)	-22.466	-43.041
4	Serra da Bocaina 2	SdBc2	(Behling *et al.*, 2007)	-22.714	-44.567
5	Serra da Bocaina	SdBoc	(de Oliveira Portes, Safford and Behling, 2018)	-22.734	-44.644
6	Morro de Itapeva	MdIta	(Behling, 1997a)	-22.783	-45.533
7	Serra de Botucatu	SdBot	(Bissa and de Toledo, 2015)	-23.012	-48.378
8	Jacarei	Jacar	(Garcia *et al.*, 2004)	-23.283	-45.967
9	Lagoa Fazenda	LaFaz	(Fernandes, 2009)	-23.509	-52.404
10	Colônia	Colon	(Ledru, Mourguiart and Riccomini, 2009)	-23.867	-46.706
11	Curucutu	Curuc	(Pessenda *et al.*, 2009)	-23.983	-46.746
12	Águas dos Papagaios	AgPap	(Ladchuk, Parolin and Bauermann, 2016; Luz *et al.*, 2019)	-24.098	-52.396
13	Lagoa Vermelha	LaVer	(Saia, 2006)	-24.388	-48.529
14	Serra Campos Gerais	SCaGe	(Behling, 1997b)	-24.619	-50.240
15	Turvo	Turvo	(Rasbold, Parolin and Caxambu, 2016a)	-25.049	-51.556
16	Morro Capivari Mirim	MCapM	(Heese, 2016)	-25.132	-48.820
17	Aroeiras	Aroei	(Silva, 2018)	-25.235	-51.224
18	Caratuva Peak PCII	CarP2	(Scheer *et al.*, 2014)	-25.241	-48.829
19	Serra do Araçatuba	SdAra	(Behling, 2006)	-25.908	-49.002
20	Buriti	Burit	(Bertoldo, 2010; Bertoldo, Paisani and Oliveira, 2014)	-26.185	-52.764
21	PP Cruce Caballero	CruCa	(Gessert *et al.*, 2011)	-26.515	-53.996
22	Coxilhao	Coxil	(Silva, 2018)	-26.578	-51.695
23	GeoB2107-3	GeB23	(Gu *et al.*, 2017)	-27.180	-46.450
24	Botuverá	Botuv	(Bernal *et al.*, 2016)	-27.223	-49.158
25	Heraldo	Heral	(Robinson *et al.*, 2018)	-27.659	-50.722
26	Abreu e Garcia	AbGar	This study	-27.671	-50.743
27	Baggio	Baggi	(Robinson *et al.*, 2018)	-27.696	-50.788
28	Serra da Boa Vista	SdBoV	(Behling, 1993, 1995)	-27.700	-49.154
29	Amaral	Amarl	This study	-27.709	-50.770
30	Luis Carlos	LuiCa	(Robinson *et al.*, 2018)	-27.730	-50.801
31	Tabuleiro Summit	TabSu	(Behling and de Oliveira, 2018)	-27.754	-48.844
32	Moor Mirante	Miran	(Jung, 2008)	-27.811	-48.878
33	Pinhal da Serra	PindS	This study	-27.842	-51.173
34	Ciama 2	Ciam2	(Jeske-Pieruschka *et al.*, 2013)	-27.897	-48.868

35	Morro da Igreja	MdIgr	(Behling, 1993, 1995)	-28.127	-49.481
36	Serra do Rio Rastro	SdRRa	(Behling, 1993, 1995)	-28.387	-49.548
37	Cachoeira do Puma	CaPum	(Fischer, 2015)	-28.600	-50.002
38	São José dos Ausentes	SJdAu	(Jeske-Pieruschka *et al.*, 2010)	-28.938	-50.044
39	Cambará do Sul	CamSu	(Behling *et al.*, 2004)	-29.055	-50.068
40	Banhado Amarelo	BanAm	(Scherer and Lorscheitter, 2014)	-29.313	-50.137
41	Serra das Pedras Brancas	SPedB	(Spalding and Lorscheitter, 2015)	-29.318	-50.138
42	Fazenda do Pinto	FazdP	(Behling, Bauermann and Neves, 2001)	-29.385	-50.533
43	São Martinho da Serra	SMadS	(Bauermann *et al.*, 2008)	-29.456	-53.698
44	Alpes de São Francisco 1	AdSF1	(Scherer and Lorscheitter, 2014)	-29.457	-50.616
45	Rincão das Cabritas	RidCa	(Jeske-Pieruschka and Behling, 2012)	-29.476	-50.573
46	CPCN Pro Mata	ProMa	(Dümig *et al.*, 2008; Silva and Anand, 2011)	-29.481	-50.172
47	Alpes de São Francisco 2	AdSF2	(Leonhardt and Lorscheitter, 2010)	-29.493	-50.622
48	São Francisco de Assis	SFdAs	(Behling, Pillar and Bauermann, 2005)	-29.587	-55.217
49	Caçapava do Sul	CacSu	(Behling *et al.*, 2016)	-30.333	-53.300
50	GeoB6211-2	GeB62	(Gu *et al.*, 2018)	-32.510	-50.240

Table S3.3.1: Information on the sites used in the palaeoecological synthesis: their number in figs. 1 and S3.3.1; name; code in the Supplementary Data folder; original publication; and coordinates. In some instances, published coordinates have been corrected based on maps or images in the original studies.

S3.4. New palaeoecological data

We present new multiproxy palaeoecological data from three sites toward the centre of southern Brazil's highland plateau. These records provide critical insights into previously un(der)investigated aspects of Araucaria Forest-Campos dynamics in two main ways. Firstly, the most intensely studied area in southern Brazil's highland region is its south-eastern corner, where 13 sites lie 20 km of the plateau's edge; the new sites are >130 km from the eastern escarpment, further from core Campos areas, closer to more contiguous Araucaria Forest, and in areas predicted to have experienced more dynamic past vegetation change (Wilson *et al.*, 2021). Secondly, the new locations are all extremely close (<1 km) to well-studied archaeological sites in the Canoas-Pelotas basin, which has the most archaeological evidence for pre-colonial southern Jê occupation of anywhere in the highlands (de Souza, Robinson, *et al.*, 2016). Conversely, the great majority of other palaeo-vegetation proxy records come from areas with far fewer archaeological sites, and no other pollen record has a close link with archaeological evidence.

S3.4.1. Site overviews

The three new sites – Abreu e Garcia, Amaral, and Pinhal da Serra – are peat bogs in small depressions, which were specifically selected to provide vegetation histories from landscapes known to have been occupied by southern Jê communities.

Abreu e Garcia (27.6710° S, 50.7431° W, 931 m elevation) is a 200 x 40 m bog within a shallow depression, located on a promontory >50 m above the surrounding landscape, and approximately

20 m away from two southern Jê funerary mound and enclosure complexes (MECs) (Robinson *et al.*, 2017). The surrounding catchment has gentle slopes ca. 5-10 m high, which are deforested and currently used for cattle pasture and a vineyard. The bog is oriented N-S and drains southward down a steep 30 m escarpment covered in mixed Araucaria woodland. A 50 cm core was collected with a Russian corer.

Amaral (27.7090° S, 50.7702° W, 867 m elevation) is a small 20 x 40 m bog within a shallow depression covered with grasses, sedges, and small woody shrubs. It is located about 800 m from a "large, dense, and well-planned" pit house settlement which was occupied without major abandonment for about 500 years until the late 18th Century (ca. 595-160 cal BP) (de Souza, Robinson, *et al.*, 2016; de Souza, 2018). The bog is located at the head of a valley and fed by small streams from the surrounded slopes, which are covered in a plantation of non-native pines (*Pinus* sp.). A 65 cm sequence of overlapping cores was collected with a Russian corer.

Pinhal da Serra (27.8421° S, 51.1728° W, 920 m elevation) is a small, circular, 50m diameter bog, located in a horseshoe-shaped basin surrounded by 10 m high slopes and with a single out-flowing stream. The bog is surrounded by agricultural fields and lies approximately 40 km south-west of the Abreu e Garcia and Amaral sites. It is located only 200 m away from a pit house village and 500 m away from an MEC. A 200 cm sequence of overlapping cores was collected with a Russian corer.

S3.4.2. Radiocarbon dating

Site	Lab code	Depth (cm)	Uncalibrated age BP/pMC	Calibrated age BP 2σ
Abreu e Garcia	Beta-436684	4-4.5	100.9 pMC ± 0.3	Modern
	Beta-457741	6.5-7	890 ± 30	728-906
	Beta-441944	10-10.5	2,070 ± 30	1,942-2,118
	Beta-457740	15-15.5	2,370 ± 30	2,338-2,490
	Beta-441945	20-20.5	4,200 ± 30	4,620-4,884
	Beta-441947	30-30.5	5,320 ± 30	5,997-6,257
	Beta-436685	34-34.5	4,930 ± 30	5,594-5,720
Amaral	Beta-457742	9.5	106.7 pMC ± 0.4	Modern
	Beta-441947	15	690 ± 30	562-678
	Beta-457743	17	880 ± 30	723-905
	Beta-457744	27	1,520 ± 30	1,314-1,515
	Beta-441948	30	3,710 ± 30	3,933-4,150
	Beta-457745	34.5	3,220 ± 30	3,376-3,482
	Beta-420641	60	7,853 ± 30	8,547-8,767
Pinhal da Serra	Beta-461673	10	107.2 pMC ± 0.4	Modern
	Beta-411674	30	1,000 ± 31	796-959
	Beta-401728	45	2,220 ± 30	2,146-2,334
	Beta-405341	90	9,800 ± 40	11,176-11,266
	Beta-405342	140	22,720 ± 90	26,486-27,278
	Beta-401729	192	34,200 ± 270	38,535-40,000
	Beta-405343	195	34,770 ± 200	39,470-40,466

Table S3.4.3.1: Radiocarbon dates obtained for the new sites in this study (pMC = percent modern carbon; BP = before radiocarbon present, i.e. 1950 AD).

Age-depth models were constructed in 'rbacon' using the SHCal20 calibration curve (Blaauw and Christen, 2011; Blaauw *et al.*, 2020; Hogg *et al.*, 2020). A present surface date (see S3.3) was added to constrain the upper parts of the models and prevent overshoot (S4.3).

S4. Supplementary results

S4.1. Exceptions to general trends in *Araucaria angustifolia*'s late-Holocene dynamics

In most of the region's palaeoecological records, *A. angustifolia* pollen reaches its highest percentages in the last 2,000 years, though it is not commonly a major component of the pollen spectra (S4.2). The clearest exceptions to these observations are Buriti (Bertoldo, Paisani and Oliveira, 2014), Águas dos Papagaios (Ladchuk, Parolin and Bauermann, 2016) and Lagoa Fazenda (Fernandes, 2009), all found in the centre- and north-west of the Araucaria Forest's present range (S4.2). (PP Cruce Caballero (Gessert *et al.*, 2011), in Misiones, Argentina, is similarly located but only covers the last 2,000 years; *Araucaria* pollen is rare throughout but is highest in the last 500 years.) All three sites record relative highs of *A. angustifolia* close to the mid-Holocene, with declines over time. At Buriti, *Araucaria* pollen at times exceeds 20% of the total – a proportion only matched by two sites (Cambará do Sul, Behling *et al.*, 2004; Amaral, this study), both in the last millennium.

There is currently no consensus on where (or indeed if) extensive areas supporting large *A. angustifolia* populations could have been found before the last millennia of the Holocene; the topic is rarely discussed. The differences between these three sites and those further south and east suggest that, until the late Holocene, *A. angustifolia* may have had one or more strongholds in the west of its current range, rather than being confined to refugia in the better-studied south-eastern plateau as has previously been hypothesised (Stefenon *et al.*, 2008, 2019; Barros *et al.*, 2015; Bernardi *et al.*, 2020; Souza, 2021; Wilson *et al.*, 2021). The western reaches of Araucaria Forest's present range have been much less investigated than south-eastern areas with Campos near the plateau's edge – the many important insights they could hold (see also Wilson *et al.*, 2021) should make them a priority for future palaeoecological research.

S4.2. Additional palaeo-vegetation synthesis results

The grids below show each synthesised proxy site's records. Proxy time series are shown as 'proxy ghost' plots (from the R package 'rbacon') – these blur the records according to the level of uncertainty in their site's age-depth model (see S3.3). Rows are in approximate latitudinal order (north to south), and sites are in approximate longitudinal order (west to east) within each row; sites in the same column are generally not found at similar longitudes. Each site is found at the same position in each grid, except when one location has more than one δ^{13}C or charcoal record – in these cases, neighbouring panels in the grid have also been used, and the site's records are outlined with a dashed grey line. The grids, individual sites' panels, and the age-depth models they are based on can all be viewed separately in the Supplementary Data folder.

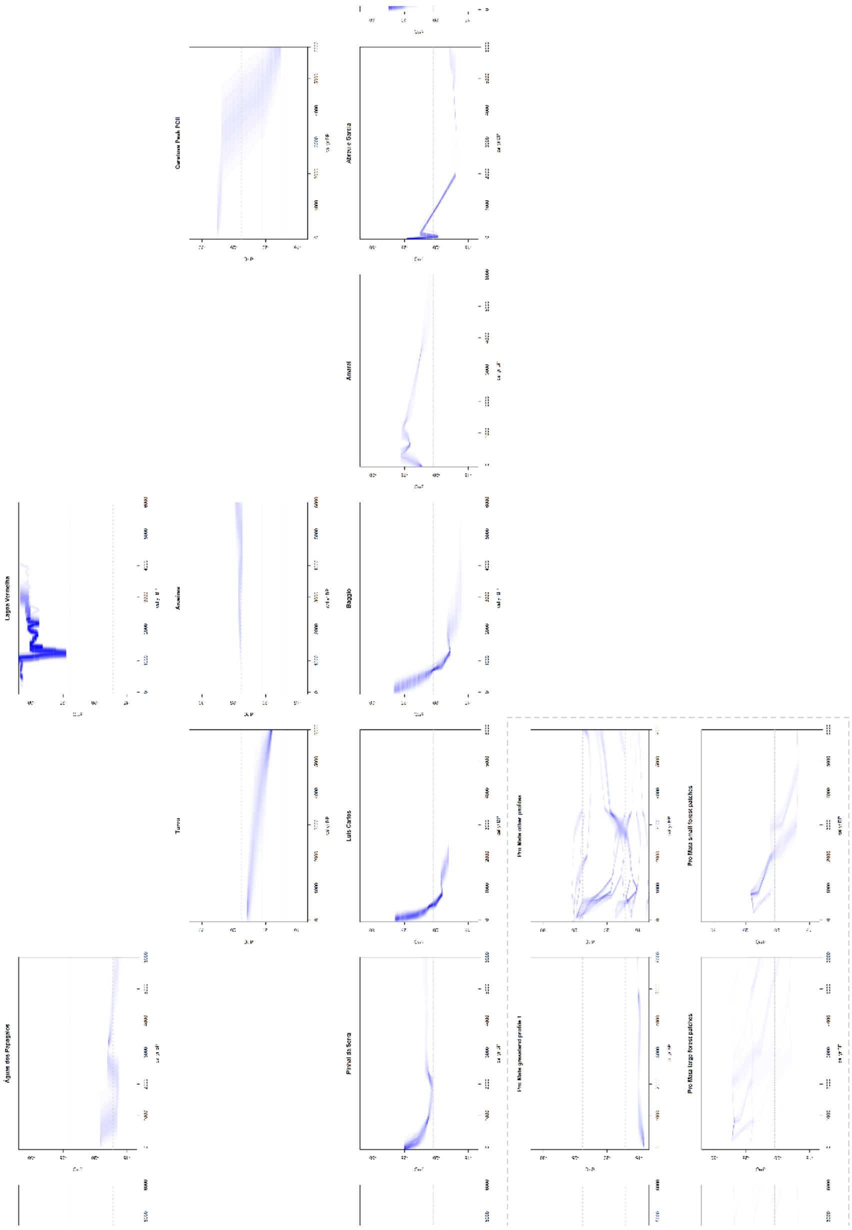


Figure S4.2.1: Synthesised $\delta^{13}C$ records. The dashed line indicates approximately equal C_3-C_4 contributions, with the dotted lines illustrating values where approximately 75% of the soil organic carbon is derived from Campos species/C_4 photosynthesisers (lower) and Araucaria Forest species/C_3 photosynthesisers (upper). These values are based on equations from Dümig et al. (2008) and are intended to be illustrative rather than definitive.

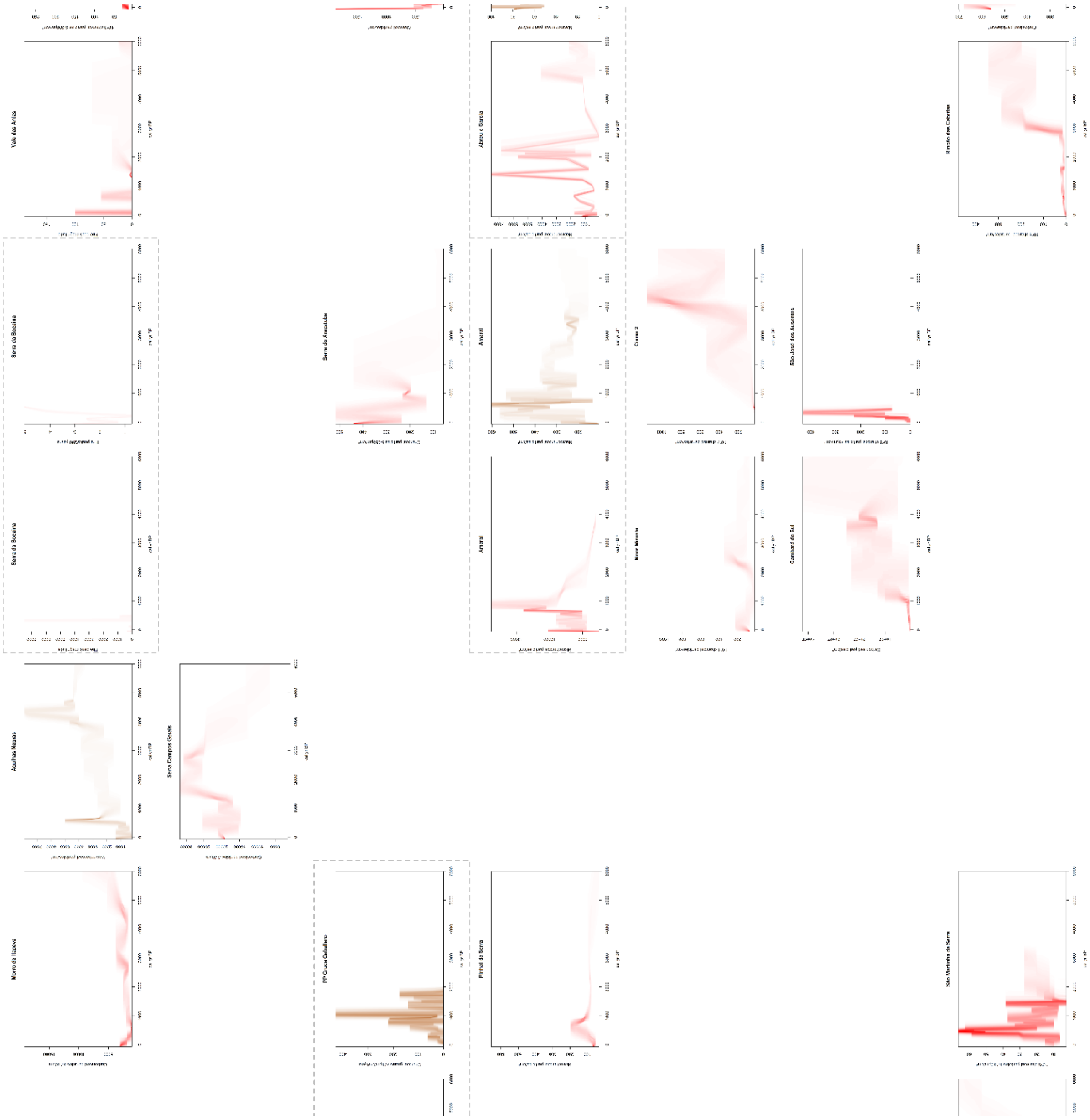


Figure S4.2.2: Synthesised fire records. Macrocharcoal records are in brown, with other records in red; the sizes of charcoal particles counted are often not specified, and even when specified they vary between studies, so plots in the same colour are not necessarily counting the same thing.

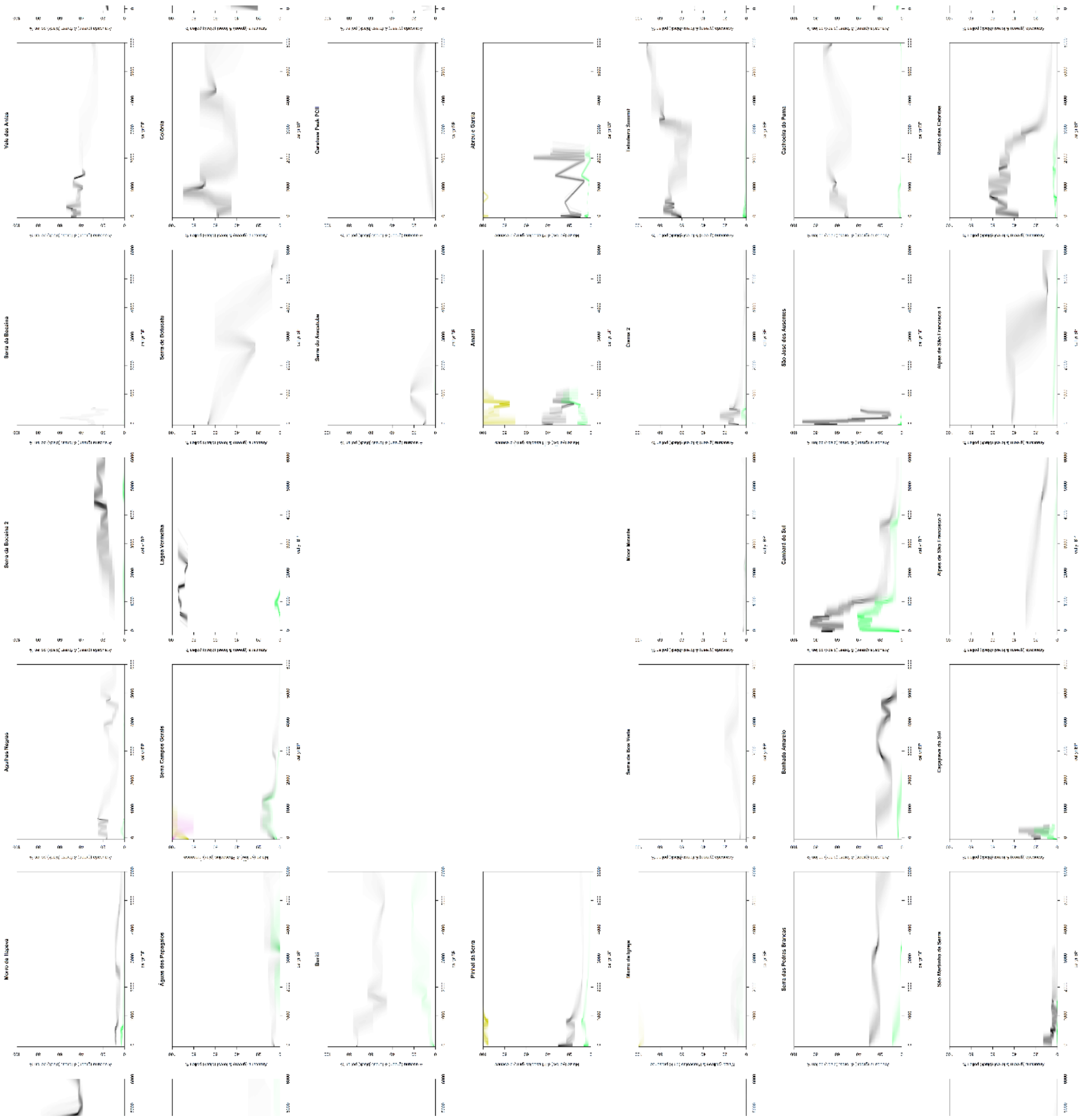


Figure S4.2.3: Synthesised pollen records. Black and green lines show forest and Araucaria pollen percentages respectively. The inverted yellow and purple lines indicate the presence of cultigen pollen (maize (Zea mays) and beans (Phaseolus), respectively); these are not percentages – rather, counts are multiplied by five and subtracted from 100% for visualisation (i.e. a value of 100 indicates absence and 90 that two pollen grains were counted).

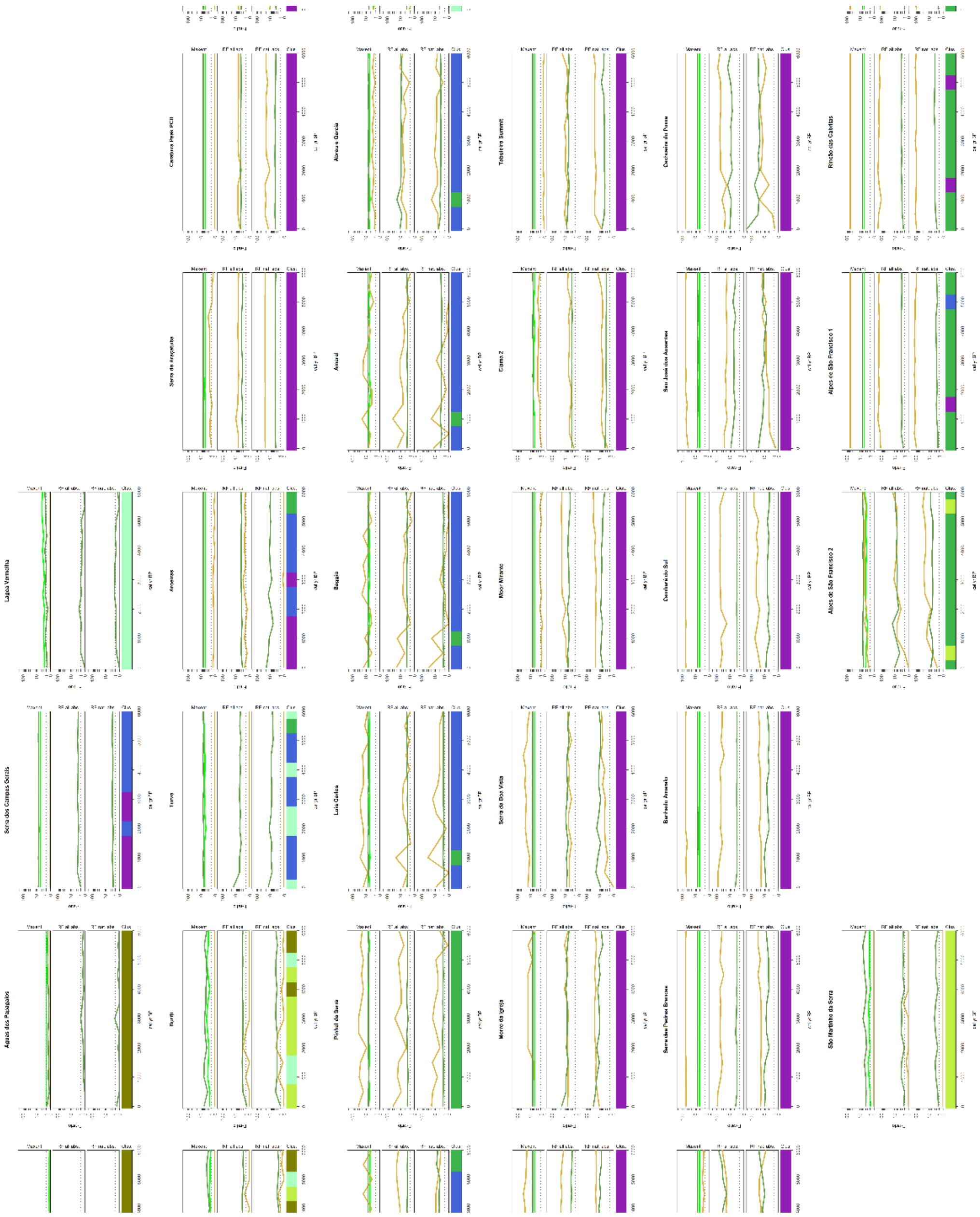


Figure S4.2.4: ENM results for the pixels containing the proxy sites. Dark green lines represent Araucaria Forest, gold lines represent Campos, and bright green lines represent Araucaria angustifolia (Maxent only). The top row in each panel shows results from Maxent models, the middle row from all-absence RF models, and the bottom row natural-absence RF models. Y-axes are F-ratios (see S3.2.3) on a logarithmic scale; an F-ratio of 1 (dotted lines) can be considered the threshold of marginal habitat suitability. The coloured bars along the bottom of each panel show modelled composition (see S3.2.3 for interpretation).

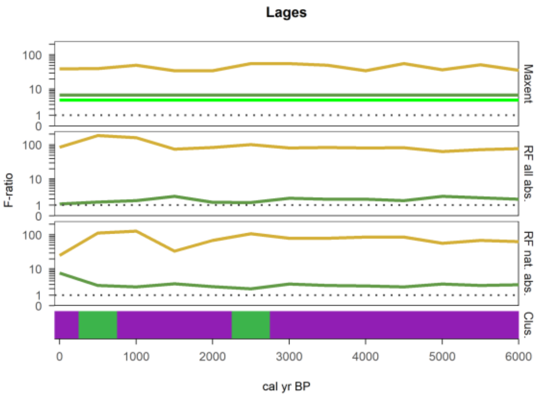
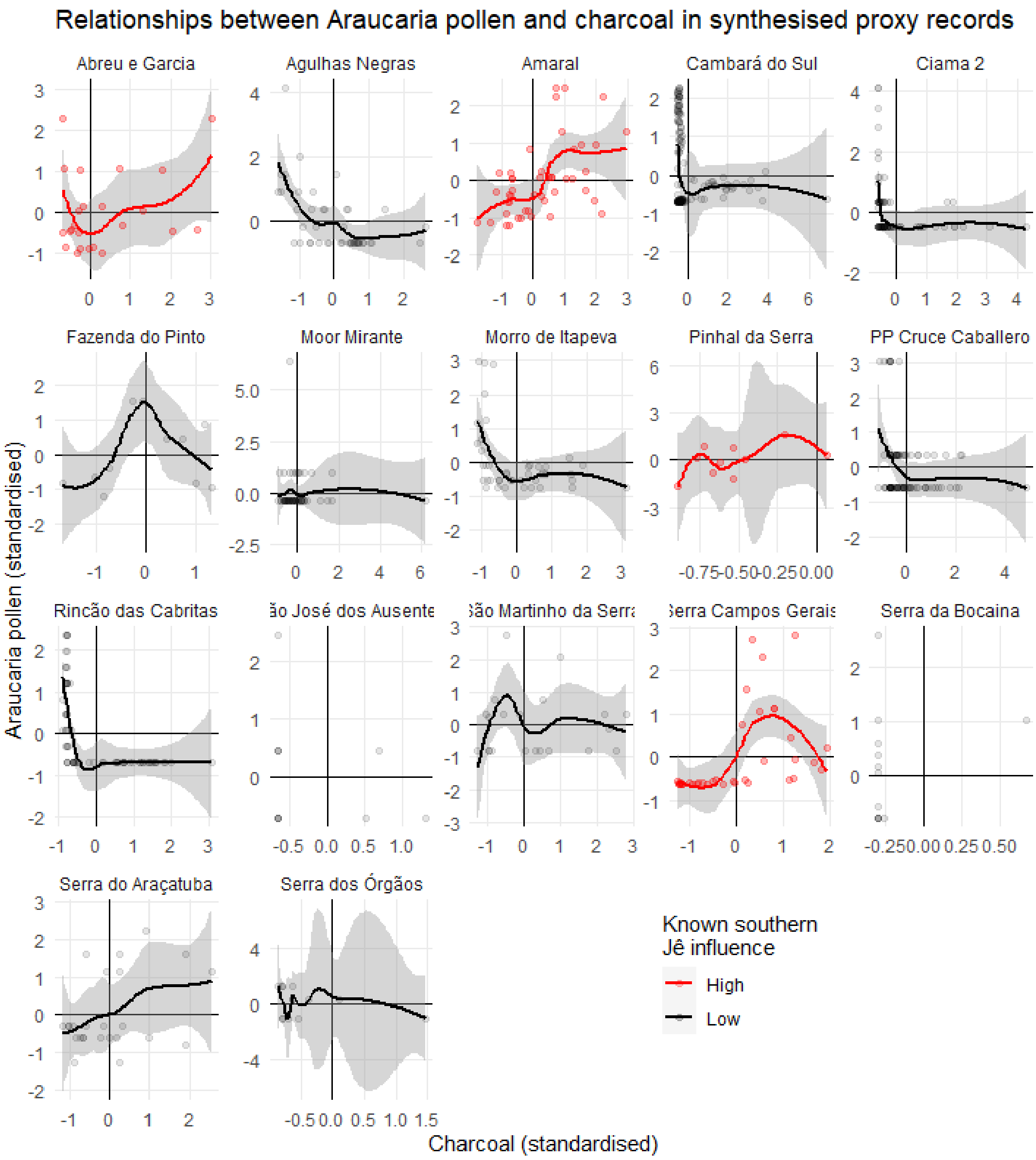


Figure S4.2.5: ENM results for Lages (Robinson *et al.*, 2018), *which is not otherwise included in our proxy synthesis as the 7,500-year record has only one date.*

There is a striking difference in vegetation-fire relationships between the four sites identified as having high southern Jê influence and the other sites for which pollen and charcoal data are both available (main text fig. 4). Fig. S4.2.6 (below) breaks down the broader trends by site. Of note, these graphs plot the relationships between every subsample with both pollen and charcoal data from each core – they are not limited to just the Late Holocene. This affects the relationship in the Serra Campos Gerais record, which is ca. 14,000 years long with less than 2,000 years influenced by humans. In the Fazenda do Pinto, Serra do Araçatuba and São Francisco de Assis records, the relationships do not clearly follow the wider negative relationship between fire and forest, despite not having significant known southern Jê influence. The Fazenda do Pinto site records no significant forest expansion, with Araucaria Forest pollen not exceeding 5%. Maize pollen was found in the São Francisco de Assis record so its pattern could conceivably be anthropogenic, but it is very unlikely to be connected to the more distant Araucaria Forests or southern Jê. Although *Araucaria* pollen at Serra do Araçatuba never reaches 2% (so is more subject to noise from the digitisation process), its positive past relationship between fire and forest cannot be easily explained – it may in fact reflect human influence, but more evidence is needed to clarify this.


Relationships between Araucaria pollen and charcoal in synthesised proxy records
Abreu e Garcia
Agulhas Negras
Amaral
Cambará do Sul
Ciama 2
Fazenda do Pinto
Moor Mirante
Morro de Itapeva
Pinhal da Serra
PP Cruce Caballero
Rincão das Cabritas
ão José dos Ausente
São Martinho da Serra
Serra Campos Gerais
Serra da Bocaina
Serra do Araçatuba
Serra dos Órgãos
Araucaria pollen (standardised)
Charcoal (standardised)
Known southern
Jê influence
High
Low

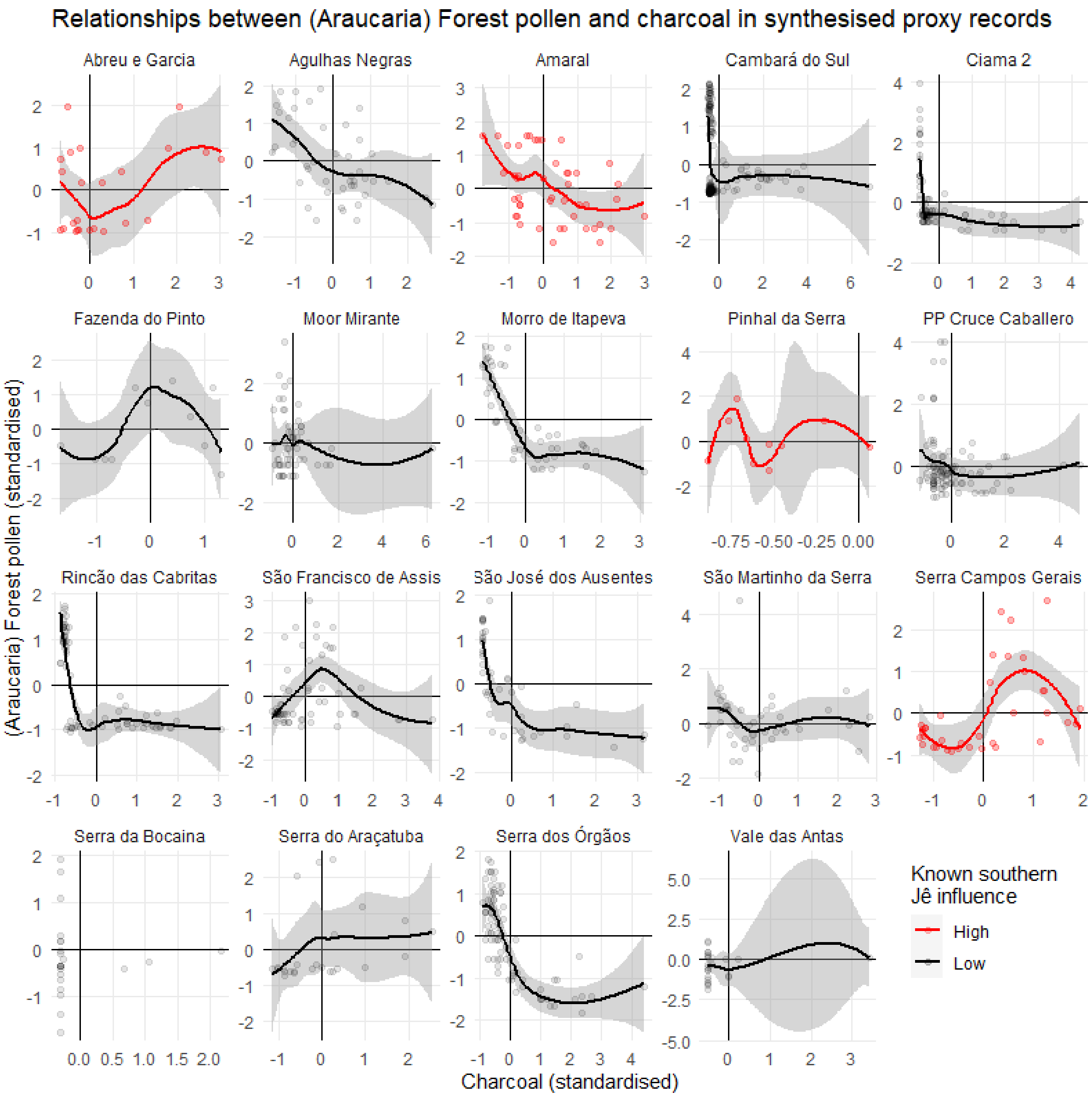


Figure S4.2.6: Site-level comparisons of Araucaria (top) and forest (bottom) pollen proportions against charcoal concentrations; all values were standardised before analysis. Lines are loess curves fitted to the points.

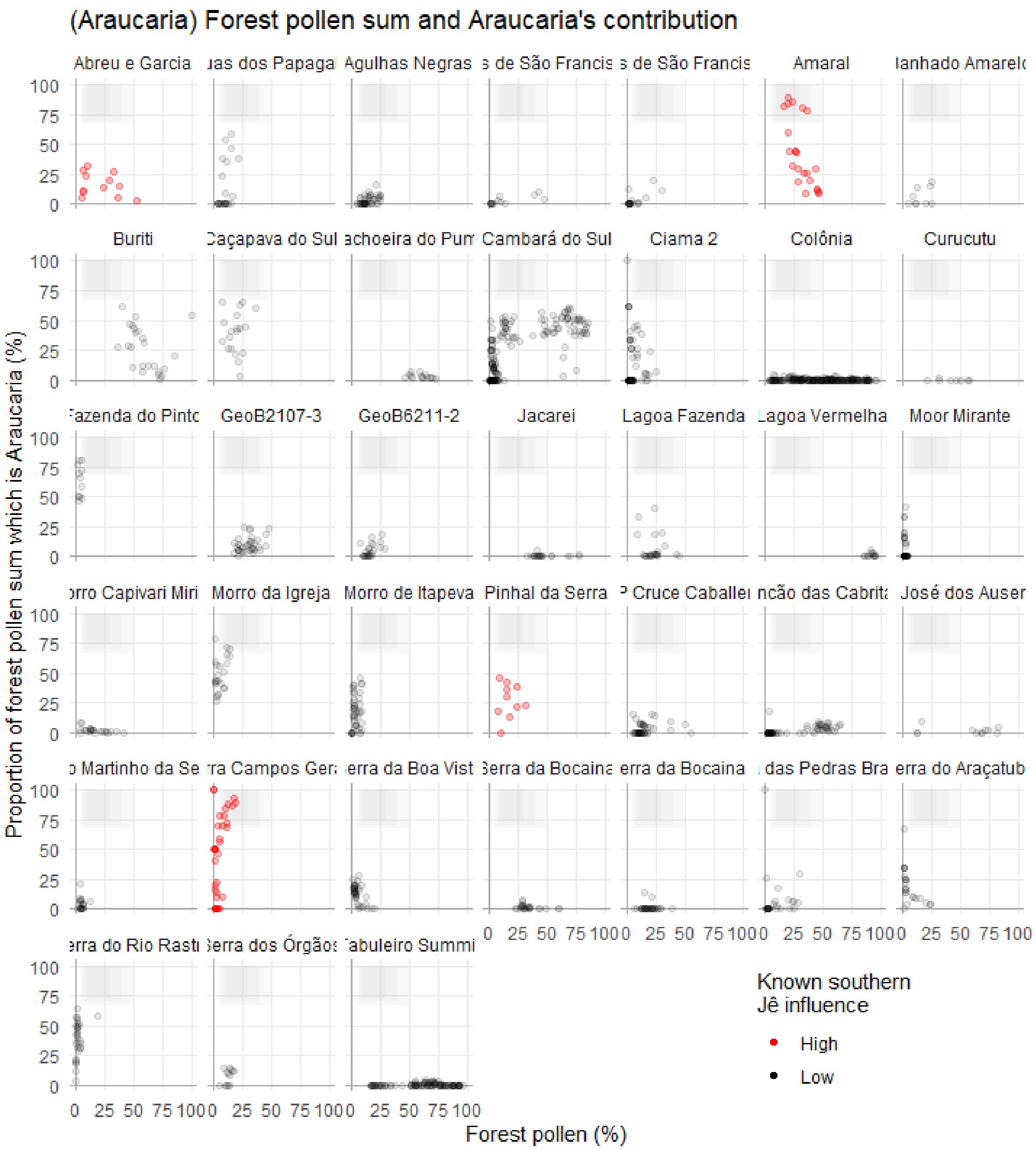


Figure S4.2.7: Site-level comparisons of (Araucaria) forest pollen and Araucaria's contribution.

S4.3. Additional results from Abreu e Garcia, Amaral, and Pinhal da Serra

S4.3.1. Abreu e Garcia

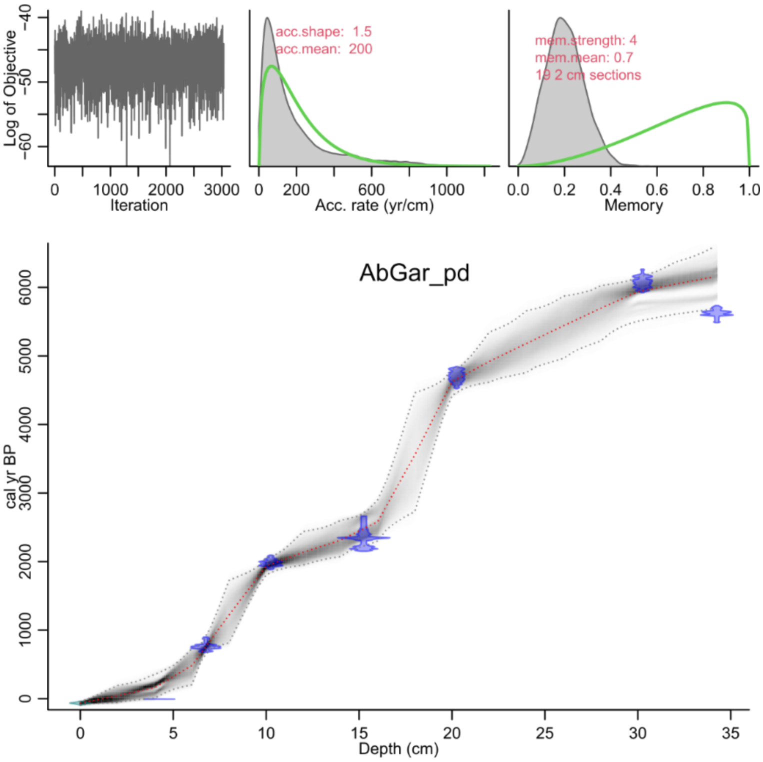


Figure S4.3.1.1: Age-depth model for Abreu e Garcia

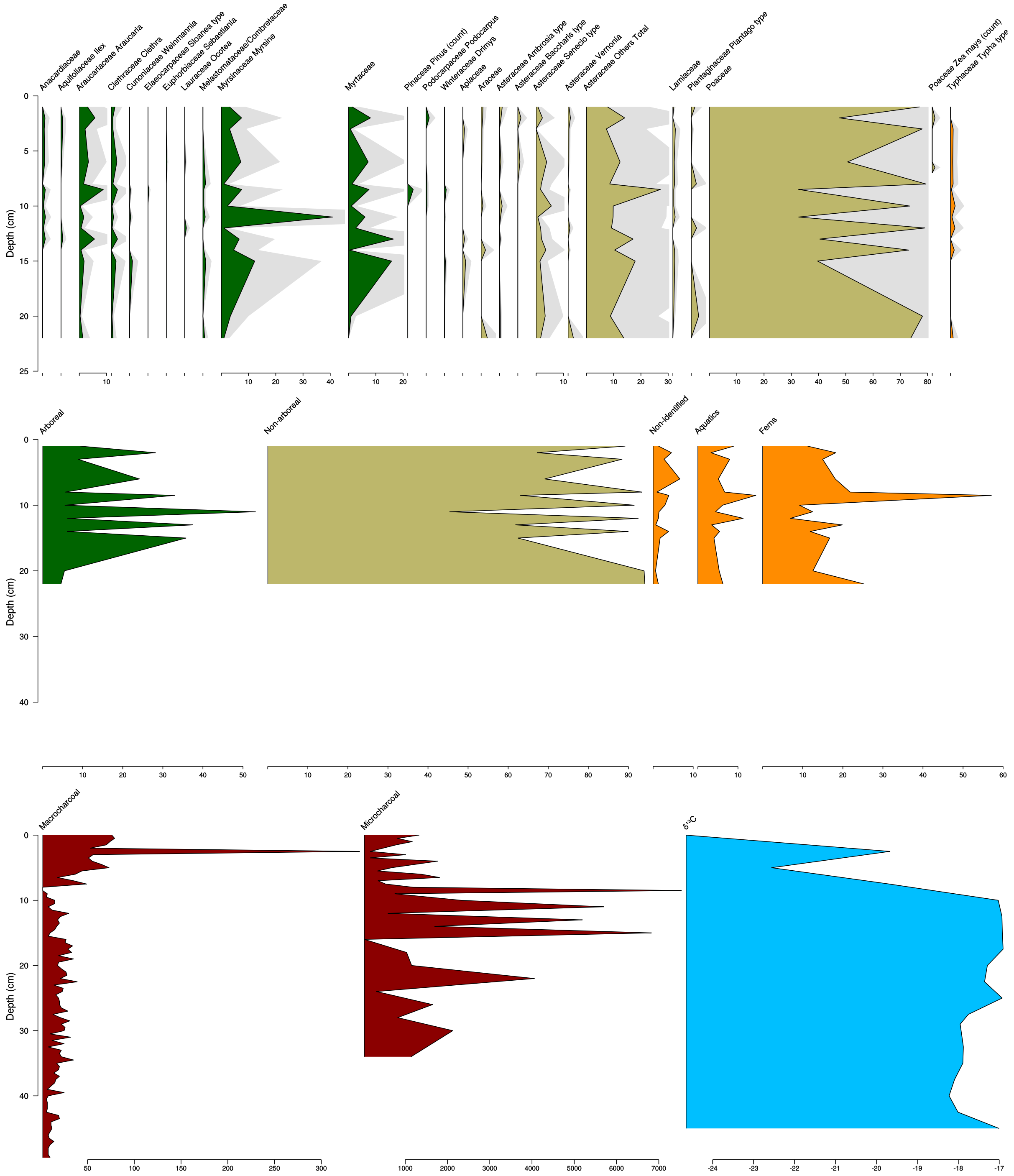


Figure S4.3.1.2: Expanded proxy diagrams from Abreu e Garcia. All pollen taxa which exceed 1% of the terrestrial sum are shown. Exaggeration is 3x. Aquatics (including Typha) and ferns are plotted as percentages of the terrestrial pollen sum (arboreal + non-arboreal + non-identified). Pine and maize pollen are counts, not percentages.

S4.3.2. Amaral

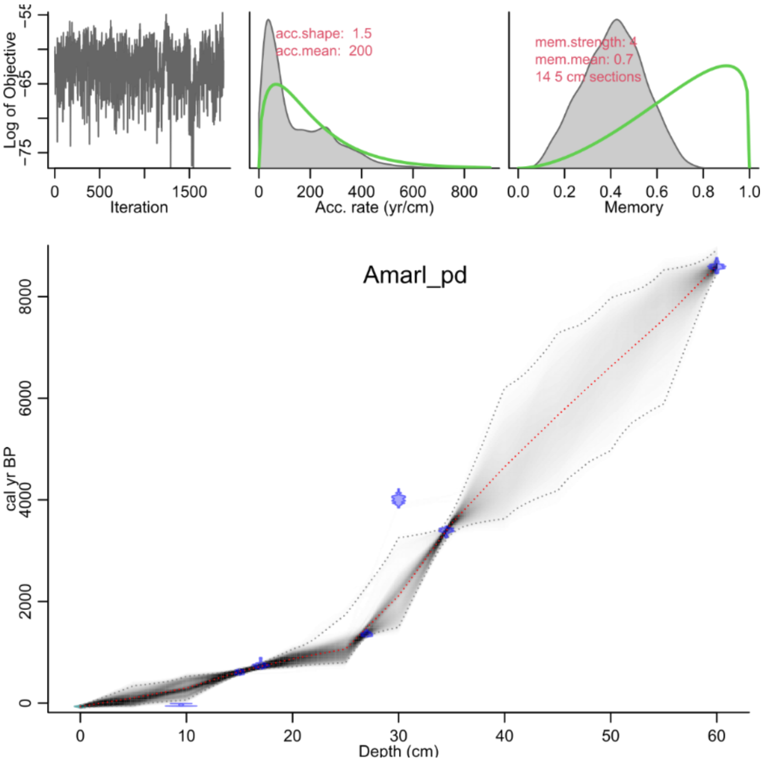
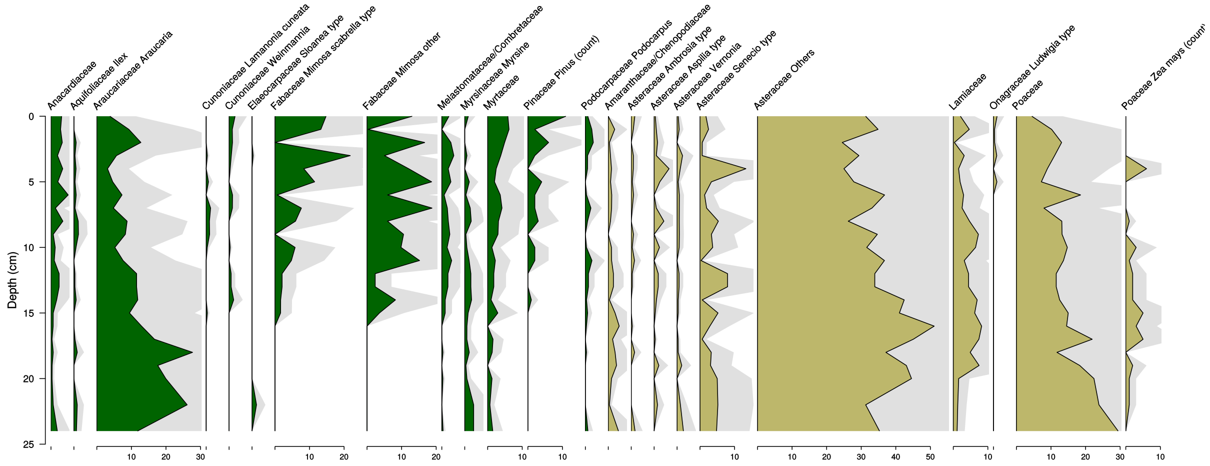


Figure S4.3.2.1: Age-depth model for Amaral.



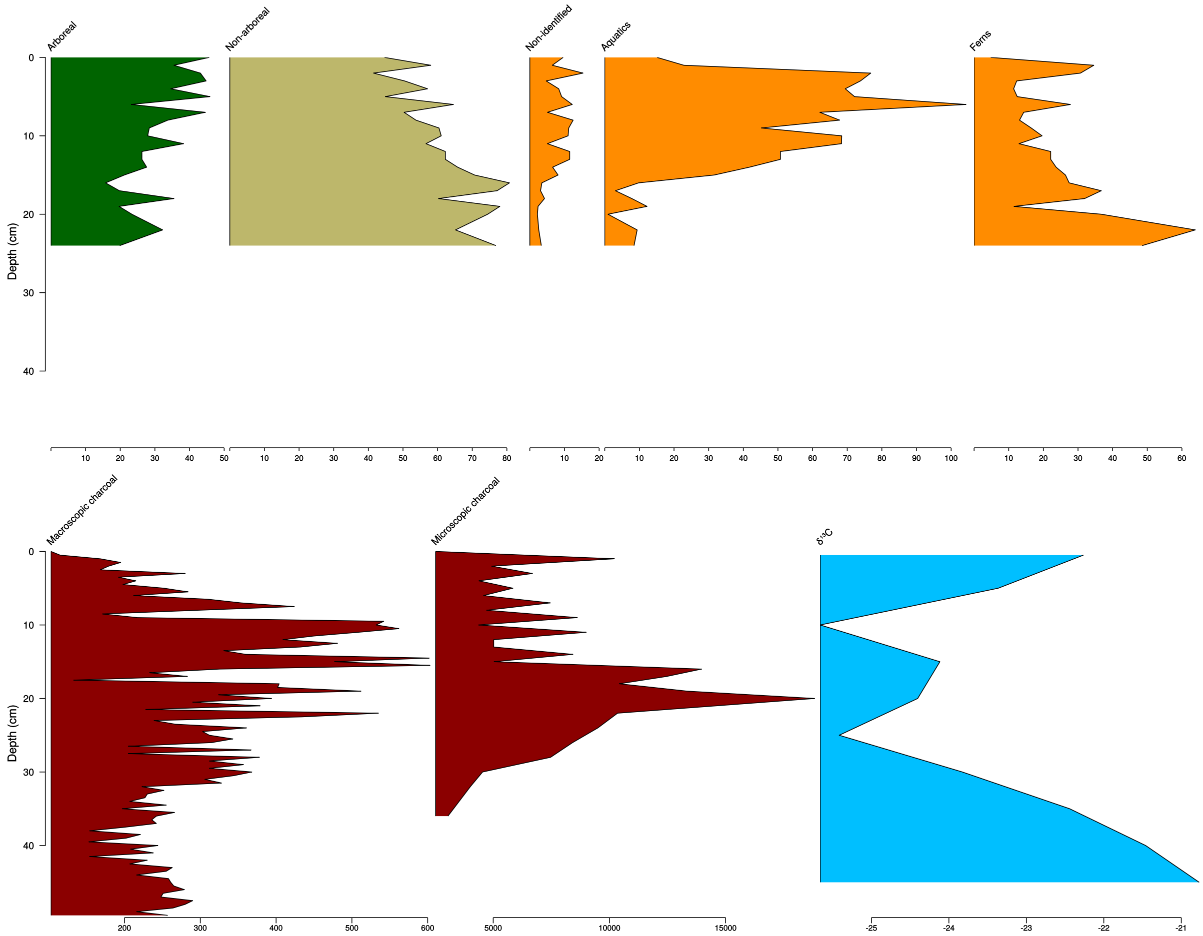


Figure S4.3.2.2: Expanded proxy diagrams from Amaral. All pollen taxa which exceed 1% of the terrestrial sum are shown. Exaggeration is 3x. Aquatics and ferns are plotted as percentages of the terrestrial pollen sum (arboreal + non-arboreal + non-identified). Pine and maize pollen are counts, not percentages.

S4.3.3. Pinhal da Serra

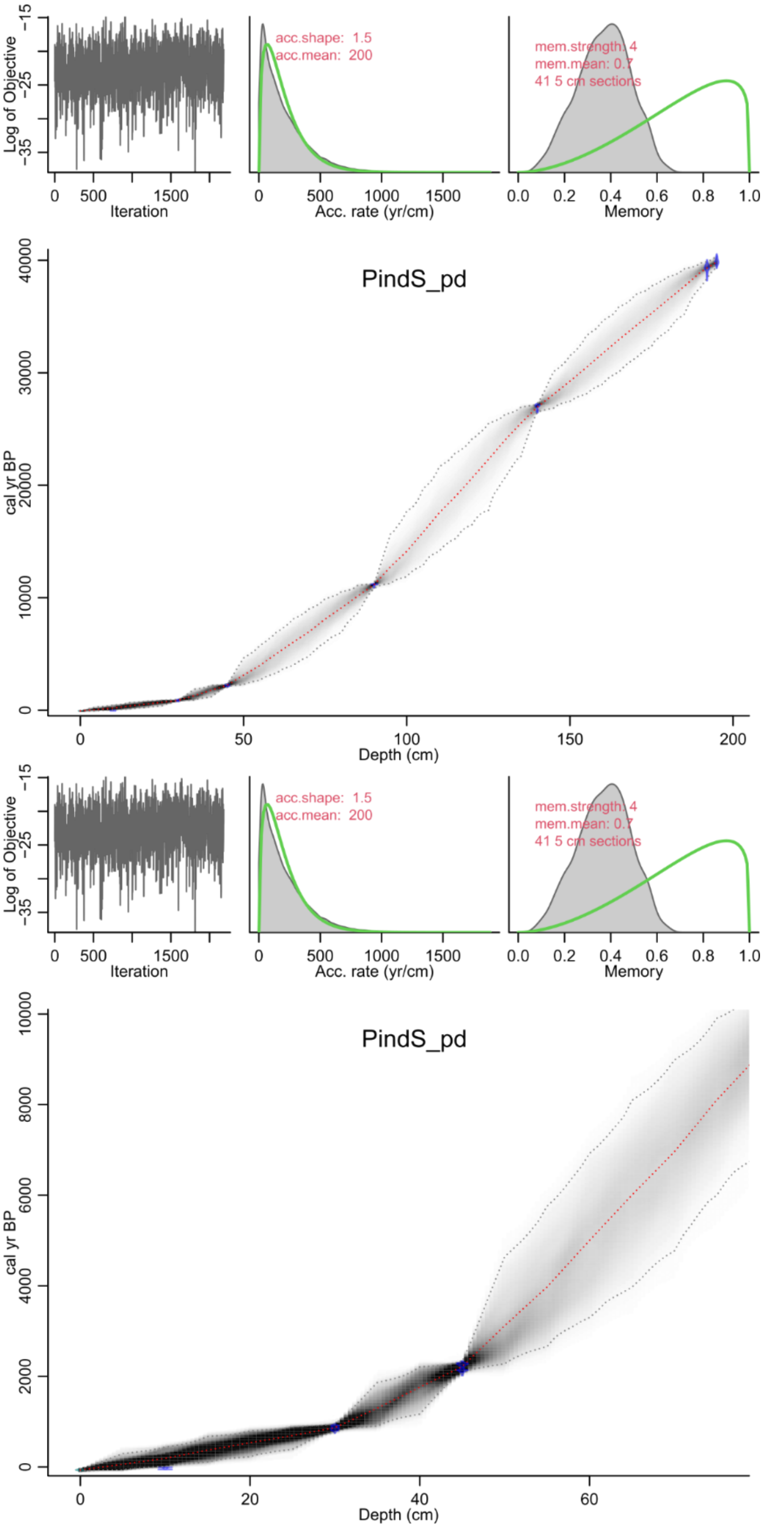


Figure S4.3.3.1: Age-depth model for Pinhal da Serra (full depth and top 75 cm only)

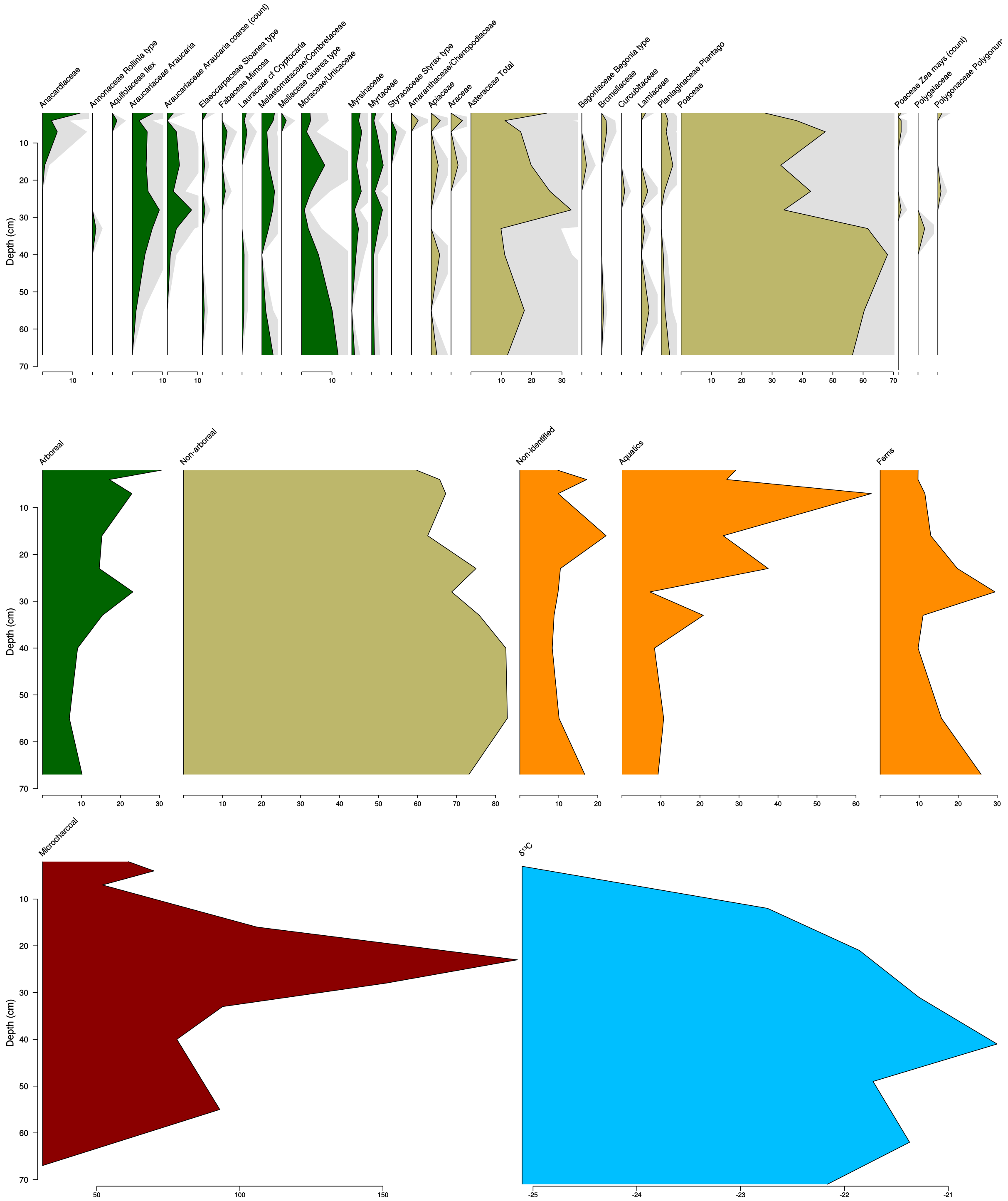


Figure S4.3.3.2: Expanded proxy diagrams from Pinhal da Serra. All pollen taxa which exceed 1% of the terrestrial sum are shown. Exaggeration is 3x. Aquatics and ferns are plotted as percentages of the terrestrial pollen sum (arboreal + non-arboreal + non-identified). Pine and maize pollen are counts, not percentages; a count of Araucaria pollen from the coarse fraction is also shown – this is independent of the percentage in the fine fraction.

S4.4. Additional ENM results

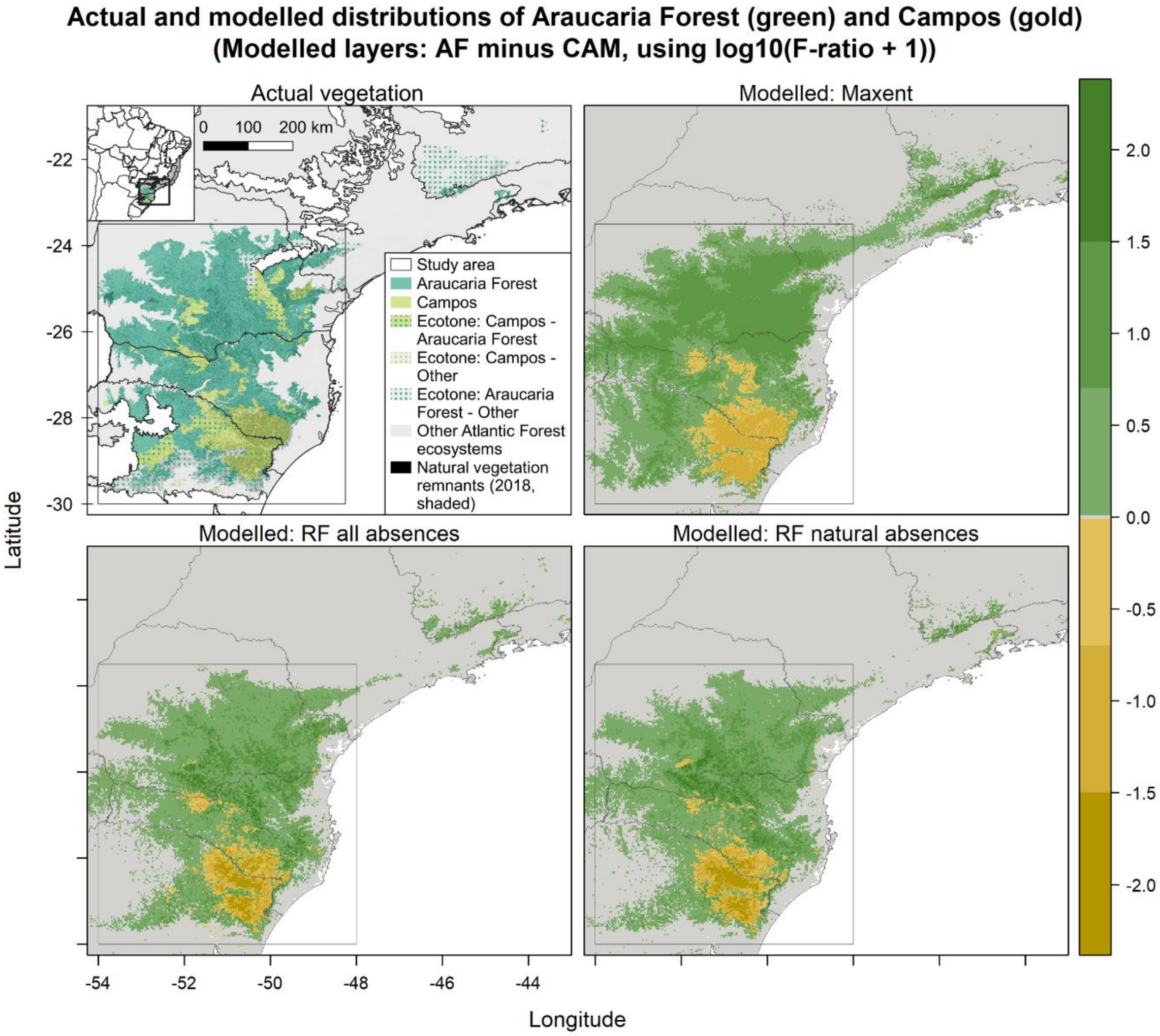
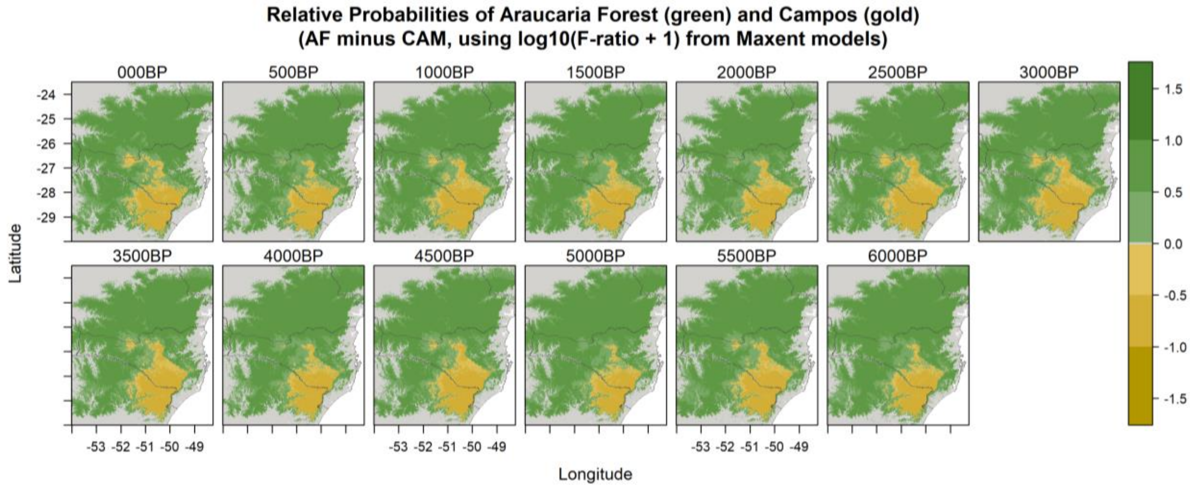
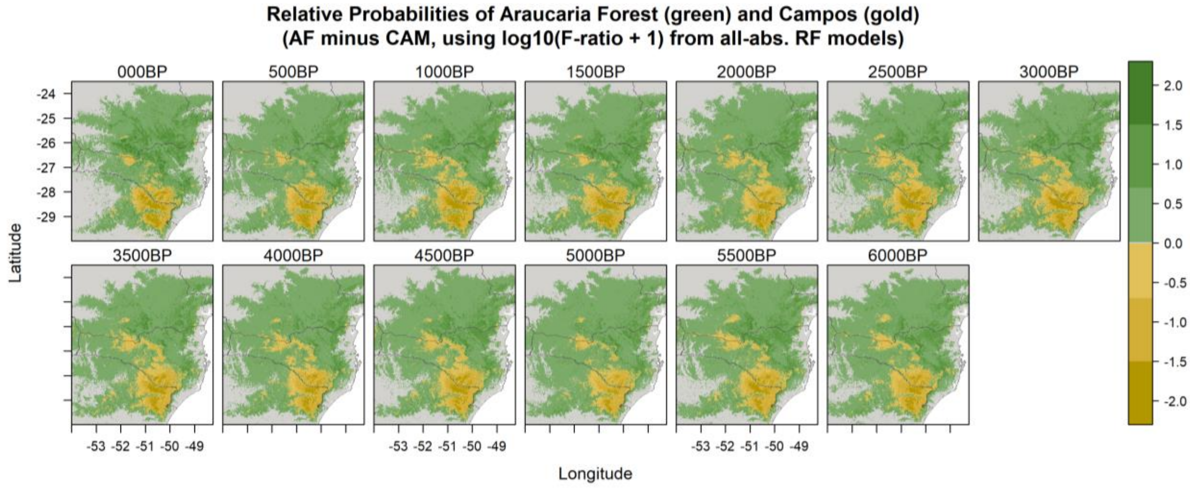


Figure S4.4.1: Actual (IBGE - Instituto Brasileiro de Geografia e Estatística, 2019; Souza et al., 2020) and modelled present-day distributions of Araucaria Forest and Campos. Green areas are more likely to be Araucaria Forest, gold areas are more likely to be Campos, and grey areas are either finely balanced between the two or both are absent (further details can be found in S3.2.3).





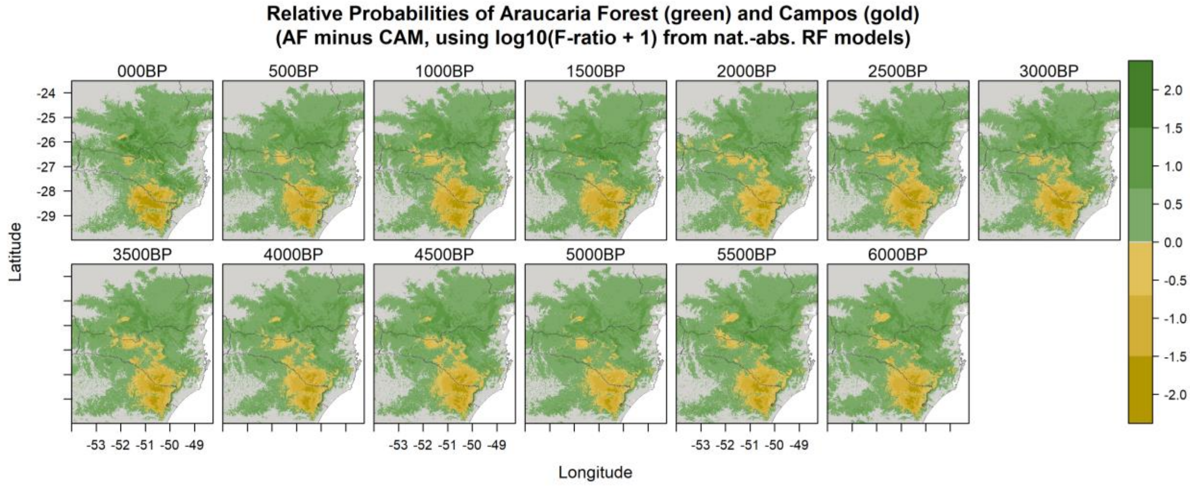


Figure S4.4.2: Ecosystem-level ENM results showing the predicted relative probability of Araucaria Forest and Campos in space and time (top-bottom: Maxent, all-absence RF, natural-absence RF).

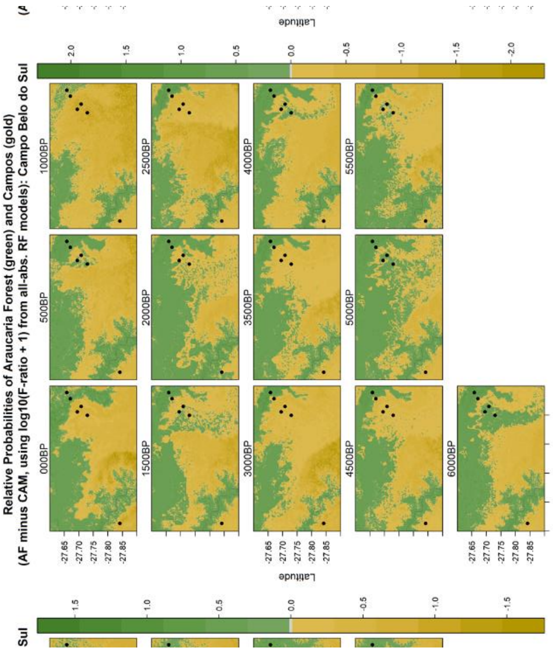


Figure S4.4.3: Model predictions for the Canoas-Pelotas basin/Campo Belo do Sul region. Proxy sites (dots) from left to right are Pinhal da Serra, Luis Carlos, Baggio, Amaral, Abreu e Garcia, and Heraldo (top-bottom: Maxent, all-absence RF, natural-absence RF).

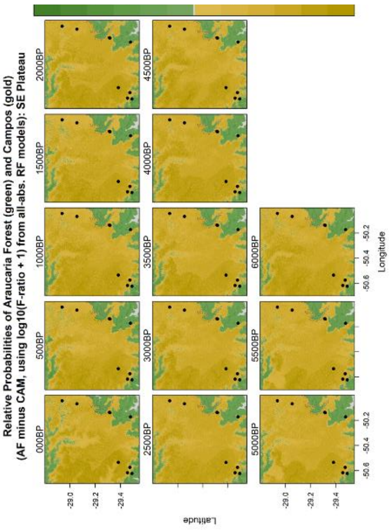


Figure S4.4.4: Model predictions for the south-east plateau region. Proxy sites (dots) from left to right are Alpes de São Francisco 2 and 1, Rincão das Cabritas, Fazenda do Pinto, CPCN Pro Mata, Serra das Pedras Brancas and Banhado Amarelo (not distinguishable at this scale), and Cambará do Sul (top-bottom: Maxent, all-absence RF, natural-absence RF).

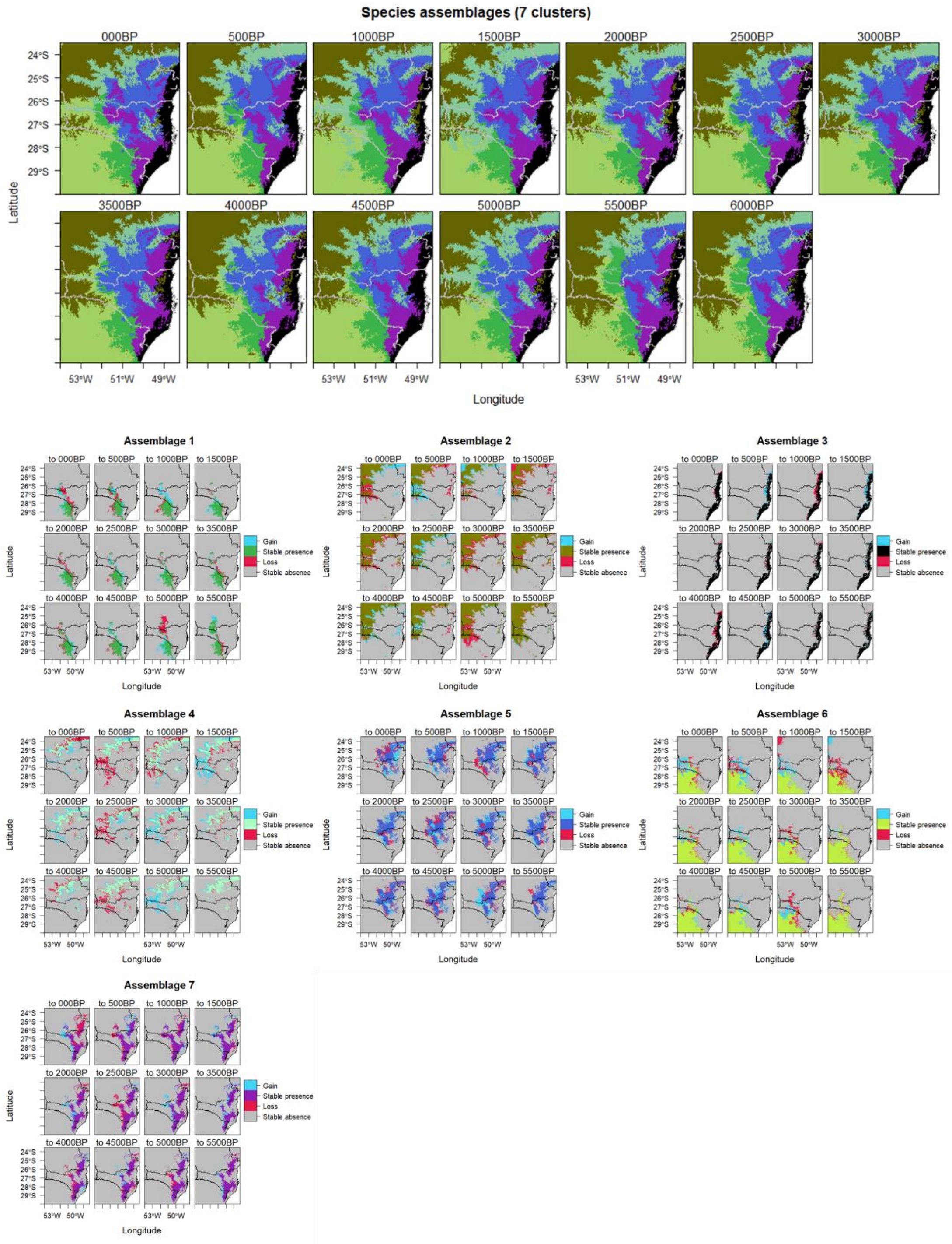


Figure S4.4.5: Predicted compositional change through space and time. For interpretation of the colours, see fig. S3.2.3.1.In the lower half of the plot, each assemblage's colour represents stable presence and grey means stable absence, while red represents area lost from the previous time point and light blue represents gained area.

S5. Supplementary discussion

S5.1. Identifying evidence of pre-colonial Indigenous impacts on Araucaria Forest

The three new palaeoecological sites studied in this paper – Abreu e Garcia, Amaral and Pinhal da Serra – are located in the area with the most archaeological evidence of pre-colonial southern Jê occupation, all within 1 km of known archaeological sites (see S3.4 and main text fig. 1d). They are therefore well placed to identify signals of land use in more intensely occupied parts of the landscape. In all three records we find increases in micro- and macrocharcoal with maize pollen around the time radiocarbon dates from nearby archaeological sites have shown southern Jê occupation. In Amaral and Pinhal da Serra, cultivation and increases in fire co-occur with relatively high percentages of Araucaria Forest pollen, of which *A. angustifolia* makes up a relatively high proportion (fig.S4.2.6-7). Together, these are strong indicators of human influence on Araucaria Forest.

Unexpectedly, we also identified the same pattern in the Serra Campos Gerais record (Behling, 1997b), 350 km away from our new study sites. Before about 700 cal BP, the site follows expected natural dynamics, with declining charcoal occurring with increases in Araucaria Forest and *A. angustifolia* pollen. After about 700 cal BP, however, charred particles reverse course and increase, cultigen pollen (maize and *Phaseolus*) appears, and Araucaria Forest (most of it *A. angustifolia*) increases. Serra Campos Gerais is not near to any known southern Jê archaeological sites but the combination of these signals is a clear indicator of past human land use.

Some other sites (fig. S4.2.7) have sustained periods where *A. angustifolia's* pollen percentages are high in absolute terms [Buriti (Bertoldo, Paisani and Oliveira, 2014) before about 2,000 cal BP] or relative to the forest pollen sum [Águas dos Papagaios (Ladchuk, Parolin and Bauermann, 2016) 4,000-2,000 cal BP] but the combination of both seems to be predominantly found in human-shaped sites. It is important to note, though, that the attribution of this pattern to human influence should not be automatic. These areas with distinctive Araucaria Forest pollen signatures are associated with more evidence of past human occupation as well as other, potentially confounding, explanatory variables – they are generally further inland at lower elevations (with attendant climatic differences), further from Campos and closer to contiguous Araucaria Forest, any of which could naturally result in floristic differences compared to the more Campos-dominated fossil pollen sites at higher elevations closer to the escarpment. Therefore, although high *A. angustifolia* pollen percentages do often appear to be associated with more intense pre-colonial Indigenous occupation, the link is not necessarily causal.

Cambará do Sul (Behling *et al.*, 2004) has both these features – for almost the entire period since 1,000 cal BP, *A. angustifolia* pollen was 20-40% of the terrestrial sum and 40-60% of the Araucaria Forest total – but the absence of fire, nearby archaeology or evidence of cultivation, and the record's congruence with natural drivers (see main text results section), suggests these are natural in this instance. Caçapava do Sul (Behling *et al.*, 2016) experiences a sudden doubling or tripling of its forest pollen percentage (7-13% to 20-36%) around 250 or 200 cal BP, driven largely by abrupt increases in *A. angustifolia* pollen (rising to make up 40-65% of the forest pollen sum). These changes are unlikely to be related to the southern Jê (the site is in the lowlands 70 km south of the plateau), and their connection to human activity is not clear: the site's fire dynamics are not recorded, and while the surrounding area had already been occupied by Guarani groups for a significant time (Bonomo *et al.*, 2015; Iriarte *et al.*, 2017), the timing of the changes also places them close to the onset of the colonial period. The only other similar site is Morro da Igreja (Behling, 1995), where, for a prolonged period, *A. angustifolia* pollen made up 3-9% of all terrestrial pollen and 38-71% of Araucaria Forest (though, as with Serra Campos Gerais, some other trees are assigned to different pollen groups), including at 8 cm depth where a grain of cultivated *Zea mays* pollen was found. However, the record's age uncertainties are so great in this period (1,000-2,900 years between maximum and minimum estimates) that it is not possible to ascribe this pattern to Indigenous land use.

S5.2. Potential Araucaria Forest transformations from low-intensity pre-colonial land use

Our study provides clear evidence of southern Jê actions transforming Araucaria Forest in intensely occupied areas close to settlements and cultivated areas, approximating the 'home' and 'clean space' domains in contemporary southern Jê ethnolandscapes (Réus Gonçalves Da Rosa, 2005; Moura, 2021). However, the design of our study does not allow us to resolve the question of how human actions affected less intensively occupied or used landscapes, such as the 'virgin forest' ('floresta virgem') ethno-landscape domain. (N.B., this term is used by contemporary southern Jê groups but is problematic in wider discourse; see e.g. Fletcher *et al.*, 2021.) There are exceedingly few Araucaria Forest palaeoecological proxy sites further inland than those we introduce in this paper, so insights into potential management in more contiguous forest areas are limited; they may have differed substantially from the better studied higher-elevation areas around Araucaria Forest-Campos ecotones and mosaics. In any case, it can be inherently difficult to determine the impacts of low-intensity human land use on forest composition – floristic changes can provide some of the clearest evidence for transient, low-impact human presence, but it is also the outcome of interest, which introduces causal circularity. Accordingly, it is not entirely unexpected that our findings indicate broad-scale vegetation changes in areas with apparently low-intensity pre-colonial southern Jê land use generally follow patterns that would be expected under natural climate changes – self-reinforcing forest expansions and reductions in fire following on from climatic changes leading to shifts from Campos grasslands towards Araucaria Forest.

Nonetheless, there are good reasons to expect that the southern Jê influenced areas of Araucaria Forest they did not use or occupy intensively (dos Reis, Ladio and Peroni, 2014; Souza, 2021). Various sources of evidence show that southern Jê groups travelled significant distances to collect, transport, trade and store pinhão (*A. angustifolia* seeds) (e.g. Henry, 1964; Wesolowski *et al.*, 2010; Cruz, 2014; Corteletti *et al.*, 2015; Fernandes and Piovezana, 2015; Gomes, 2018; Scheel-Ybert and Boyadjian, 2020; Moura, 2021). Such actions could easily start, spread or enrich Araucaria populations (for a detailed discussion of potential mechanisms, see Levis *et al.*, 2018). In this, *A. angustifolia* has a clear analogue in Amazonia's Brazil Nut tree, *Bertholletia excelsa* (an analogy also noted by Lauterjung *et al.*, 2018).

Both *A. angustifolia* and *B. excelsa* are floristically dominant, tall, canopy-emergent trees with significant cultural importance to Indigenous groups, who do and/or did travel long distances to collect the trees' abundant, large and nutritious seeds, which are otherwise mainly dispersed by gravity and scatter-hoarding rodents (Shepard and Ramirez, 2011; dos Reis, Ladio and Peroni, 2014; Ribeiro *et al.*, 2014; Thomas *et al.*, 2015; Souza, 2021). Low-intensity harvesting by contemporary Kayapó Brazil Nut collectors has shaped *B. excelsa* distributions, with deliberately planted and unintentionally dropped seeds increasing recruitment within *B. excelsa* groves and along paths that lead back to Kayapó villages (Ribeiro *et al.*, 2014). At a regional-scale, *B. excelsa*'s distribution appears to have been significantly shaped by pre-colonial Indigenous people (Shepard and Ramirez, 2011; Thomas *et al.*, 2015). The similarities between the two species' socio-ecological traits strongly suggests the southern Jê could have similarly influenced *A. angustifolia* in the pre-colonial era. For example, although increases in C3 contributions to soil carbon in the $\delta^{13}C$ record at Baggio (Robinson *et al.*, 2018) are compatible with climatic drivers (see main text and S3), these increases in forest in the last 500 years could still be connected to the establishment of the Baggio 1 pit-house village (de Souza, 2018; Robinson *et al.*, 2018). Araucaria pollen declined in the nearby Amaral site after the settlement was founded so people probably had to travel further afield to collect pinhão; if the Baggio valley held riverine forests (plausible but not made explicit in Robinson *et al.*, 2018), many decades of travel to and from the village and this area could have led to rapidly expanded or newly established Araucaria Forest areas.

Finally, some contemporary ethnoecological research and Indigenous knowledge suggests the southern Jê may have deliberately manipulated *A. angustifolia* populations in areas with less intense occupation (as well as, e.g., planting Araucaria trees in villages; Gomes, 2018). Gomes (2018, p. 237) reports two isolated adult Araucarias near to an old road and gardens, which a Xokleng-Laklãnõ elder indicated may have been connected with past pinhão-collecting expeditions. In a news interview (https://www.plural.jor.br/noticias/vizinhanca/povos-indigenas-lutam-pela-permanencia-na-floresta-estadual-metropolitana-em-piraquara/), Kretã Kaingang, a Kaingang political leader, stated that 'The araucaria is a territorial symbol because, in Brazil, they were planted by our Kaingang ancestors.' (Original: 'A araucária é um símbolo territorial porque, no Brasil, elas foram plantadas pelos nossos ancestrais Kaingang.') The elaboration of such understandings of past human-environment relationships could serve to advance our knowledge of how southern Jê (and Guarani) people shaped Araucaria Forests and Campos before European colonisation. External interpretations of southern Jê ethnoecology are useful – as in this study and others (e.g. de Souza, Corteletti, *et al.*, 2016; Robinson *et al.*, 2017), they provide a valuable lens for interpreting archaeological and palaeoecological evidence – but an additional promising avenue for future research would be the collaborative combination of 'classically scientific' and Indigenous ecological knowledge systems to improve our understanding of past vegetation dynamics in southern Brazil, cf. Richer and Gearey (2017) (as with Zurita-Benavides, Jarrín–V and Rios, 2016; and Machado, Tschucambang and Fonseca, 2020, and Xokleng-Laklãnõ archaeological artifacts).

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