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LATE PLEISTOCENE/HOLOCENE EVOLUTION OF BRAZILIAN ECOSYSTEMS: CLIMATIC CHANGES AND PLANT MIGRATIONS

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Apresentação

Esta tese foi elaborada como um dos requisitos parciais para inscrição no Concurso de Livre Docência no Instituto de Geociências da Universidade de São Paulo (USP) em março/abril de 2018 e reúne estudos inéditos ou publicados a partir de 2013 sobre mudanças na vegetação e clima durante o Pleistoceno Tardio de quatro ecossistemas brasileiros - Cerrado, Mata Atlântica, Caatinga, e Floresta Amazônica – a partir de análises palinológicas em sedimentos lacustres e em depósitos de turfeiras.

O primeiro trabalho **(Manuscrito 1)**, intitulado “Ice-Age forest connections: a mechanism for Atlantic-Amazonian speciation”, submetido recentemente ao periódico científico Nature Geosciences, contém uma reavaliação do registro palinológico do Lago de Serra Negra (MG), parte integrante da tese de doutoramento (1987-1992) no Departamento de Botânica e Zoologia da Ohio State University, Columbus, Ohio (EUA). Essa reanálise teve início durante os anos de pós-doutoramento (1993-1995) no Museu de História Natural de Chicago (EUA), mas não fora concluída. A partir de 2016, já no IGC/USP, esse estudo foi estimulado pela concessão de verba de pesquisa através do Projeto Temático FAPESP Proc. 2015/50683-2, intitulado “Vulnerability of Populations Under Extreme Scenarios”, que tem este pesquisador como Coordenador e Reponsável. Este projeto temático visa o entendimento da história das florestas montanas brasileiras frente às mudanças climáticas do Pleistoceno Tardio/Holoceno, tema totalmente compatível com os objetivos da reavaliação do registro palinológico do Lago de Serra Negra, que engloba praticamente o último ciclo glacial, i.e., os últimos 100.000 anos. O atraso na publicação dessa reavaliação dos dados desta importante localidade para os estudos do Quaternário do Brasil foi benéfico a este pesquisador devido ao emprego de várias técnicas de análise não disponíveis nos anos 90. Uma delas é o modelo de idade radiocarbônica que permite ao estabelecimento de idades para amostras não datadas, mas inseridas em um intervalo com controle de datação

^{14}C. Outra vantagem tem a ver com a maior disponibilidade de registros paleoambientais para comparação dos resultados obtidos, que fornecem uma visão muito mais ampla das paisagens quaternárias ao contrário dos anos 90, quando não havia no Brasil mais do que três estudos pertinentes a este tema. Este trabalho tem como resultado mais significativo a comprovação da expansão de florestas úmidas e frias na região Sudeste do Brasil em sincronia com a última glaciação no hemisfério norte e nas grandes elevações do hemisfério sul (Andes). Os resultados invalidam a controversa ideia da aridez pleistocênica proposta para o Brasil central por uma geração de pesquisadores que foram altamente impactados pelos trabalhos do geógrafo Ab´Saber (1982). Em nenhum momento desse registro, depositado praticamente nos últimos 1000.000 anos, há evidência de um único grão de pólen de espécies da Caatinga. Os dados apresentados não só invalildam a hipótese como mostra um cenário climático e vegetacional oposto ao que foi proposto pelos refugialistas, ou seja a região nuclear de cerrado foi impactada por climas frios e úmidos de modo que o Cerrado sofreu vários ciclos de substituição por florestas ombrófilas mixtas. Outra importante contribuição deste paper é a proposta de um mecanismo ecológico teórico de especiação vegetal, com base em mudanças climáticas, que gerem contração e expansão de vegetação florestal tropical durante fases glaciais durante todo o Quaternário.

O segundo trabalho **(Manuscrito 2)**, intitulado “The Brazilian Atlantic Dorest During the Late Quaternary: Expansion Induced by Tropical Incursion of Polar Air Masses”, também inédito, a ser submetido à Nature Geosciences, está também inserido diretamente no âmbito do Projeto Temático FAPESP, Proc.2015/50683-2. Este manuscrito, considerado um dos produtos mais importantes desse projeto temático, tem como objetivo principal o teste da hipótese de que vários padrões biogegráficos modernos, especialmente em relação à distribuição disjunta, de populações separadas por muitos milhares de quilômetros, de táxons vegetais montanos adaptados a altas taxas de umidade e baixas temperaturas, foram estabelecidos principalmente durante a última fase glacial e não a mudanças climáticas do Paleogeno, como sugerido por Maguire

(1970). Para isso foram levantados todos os trabalhos palinológicos quaternários, publicados ou não, disponíveis para o Brasil para a obtenção de uma visão geral dos ecossistemas brasileiros durante o Pleistoceno Tardio. Com este levantamento foi possível notar rotas de migrações de várias espécies e verificar que durante o último ciclo glacial alguns elementos florestais migraram grandes distâncias no Sudeste/Centro Oeste/Nordeste do Brasil. Esse deslocamento de populações possivelmente permitiu troca genética entre populações hoje isoladas pelas mudanças climáticas subsequentes. Através dessa análise foi possível estabelecer para as fases mais frias da última glaciação, Último Máximo Glacial- Heinrich 1 (c. 25 – 17,5 K anos cal. A.P.; 17,5 K – 14,6 K anos cal. A.P.), duas rotas principais de migração de espécies vegetais: uma rota que conecta as regiões Sul e Sudeste, via Serra da Mantiqueira, derivando-se para a Serra Geral em direção ao leste da Amazônia e outra rota Serra do Mar/Mantiqueira, conectando-se à Serra do Cipó, Serra do Espinhaço, Chapada Diamantina até o coração do semi-árido Nordestino. Com essas rotas, cria-se um modelo teórico para explicar disjunções florísticas entre o sul, sudeste do Brasil com a Amazônia, e disjunções que se extendem às Guianas e Venezuela assim como outras entre o Sul /Sudeste e a florestas úmidas, mantidas como enclaves úmidos (brejos de altitude), em áreas elevadas da região semiárida do Nordeste.

O terceiro trabalho **(Manuscrito 3)**, também inédito, intitulado “Late Pleistocene/Holocene Evolution of a Forest/Altitude Savana Mosaic in the southern Brazilian Atlantic Forest”, retrata estudos palinológicos e paleoclimáticos realizados no Parque Estadual Serra do Mar, Núcleo Curucutu, conduzidos inicialmente pela então aluna de Iniciação Científica Vanda Brito de Medeiros, do curso de Ciências Biológicas na Universidade Guarulhos, entre os anos de 2004 e 2005. Essa análise foi posteriormente ampliada pelo aluno Maicon Alicrin Silva, da Universidade São Judas Tadeu, durante seu projeto de Inciação Científica, com Bolsa FAPESP, no IGc/USP, entre os anos de 2016 e 2017. Dessa forma aumentamos a resolução das análises do testemunho coletado em 2006 que gerou um registro paleoambiental com maior detalhamento das variações vegetacionais e climáticas no setor sul da Floresta Atlântica do Brasil, em relação à primeira publicação (Pessenda et al., 2009) desses resultados, que contou com reduzidas informações palinológicas. Entre os principais resultados do Manuscrito 3 está a comprovação de mudanças significativas da paisagem do setor sul da Floresta Atlântica devido ao esfriamento glacial, impulsionado e controlado possivelmente pela intensificação das incursões de massas de ar de origem polar. Entre as várias conclusões obtidas está o fato de que o atual mosaico Floresta/campo de altitude em áreas elevadas da Serra do Mar é muito antigo e não pode ser explicado como relicto de um passado árido durante o Pleistoceno Tardio. Os resultados também sugerem que outros mecanismos, possivelmente relacionados a características geomorfológicas e edáficas, devam estar envolvidos no estabelecimento desse padrão vegetacional. Além disso, os dados palinológicos mostram claramente que os campos de altitude no Curucutu têm coexistido lado a lado com florestas, que tiveram suas características florísticas alteradas conforme as mudanças climáticas, ora de caracter ombrófilo mixto, ora de caráter de florestas ombrófilas densas com menor representação de gimnospermas (*Araucaria* e *Podocarpus*).

O **Manuscrito 4**, intitulado “Paleoclimates of Amazonia: an Ice-Age View, foi publicado como capítulo do livro Paleontologia: Cenários da Vida – Paleoclimas, editado por Carvalho et al. (2014), versa sobre uma ampla revisão sobre o conhecimento atual sobre as mudanças da vegetação em função das variações climáticas do Pleistoceno Tardio sobre a Amazônia, incluindo dados paleoecológicos para países vizinhos, por um grupo de palinólogos, incluindo o autor desta tese. Este artigo também tem como objetivo convencer a comunidade científica de que não existem evidências para a suposta transformação da atual paisagem florestal muito heterogênea composta por vários tipos de fisionomia em paisagem semi-árida durante o Pleistoceno Tardio. A revisão abrangente neste manuscrito traça um histórico dos desenvolvimentos científicos sobre a vegetação da Amazônia e mostra gradualmente de o desenvolvimento de novas análises paleocológicas, que também não conseguiram alterar a visão de uma Amazônia sempre úmida durante a última glaciação. É importante destacar que este trabalho destaca o problema da interpretação de termos como “dry” e “drier”, que por serem relativos podem levar alguns pesquisadores a visualizar condições extremas como por exemplo o clima semi-árido do Nordeste do Brasil ou até mesmo desértico para áreas da Amazônia durante o período cronológico de intensificação de condições glaciais no hemisfério norte e nas grandes elevações do hemisfério sul. Esta contribuição também trata rapidamente de um dos mais importantes conhecimentos ecológicos derivados das análises palinológicas como o conceito de comunidades não-análogas (ver item 1.3), que permeia esta tese de Livre Docência.

O **Manuscrito 5**, intitulado “The Holocene of the Amazon”, também foi publicado como capítulo do livro Paleontologia: Cenários da Vida – Paleoclimas, editado por Carvalho et al. (2014). O objetivo deste trabalho foi destacar o conhecimento sobre as grandes variações climáticas e vegetacionais ocorridas na Amazônia nos últimos 10.000 anos, com destaque para o debate sobre a influência humana sobre os ecossistemas amazônicos, incluindo o significado paleoambiental, ainda muito controverso, da *terra-preta-do-índio*. Este texto destaca a grande variabilidade climática e vegetacional na Amazônia, ao se apoiar em um grande número de estudos, uma vez que registros palinológicos e paleoecológicos para o Holoceno são mais abundantes na literatura científica do que aqueles para o Pleistoceno Tardio. Entre as grandes alterações destaca-se o aumento generalizado da temperatura global, as grandes variações no nível relativo do mar e a relação entre populações humanas e o registro de partículas carbonizadas encontrados em sedimentos depositados nos últimos milhares de anos. No geral, este documento teve entre os seus vários objetivos o de mostrar a posição de paleobiólogos sobre a questão do impacto humano na Amazônia, ou seja, de sustentar a ideia de que até tempos históricos a Amazônia foi pouco impactada pelas populações humanas, ideia que este autor já não mais acredita em face de evidências botânicas e arqueológicas recentes (*e.g.* geoglifos do Acre e novos sítios arqueológicos no Parque Nacional do Xingu, Brasil). Estes últimos estudos evidenciam grande manupulação da vegetação no passado, com a criação de sofisticados centros de domesticação de plantas, estabelecimento no Holoceno Tardio de florestas culturais e de sistemas urbanos organizados, aliados a sistemas agro-florestais que alteraram várias regiões amazônicas como o Alto Xingu e Acre e que chocam diretamente com a visão proposta de uma Amazônia intocada pelo *Homo sapiens*.

O **Manuscrito 6** traz uma contribuição inédita aos estudos do Quaternário com o uso do fungo, pertencente ao gênero *Sporormiella*, que cresce exclusivamente em fezes de grandes herbívoros e que tem sido usado por vários pesquisadores internacionais como um proxy para a determinação da presença de megafauna de herbívoros em localidades e regiões sem registro fóssil. Este estudo, publicado recentemente no periódico internacional Quaternary Research, traz várias evidências vegetacionais que mostram uma fortecorrelação entre o ínicio do declínio das populações de grandes herbívoros milhares de anos antes da transição Pleistoceno/Holoceno, possivelmente devido às mudanças climáticas globais, que no caso do Sudeste do Brasil, indicam condições úmidas e frias. Estas alterações ambientais tiveram grande impacto nas comunidades vegetais, que passaram a ter composições florísticas sem análogos modernos (ver item 1.3). As hipóteses lançadas neste trabalho sugerem que a extinção da megafauna plesitocênica no Sudeste do Brasil foi consequência da somatória de vários fatores, tais como mudanças climáticas globais no final do Pleistoceno que coincidiram cronologicamente com a chegada dos primeiros assentamentos de grupos humanos. Estes aceleraram o processo de extinção que já havia sido iniciado há milhares de anos antes da transição Pleistoceno/Holoceno.

O último documento, **Manuscrito 7**, intitulado “New Holocene pollen records from the Brazilian Caatinga”, foi aceito para publicação nos Anais da Academia Brasileira de Ciências, e deverá aparecer em uma das próximas edições desse periódico em 2018. Este trabalho tem como primeiro autor a aluna de doutorado Vanda Brito de Medeiros e tem co-autoria de Rudney de Almeida Santos, também doutorando no IGc/USP. Esta contribuição tem grande importância aos estudos do Quaternário Tardio devido à dificuldade de se encontrar, na região semi-árida do Nordeste do Brasil, registros sedimentares orgânicos com conteúdo palinológico preservado. A área de estudo permaneceu imune à tendência geral de semi-aridização da paisagem de grandes áreas do Nordeste do Brasil nos últimos 4000 anos, graças a uma falha geológica que expõe seções de um aquífero, que permitiu a manutenção contínua de uma área alagada e coberta por buritizais, grandes adensamentos da almeira *Mauritia flexuosa* (syn. *Mauritia vinífera*). Nessas áreas úmidas, com acumulação de matéria orgânica, durante os últimos 10.000 anos na região do Vale do Catimbau, em Pernambuco e em uma localidade no sul do Piauí, também com exposição superficial de lençóis freáticos profundos, foram preservados os conteúdos palinológicos da vegetações circundantes. Apesar de sua situação inusitada, em termos de umidade, os dois registros contém sinais que puderam ser correlacionados com outras áreas do semiárido e que denotam mudanças climáticas de grandes proporções durante o Holocene do Nordeste do Brasil. Entre os resultados mais significativos está a validação do modelo climático em direção ao atual clima semiárido no Nordeste do Brasil a partir dos últimos 4000 anos, como indicado por registros paleoclimáticos obtidos a partir da variação de razões isotópicas de Oxigênio , preservados em espeleotemas.

Os sete manuscritos são precedidos pelo Capítulo 1, que contém uma introdução geral a conceitos ecológicos, florísticos, e palinológicos que sustentam as discussões e argumentações explicitadas nos textos que formam o cerne desta tese de Livre Docência.

CHAPTER 1

1. General introduction and conceptual framework

This chapter contains a conceptual framework concerning the knowledge on ecosystem changes during the Late Pleistocene/Holocene in Brazil as well as different topics on Ecology and Biogeography, which are essential to an understanding of the goals and methods in each of the manuscripts, herein presented. Among these topics are: a). The unresolved biodiversity problem of the neotropics, b).Unexplained plant and ecossystem´s disjunctions in Brazil, c).No-analog plant communities of the past and their impact on the biota; d). Problems related to the interpretation and significance of certain plant taxa in Late Quaternary pollen records, and finally, e). The test of the Pleistocene Forest Refuge Hypothesis as well as of the hypothesis of past humid corridors, established durintg the Late Quaternary, allowing long distance migration by various botnaical taxa. as a possible mechanism for various unresolved modern biographic disjunct distributions.

The knowledge on the evolution of the Brazilian ecosystems has progressed a great deal after the 1990´s with the publication of the first pollen diagrams unveiling Late Pleistocene/Holocene vegetation and climatic histories for Amazonia (Absy et al., 1991; Colinvaux et al., 1996), Central Brazil (Barberi et al. 2000; Barberi 2001; Ferraz-Vicentini, 1993, 1999; Ledru, 1993; De Oliveira, 1992), the Atlantic Forest region (Pessenda et al., 2009; Behling,1995, 1997), the Caatinga of Northeastern Brazil (De Oliveira et al., 1999; Behling et al., 2000), the Pantanal (Bezerra & De Oliveira, 2014) and southern Brazil (Behling, 1995). One of the driving forces for such development was undeniably the need to test, by means of pollen analyses, the well known Pleistocene Forest Refuge Hypothesis model (sensu Haffer, 1969; Ab´Saber, 1982; Prance et al. 1982; Haffer & Prance, 2001). Before the first pollen diagram became available for Brazil, Liu & Colinvaux (1985) published palynological results from a locality known as Mera, that immediately reverberated among tropical quaternarists due the discovery of plant megafossil in a sedimentary profile containing palynological evidence of a mixed forest community during the Last Glacial Maximum (LGM) of Ecuadorian Amazonia. Their results collided with the previsions of the Refuge Hypothesis, in vogue during the mid 1980´s among paleocologists, due to the powerful evidence in northwestern Amazonia of allopatric forest taxa living in sympatry in area of the tropical lowlands which was thought to have had caatinga/savanna-like vegetation during the time of maximum expansion of glaciers in the northern hemisphere. The mixture of Andean and Amazonian plant taxa in the Mera record, shown to be coexisting in plant associations, would require a temperature depression of at least 5^{o}C in annual mean average for the Amazonian lowlands to permit the descend of montane taxa into the lowlands. These results were somehow very similar to those observed in North America (Davis, 1981) depicting widespread plant species migrations migrating individually according to their ecological and environmental recquirements supported Gleason´s Individualistic Concept of Plant Associations (1926), now applied for the first time to the neotropical vegetation (see item 1.3). The first generated scenarios, derived from early palynological studies in Brazil in the 1990´s later created two polarizing points of view. The first refutes the hypothesis due to overwhelming evidence of maintenance of tropical forests during glacial times, with very different floristic composition, when compared to modern floristic patterns, with no modern analogs under reduced temperatures (De Oliveira, 1992; Colinvaux et al., 1996; Colinvaux et al., 1999; Bush & De Oliveira, 2006). At the other pole lied the acceptance of the Refuge Model of drier landscapes and reduced arboreal vegetation cover during glacial times by some palynologists and ecologists.This dissension however is easily explained as a natural consequence of opposing interpretations of pollen signals dominated specially by grasses, as previously taken into account by Colinvaux et al. (1996), Colinvaux et al. (1999), Bush (2002), Colinvaux & De Oliveira (2000), De Oliveira et al. (2005), as discussed in item 1.4 of this introduction.

With the advent of geochemical analysis in very high temporal resolution, mainly oxygen isotope ratios in cave speleothems, deposited during the Late Pleistocene/Holocene in Brazil (Cruz et al., 2005; Cruz et al., 2006; Cruz et al., 2009; Wang et al., 2017, among others), an independent methodology gave paleocologists a much clearer view of climatic changes during the Late Quaternary. The results of this geochemical methodology thus soon started to provide palynologists with more robust climatic scenarios with very high temporal resolutions for the interpretation of pollen signals, usually with low temporal resolution, in lake and peatbog sediments.

Despite of these remarkable scientific developments, the fragmented information on vegetation histories for Brazil produced by different investigators has not been fully integrated to address important questions that remain unresolved, especially those concerning the biodiversity problem of the neotropics and disjunct vegetation patterns found in various Brazilian ecosystems, that appear to be intrinsically related to large scale climatic changes (item 1.2).

In order to provide an integrated view of the history of the Brazilian landscapes, this contribution brings new pollen analyses in strategic geographical and ecological locations such the Southern Atlantic Rainforest (Curucutu, São Paulo) and in the hyperxerophytic Caatinga region (Catimbau, Pernambuco and Bom Jesus, Piauí) as well as important results for Amazonia. In addition, the long pollen record of Lake Serra Negra (De Oliveira, 1992) was reanalyzed under the light of an unpublished sediment chronology model and of the late glacial climatic settings in different regions of Brazil, based on oxygen isotopic ratios in cave speleothems. All these new results were then integrated to a revision of published and unpublished Brazilian pollen records of glacial age (Manuscript 2). These analyses generated a broad and integrated view of the evolution of the Brazilian ecosystems during the Late Pleistocene and Holocene offering new insights on the origin of tropical biodiversity and important evidence to test important hypotheses to unveil possible ecological mechanisms and climatic changes, concealed withing modern vegetation disjunction patterns.

1.1. The biodiversity problem

The mechanisms controlling speciation of plants and animals and their biogeographic patterning in hyperdiverse systems such as those found in the South American neotropics remain as an enigma. The sub-continental scale of these ecosystems ensures that a single mechanism will not provide a single answer accounting for all patterns (Colinvaux, 1989). Tectonics (Gentry, 1982; Cracraft & Prum, 1988), fluvial isolation (Endler, 1982) and climate change (Haffer, 1969; Colinvaux et al., 1996) are all potential drivers of speciation. Tectonic uplift of the Andes separates Amazonian and other large ecosystems in Brazil from Central American and Pacific coastal populations, providing the allopatry that fosters speciation has been discussed and shown by Hoorn et al.(2010) and Ribas et al. (2007). Undoubtedly tectonic folding that extends into the Amazon Basin may be an important source of population isolation in much of western Amazonia (Gascon et al., 2000). Rivers bound some of the classic biogeographic regions of Amazonia (Cracraft & Prum, 1988) but do not appear to be a major barrier to gene transfer (Hewitt, 2000), especially in headwater regions (Peres et al., 1996). Climate change offers the potential for truly large-scale habitat alteration and could provide an overarching means to create allopatry, and hence fuel speciation or alternatively to induce niche adaptation through local extinctions or range expansions (Holt, 2009).

The largest changes in climate, over the last few million years, have been glacial-interglacial cycles, and these have become the center of climate-based speciation arguments. The most influential climate-based explanation of tropical diversity was the refugial hypothesis (Haffer, 1969) which suggested that ice-age aridity resulted in the rainforest contracting into isolated pockets surrounded by savanna grasslands. Speciation events are hypothesized to have occurred particularly frequently in these isolated forest fragments. When wet conditions returned, allopatry gave way to the observed modern parapatry. Although an elegant hypothesis, the forest fragmentation and isolation needed for this speciation pump was unsupported by paleoecological data (Colinvaux et al., 1999; Colinvaux et al., 2001).

Subsequent genetic studies have also shown that much of the speciation in Amazonia was actually far more ancient, taking place not in the Quaternary ice ages, but in the warmer phases of the Miocene or Pliocene (Santos et al., 2009; Ribas et al., 2005) or was at least continuous without an acceleration in the Quaternary (Zink et al. 2004; Rull, 2008). Nevertheless, mid- or late-Pleistocene speciation was evident in some clades, often including relatively recently derived separations between Atlantic forest and Amazonian forest species (Ribas et al., 2011). Such a close relationship of Atlantic and Amazonian forests suggested physical linkage, but aridity-based explanations of speciation would have deepened the separation of these systems rather than provided connectivity. Many genera, ranging from birds and rodents to butterflies and plants, have phylogenetic histories that indicate the movement of individuals between the Amazonian and Atlantic rainforests across what today would appear to be inhospitable cerrado (Ribas et al., 2005; Costa, 2003; Moritz et al., 2000). Several different migratory corridors have been suggested connecting these biomes (Por, 1992; Sternberg, 2001). But such a connection requires that the systems are functionally wetter-than-modern, i.e., evapotranspiration rates have to fall to the point where forest can establish on cerrado (Sternberg, 2001).

1.2. Unexplained biogeographical and disjunction patterns in Brazil

The origin of disjunct vegetation types in mountainous landscapes of southeastern and central Brazil displaying strong affinity to humid montane floras of northern South America still remains unknown. Earlier hypotheses suggested ancient cold and humid migration corridors possibly in the Eocene or Miocene (Maguire, 1970), later affected by Quaternary climatic change (Harley, 1995), could have allowed ancient contact between populations now isolated in mountain tops by climate.

Among the various objectives of this present work is the understanding the relationship between the distribution of cold-adapted montane tropical taxa belonging to the Atlantic Rainforest domain of southern/southeastern Brazil and climatic scenarios characterized by enhanced precipitation as suggested by oxygen isotopic ratios in speleothems of South America (Cruz et al., 2005, 2006, 2009; Wang et al., 2017) under lowered temperatures, ca. 5°C depression (Stute et al., 1995; Colinvaux et al., 1996; Colinvaux & De Oliveira, 2000; De Oliveira, 1992), during the Last Glacial Maximum (LGM), c. 25 – 17.5 K cal. Yrs BP.

One of the hypotheses to be tested is that during the late glacial cycle more intensified polar circulation with incursions of polar air masses into South America mainland, under a less intensified Hadley circulation over South America and relatively reduced insolation levels, promoted conditions suitable for the establishment of migration corridors for the expansion of montane forest niches (Manuscript 2). These former connections, between southeast and central Brazil (31° to 22 °S) and southeastern Amazonia, could therefore explain much of the modern occurrence of disjunct distribution of humid and cold-adapted taxa in elevated areas of cerrado and in semi-arid caatinga reaching 4°S, with counterparts in the tepuis of the Guyana Shield, including those in Roraima and Venezuela (Harley, 1995).

In southern and southeastern Brazil, large tracts of cold-adapted forests range from 1000 to 2000 m in elevation with a typical architecture dominated by gymnospermous taxa forming a 35-50 m height emergent layer of *Araucaria angustifolia* and lower canopy of *Podocarpus lamberti* or *P.sellowii* reaching 20 to 30 m (Hueck, 1966; Klein, 1975; De Oliveira, 1992). At the northernmost edge of this distribution range, *Podocarpus* is found in relictual populations in orographically controlled humid islands within semi-arid climates, isolated in the Pleistocene, as indicated by genetic data (Dantas et al. 2015). Pollen data from a peatbog located within the semi-arid caatinga domain of Northeastern Brazil (De Oliveira et al., 1999) indicate the presence of rainforest vegetation during the Late Pleistocene/Holocene, thus reinforcing the hypothesis of former connections between Amazonia and the Atlantic Rainforest via a then humid Caatinga. The discovery of fossilized leaves of rainforest taxa found in the late glacial calcareous tuffs in a modern Caatinga region by Cristalli (2006) added more support for this mechanism.

1.3. No-analog communities: ecological implications and significance

The concept of no-analog biological communities, i.e. communities compositionally unlike any found nowadays, was one of the most important conclusions derived from the analyses of Late Pleistocene/Holocene pollen records from lake sediments in North America by Davis (1981); Davis & Shaw (2001) and Huntley & Webb III, 1989). After examining the composition of former plant communities in over 700 geographical locations as ice expanded southwards due to establishment of the Würm/Wisconsin glaciation, it became clear that different forest species migrated following different routes in the North American continent forming plant associations without modern counterpart or analogs. This reshuffling of taxa was essential to bring light to the controversy on one of the most fundamental concepts in Ecology, i.e., the nature of biological communities. The prevailing and divergent points of view were given by Clements (1916) and Gleason (1926). The first, known as the Closed Community Concept, advocated that biological communities are fixed and unchanged through time, a concept that further permitted the elaboration of other important ecological concepts such as plant succession and climax community. The second, known as the Individualist Concept, supported by Gleason´s continuum model of plant distributions, i.e., that it is nearly impossible to devise where a community starts and ends due to the fact that their composition is not fixed through time as species' distributions (continuum) are controlled by their individual ecological requirements.

Similarly to this development in North America, former Late Pleistocene no-analog communities were also detected in palynological records in 1980´s and 1990´s in Ecuadorian Amazonia (Liu & Colinvaux, 1985; Bush et al., 1990), in the Brazilian Amazon (Colinvaux et al., 1996), in the Cerrado region of Southeastern Brazil (De Oliveira, 1992; Ledru, 1993) and in the semi-arid Caatinga (De Oliveira et al., 1999; Behling et al. 2000).

These novel associations of species during the Late Pleistocene probably impacted ongoing ecological relationships and plant distributions. For instance, in

Manuscript 6, a new line of evidence suggests that in southeastern Brazil, megafaunal populations started to decline much earlier than the Pleistocene/Holocene boundary, as a probable side-effect of changing plant communities (no-analogs) .and that the declining populations of large mammals did not support human predation, finally going extinct after the arrival of the first populations (Raczka et al., 2017).

1.4. Interpretation of Poaceae, Asteraceae in paleoclimatic studies

The dry facies of neotropical vegetation, principally savanna, but including the more wooded forms known as Cerradão, Caatinga and others, all have ground covers of grass and other herbaceous taxa and all yield pollen spectra in which Poaceae (Gramineae) pollen is predominant, possibly at 50% or more. Thus, any pollen spectra from the Amazon, Caatinga, Cerrado or Atlantic Forest regions without large grass percentages cannot represent dry habitats or climates. The converse proposition, however, that high Poaceae (Gramineae) always means drying, is not true. A common habitat for grasses in the humid tropical vegetation types of the lowlands in almost any Brazilian ecosystem is the floating mats that form in shallow lakes or slow-moving streams. The grass species that form much of the matrix of these mats are, of course, not the same species that grow in drier savannas, but their pollen cannot be distinguished with a light microscope—both sets of grasses appear simply with the classical morphology of Poaceae (Gramineae), i.e. unidstinguishalbe monoporate psilate grains. Other common habitats for grasses are low islands and mud-banks exposed by movements of river channels, which are often colonized by dense stands of savanna-like grasses and composites (Asteraceae). Both floating mats and mud bank islands inject grass pollen into what might well be a primary pollen signal for lowland tropical forest. When interpreting Poaceae and Asteraceae in a pollen diagram, therefore, the guiding principal should be the use of the entire pollen spectrum of each sample. If forest taxa continue alongside the expanded Gramineae spectra, the grass pollen cannot be considered evidence for drying or open landscapes. One good example of this problem is found within modern late successional

Araucaria forests of the Serra da Mantiqueira where various native species of bamboo grown on the dark ground level. Examples of forest bamboos are the genera *Merostachys* and *Chusquea*.

Another more subtly wrong interpretation of Poaceae maxima is inherently likely in pollen diagrams of bog or marsh deposits. Unlike sediments in deeper lakes, bog deposits are subject to surface drying from small changes in precipitation or from changes in drainage patterns in the local landscape. A result is that grasses and other weeds grow densely on the dry bog surface, resulting in local overrepresentation of grass and other herb pollen. Percentage statistics then require that the percentages of all other taxa in the pollen sum are reduced to accommodate the increased influx of grass and herb pollen derived from plants growing on the dried surface of the bog. Pollen analysts have sometimes fallen into the trap of using summary diagrams from such bogs to suggest that regional grasslands were expanding at the expense of forest, when the only real change was the drying of the sampled bog—possibly from climatic change, but possibly not.

Poaceae pollen (or sum herb pollen), therefore, cannot be used as an index fossil for savanna or other dry vegetation type. Nor are other herb pollen taxa useful as index fossils for savanna. One candidate pollen index fossil for savanna that has been proposed is the genus *Cuphea* (Lythraceae) (Absy et al., 1991) which has the nice advantage of being an easily identified pollen type. It is true that *Cuphea* species might be prominent in savannas and *Cuphea* pollen has recently been shown to reach 40% in some caatinga pollen spectra from northeastern Brazil (De Oliveira et al., 1999). However, many species of *Cuphea* occur in waterlogged conditions such as the Brazilian Pantanal during the wet season (Pott & Pott, 1994). Moreover, *Cuphea* shares with *Podocarpus,* Melastomataceae, and many other pollen taxa the property of having species adapted to many habitats. Some *Cuphea* species are understory shrubs of tropical forest. Moreover, some species are weeds of moist sites like stream banks, plants of which probably account for the few percent of *Cuphea* in the Late Pleistocene/Holocene Crominia pollen diagram (Ferraz-Vicentini, 1993), in central Brazil. More importantly, other *Cuphea* species are weeds of drying bogs. Thus a bog with a dry surface is likely to yield pollen spectra rich in Poaceae, supported by a few percent of *Cuphea* pollen, and probably with other common tropical weeds like *Borreria* as well. These taxa, severally or individually, are not index fossils for savanna. Thus, although a high percentage of grass pollen, probably with associated herbs, is always present in savanna or cerrado pollen profiles, high percentages of these herbs can be present for other reasons and do not stipulate regional aridity. When these pollen types are produced in floating mats or on river banks, they may not imply drying at all.

Asteraceae (Compositae) signals represent another line of contention between paleocologists not trained in Plant Sociology or Phytosociology. Although this plant family is traditionally interpreted in pollen analyses of northern hemisphere vegetation as indicator of herbs and open landscapes, the same rationale cannot and should not be applied in neotropical studies for many asteraceous taxa are actually trees of high elevation areas, as well as other habitats over large geographical areas in Brazil. Examples are the tree species *Dasyphyllum spinescens* and *Dasyphyllum tomentosum* which occur in high elevation Araucaria forests, *Eremanthus arboreus*, common in high elevation cerrados, *Eremanthus erythropappus*, an arboreal taxon typical in high elevation semidecidous forests as well as in the Atlantic Rainforest, *Gognatia polymorpha*, which displays high geographical amplitude*, Piptocarpha angustifolia* and *P. axilaris*, commonly found in high elevation and Araucaria forests, *Stifftia chrysantha*, which is found in high elevation Atlantic Rainforest, *Stiftia fruticosa* in the Atlantic Rainforest, *Vernonia discolor, in s*emi-decidous forest and high elevation Araucaria forest and *Wunderlichia cruelsiana*, a typical taxon of high elevation moist savannas (campos rupestres) of Central Brazil (Lorenzi, 2009, 1998, 1992). Although interpreted as arboreal, Asteraceae (Compositae) is generally included only in herb pollen percentages and displayed in the diagrams as such.

The pollen of three woody plant genera is useful as indicators of savanna, when considered in the context of the rest of the pollen spectra in which they appear. They are *Curatella* (Dilleniaceae), *Stryphnodendron* (Mimosoideae), and *Caryocar* (Caryocaraceae). The genus *Curatella* has only two species in the neotropics, both of which are plants of dry habitats, and *Curatella americana* being characteristic of savannas. *Stryphnodendron* pollen is dispersed in polyads like most of the large subfamily Mimosoideae, but distinctive enough to identify at the genus level. Both of these genera are strongly suggestive of savanna if the rest of the pollen spectra are also consistent with this vegetation type. But *Caryocar* has to be used, with more caution. *Caryocar* trees are an important constituent of savanna such that their pollen is expected to show in savanna pollen diagrams. Yet the genus also provides some of the largest trees in lowland tropical rain forest such *Caryocar edule* in the Atlantic Rainforest, so that the presence of the genus in a pollen diagram is not, by itself, an indicator of savanna (Prance, 1990). In the LGM record of Lake Pata (Colinvaux et al., 1996), *Caryocar* appears in the pollen diagram at the same time the local biota is represented entirely by lowland rainforest taxa in consortium with downslope migrating montane taxa such as *Podocarpus*, *Hedyosmum* and others. It is therefore necessary to interpret the presence of all supposed index taxa in the context of the whole pollen spectrum.

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CHAPTER 2

MANUSCRIPT 1 (unpublished)

Ice-Age forest connections: a mechanism for Atlantic-Amazonian speciation

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Abstract

The mechanisms that generate and maintain Amazon rainforest diversity are unresolved. Available paleoecological records from Amazonia do not provide evidence of mechanisms that generate speciation; yet regional species distributions and diversity are clearly not homogeneous. While congeners have distinctive distributions within Amazonia, many are also represented in the Atlantic rainforest, separated from modern Amazonia by dry cerrado vegetation. Biogeographic and genetic studies suggest a past linkage between the Amazonian and Atlantic forest systems, but the timing of that connection is not known. Here we report a fossil pollen record spanning two glacial cycles from the modern cerrado that shows the repeated expansion and contraction of forest during ice ages. The forest that occupied the cerrado region was a mixture of rainforest, cerrado, and cold-tolerant tree species without modern analog. Each range extension of forest into the cerrado held a slightly different balance of tree species, suggesting unique migrational opportunities for plants and animals. The most recent period of likely connection was between c. 114,000 and 70,000 years ago. We propose a bridge hypothesis as a mechanism promoting gene flow between the two forest regions during cool, mesic periods. The repeated opening and closing of forest corridors within ice-ages provides a mechanism creating alternating sympatry and allopatry: the ideal ingredients of a speciation pump.

Keywords: *Araucaria*, Atlantic rainforest, Cerrado, Pleistocene, Speciation, Brazil

INTRODUCTION

The mechanisms underlying the speciation of plants and animals and their biogeographic patterning in hyperdiverse systems such as Amazonia remain a conundrum. The sub-continental scale of Amazonia ensures that a single mechanism will not provide a single answer accounting for all patterns [1]. Tectonics [2,3], fluvial isolation [4], and climate change [5,6], are all potential drivers of Amazonian speciation. Tectonic uplift of the Andes separates Amazonian from Central American and Pacific coastal populations, providing the allopatry that fosters speciation [7,8]. Indeed, tectonic folding that extends into the Amazon Basin may be an important source of population isolation in much of western Amazonia [9]. Rivers bound some of the classic biogeographic regions of Amazonia [3], but do not appear to be a major barrier to gene transfer [10], especially in headwater regions [11]. Climate change offers the potential for truly large-scale habitat alteration and could provide an over-arching means to create allopatry, and hence fuel speciation or alternatively to induce niche adaptation through local extinctions or range expansions[12]. The largest changes in climate over the last few million years, have been glacial-interglacial cycles, and these have become the center of climate-based speciation arguments.

The most influential climate-based explanation of tropical diversity was the 'refugial hypothesis'[5], which suggested that ice-age aridity resulted in the rainforest contracting into isolated pockets surrounded by savanna grasslands. Speciation events are hypothesized to have occurred particularly frequently in these isolated forest fragments. When wet conditions returned, allopatry gave way to the observed modern parapatry. Although an elegant hypothesis, the forest fragmentation and isolation needed for this speciation pump was unsupported by paleoecological data [13]. Subsequent genetic studies have also shown that much of the speciation in Amazonia was actually far more ancient, taking place not in the Quaternary ice ages, but in the warmer world of the Miocene or Pliocene [14,15] or was at least continuous without an acceleration in the Quaternary [16,17]. Nevertheless, mid- or late-Pleistocene speciation was evident in some clades, often including relatively recently derived separations between Atlantic forest and Amazonian forest species [18,19]. Such a close relationship of Atlantic and Amazonian forests suggested physical linkage, but aridity-based explanations of speciation would have deepened the separation of these systems rather than provided connectivity.

Many genera, ranging from birds and rodents to butterflies and plants, have phylogenetic histories that indicate the movement of individuals between the Amazonian and Atlantic rainforests across what today would appear to be inhospitable cerrado [15,18,20]. Several different migratory corridors have been suggested connecting these biomes [21]. But such a connection requires that the systems are functionally wetter-than-modern, i.e., evapotranspiration rates have to fall to the point where forest can establish on cerrado [22]. Using fossil pollen analysis of ancient lake sediments, we reconstruct the vegetation history of Serra Negra Crater Lake (Fig. 1 and 2) across two glacial cycles to test whether connective forest corridors were established across the cerrado biome that currently separates Atlantic from Amazonian rainforests.

STUDY SITE

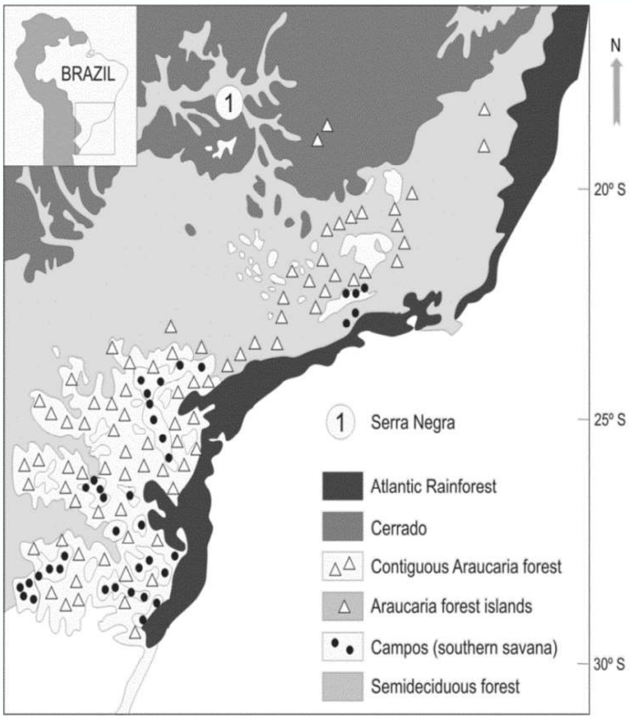

Fig. 1. Vegetation map of southeastern Brazil depicting the location of the Serra Negra Lake and aerial photograph taken of the Caldera during the 1960´s by the United States Air Force, prior to development of central Brazil.

The caldera, located between 18°55' and 19°00'S; 46°45'-46°57'W, has an approximate external diameter of 12 x 15 km and is located in the vicinity of the townships of Patrocínio and Guimarania in western Minas Gerais. Ringlike structures or dykes, surrounding the crater are composed of Precambrian/Cambrian quartzite rocks (Barbosa et al., 1970). The lake was most likely formed by collapse of the caldera due to dissolution of underground carbonatite (Barbosa et al., 1970), under a 200 m thick laterite crust (Gomes et al., 1990). Since 1989, the site was visited four times, and more recently in 2014, during both the dry and wet seasons and no significant difference in lake level was observed. Altitude of the inner crater rim varies from 1250-1273 m and elevation at the lake is 1200 m (Barbosa et al., 1970). Lake depth in most of its area is 0.50-1.00 m though 6 m deep at the coring site near its northern edge.

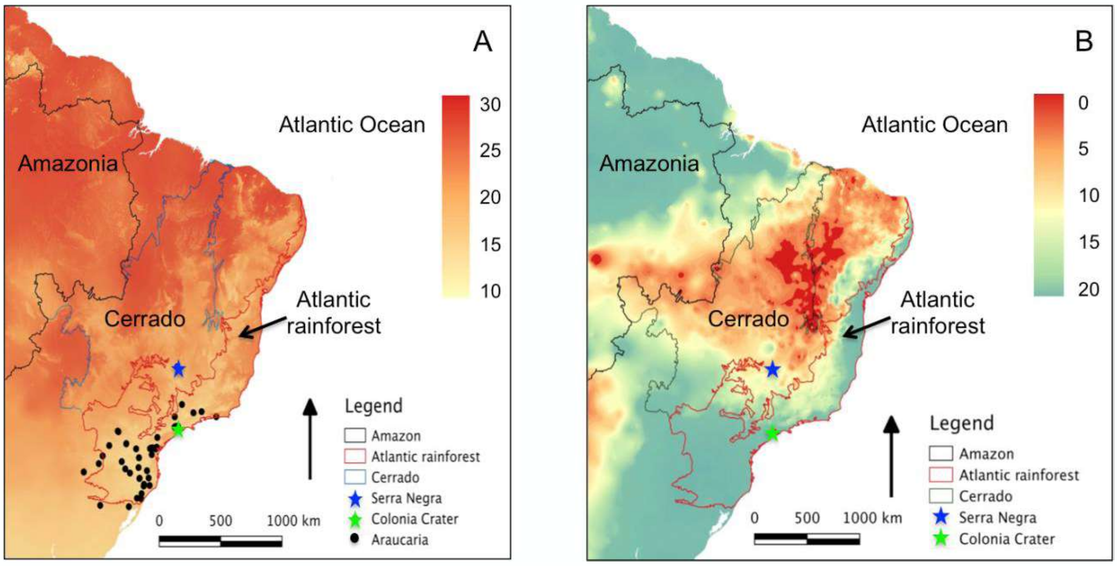

Fig. 2. Location of Serra Negra, and Colônia relative to major vegetation types in southeastern Brazil. Data are superimposed on a) temperature of the driest quarter also showing the locations of Araucaria angustifolia documented in BIEN 3.4 [23]; and b) precipitation of the driest quarter. Climatic data from Bioclim[24].

RESULTS

Pollen assemblages representing forest and cerrado conditions fluctuated on millennial scales during the two glacial cycles represented in a 7.82-m long sediment core retrieved from Serra Negra.

A sedimentary hiatus was evident at c. 1.1 m where there was almost no sedimentation between c. 32,000 and 17,000 years ago, i.e. during the Last Glacial Maximum (LGM). Pollen assemblages varied strongly through time and were divisible into warm cerrado, cool cerrado, and forest (Fig. 2). Poaceae, Cyperaceae, Asteraceae, with some woody taxa*, e.g., Mauritia, Qualea*, Malvaceae*,* Styracaceae*, Tabernaemontana*, and *Vochysia,* dominated cerrado vegetation. During the last glacial period, cold-tolerant arboreal elements, e.g. *Araucaria, Podocarpus, Myrsine*, and *Ilex* that do not normally inhabit cerrado were present in many samples indicating a cool cerrado. In forested periods a novel combination of taxa was formed by *Podocarpus*/*Myrsine*/Myrtaceae/*Ilex*-dominated forests that also contained coastal elements, e.g. *Alchornea*, together with Burseraceae (*cf. Tetragastris*) and *Astronium*, *Stryphnodendron*, *Qualea*, *Copaifera*, *Sebastiania*, *Sapium*, Arecaceae and others found more commonly in cerrado and semi-deciduous forests.

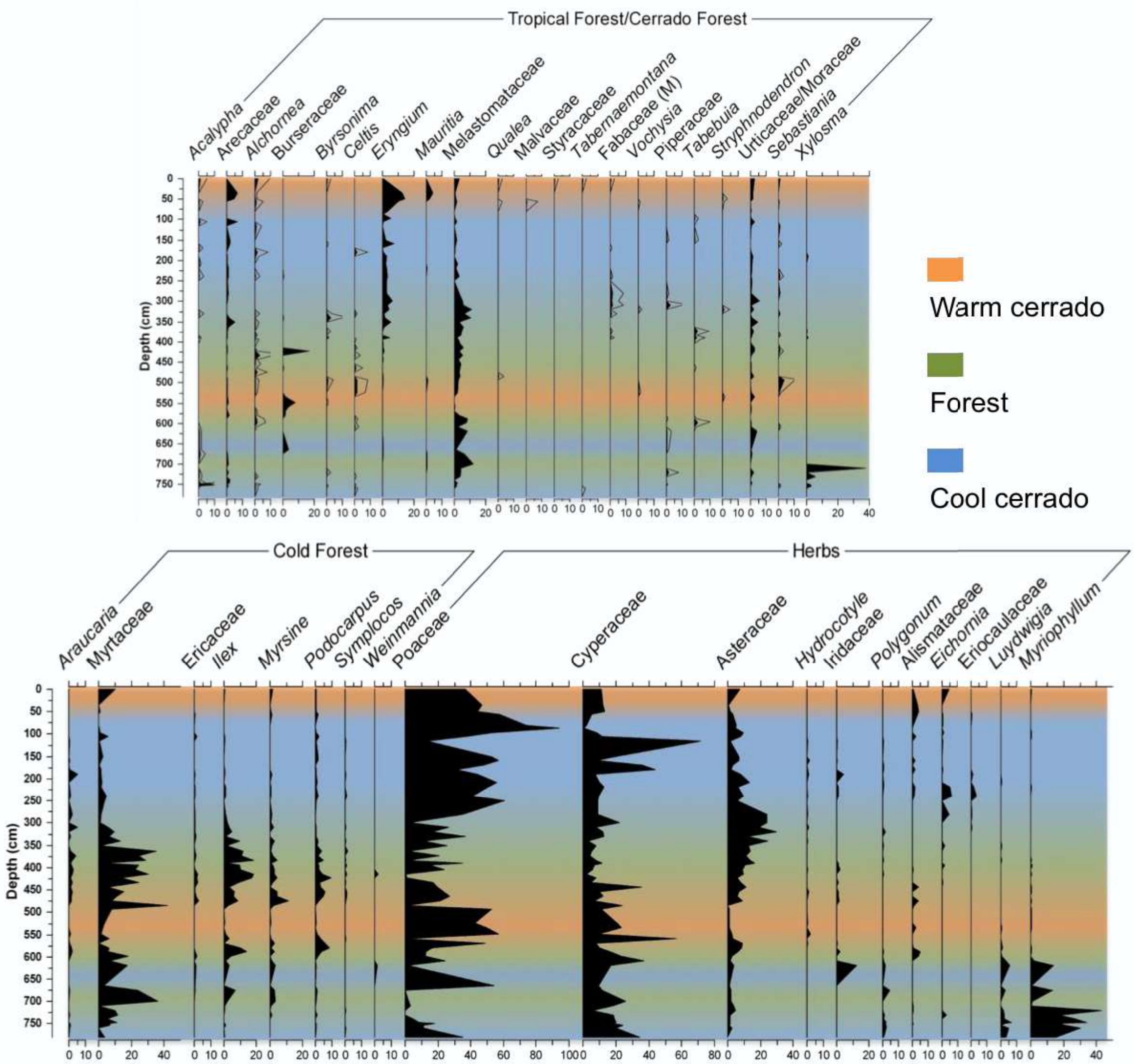

Fig. 3 Vegetation shifts between cool cerrado, forest and warm cerrado documented in the fossil pollen record from Serra Negra. Background colors indicate assemblage type. Times when Serra Negra supported forest are the most likely for conections between Amazonia and the Atlantic rainforest. Outlined values represent a 5x exaggeration.

Between core depths of 5.4 m and 5 m was the only time beyond the range of ^{14}C dating that a cerrado without cold elements occupied the site. We assume that the last interglacial was at least as warm and dry as today, and hence was a time when warm cerrado would have been present. By assigning 5.4 m core depth as the onset of the last interglacial, an age of 130,500 years was derived from the EPICA ice-core record, and used as a tie point (Fig. S2). A linear interpolation of ages between 130,500 and the limit of ^{14}C dating provides the remainder of the chronology. For simplicity, this interpolated rate was extended downcore, though no weight is placed on interpreting the age of these older events.

Forest that contained a mixture of rain forest, cerrado and cool elements occupied the Serra Negra site between c. 114,000 and 70,000 years ago. Forests also occurred during undated portions of the preceding interglacial.

DISCUSSION

Cool cerrado and forests that included elements such as *Araucaria*, *Podocarpus* and *Weinmannia*, occupied Serra Negra for longer intervals than warm cerrado. The Serra Negra fossil pollen data indicated multiple forest invasions of this modern cerrado landscape during the last two glacial cycles. The last such expansion probably occurred c. 114,000 years ago and lasted until c. 70,000 years ago (Fig. 4). Similar pollen spectra were reported from a sediment core raised at Colônia (Figs. 2 & 4) in the coastal Atlantic rainforest almost 550 km due south of Serra Negra [25,26]. The Colônia fossil pollen record spanned c. 140,000 years, and featured a forested landscape throughout the last interglacial (Fig. 3c). In the glacial inception this forest supported cool-tolerant elements, such as *Podocarpus* and *Araucaria* and, just as at Serra Negra, there was a transition from forest to more open conditions at c. 70,000 years ago. Colônia had a less continental climate than Serra Negra and so the extent of vegetation change was not as extreme.

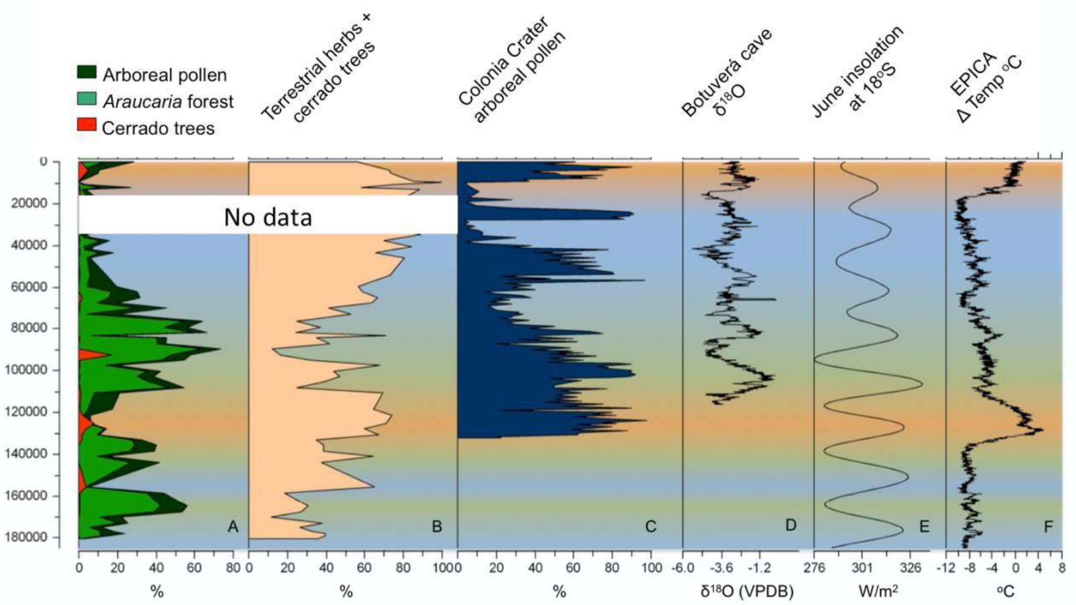

Fig. 4. Vegetation change at Serra Negra plotted against time relative to paleoclimatic and paleoecological data and Marine Isotope Stages (MIS) [27]**. Percent arboreal pollen (a) and cerrado elements (b) from Serra Negra; c)** Arboreal pollen from Colônia [26], d) precipitation data based on the speleothem isotopic record from Botuverá Cave [28], e) June insolation [29], and f) the EPICA temperature profile[30]. The background shading follows that of Fig. 3.

The interglacial forests of Colônia were similar to modern Atlantic rainforest, providing additional support for our suggestion that the interglacial Serra Negra vegetation should be similar to that of the Holocene. Consequently, the modern division between coastal Atlantic forest and Amazonian forest existed during the last interglacial. Both Colônia and Serra Negra show open vegetation between 70,000 years ago and the onset of the Holocene, but for the period between c. 114,000 years ago and 70,000 years ago there was forest at both sites and a strong probability that a forest corridor connected Amazonian and Atlantic forests.

The forested phase at Serra Negra were strongest during wet phases at Botuverá Cave (more negative isotopic values; Fig. 4d), which in turn reflected precessional forcing (Fig. 4e). However, as temperature fell below a threshold, wet events were insufficient to maintain forest and a cool cerrado formed. During the driest time in the glacial period, between 32,000 and

17,000 years ago, there was a depositional hiatus at Serra Negra, although sedimentation at Colônia appears to have been continuous. Nevertheless, even at Colônia, forest was replaced by grassland [26]. If it is assumed that both settings were primarily grasslands at this time, this would have been a brief window of opportunity for savanna species to forge connections between northern and southern populations [31,32], so long as they could acclimate to significantly colder-than-modern conditions.

The forested landscapes of Serra Negra were in continuous compositional flux through the last two glacial cycles. The density of the forest cover differed from one stadial to the next, with some being more open, e.g. at 1.1 - 1.8 m core depth, whereas others appear to have been closed-canopy systems, e.g. at 3.5 - 4.8 m depth. Throughout these episodes the Serra Negra pollen record contained mixtures of species that do not co-occur today. Known as non-analog assemblages, these mixtures of presently allopatric species were first identified as co-occurring during periods of rapid climatic change, especially deglacial warming [33,34]. In South America, non-analog floras were described from both lowland and montane settings [35,36], but in the cerrados of southeastern Brazil they were a long-term component of the landscape rather than being associated with the deglacial [37].

Our data suggest that at either glacial extreme the conditions were too dry or too cold for connections to be made between the Amazonian and Atlantic rainforests. In times of high net moisture availability, as species migrated from the Atlantic forests into the Amazonian interior or vice versa, populations crossed regions that would become a barrier to gene flow as conditions returned to a low net moisture state. This repeated expansion of populations followed by isolation provided bridging opportunities for allopatry and speciation. The mechanism we propose did not require substantially drier-than-modern conditions and forest fragmentation, but rather relied on forest expansion to connect adjacent populations. While the aridity required for the refugial hypothesis has not been supported by paleoecological data[38], evidence for glacial-age cooling and only moderate changes in precipitation are supported by proxy data from fossil pollen and isotopic records [39-42].

The refugial hypothesis [5] relied on the peaks of glacial oscillations to provide disjunctions at the glacial maximum and re-unification in the interglacial. Thus the most extreme glaciations, i.e. those of the last 650,000 years would have been the most likely to meet Haffer's model (Fig. 5). Little evidence exists, however, to support that speciation in this period was higher than in earlier times[16,43,44]. By contrast, our bridging model suggests that the peak connectivity occurred during phases of moderate cooling and evapotranspirative stress rather than at peak warming. If the timing of forest, cerrado and cool cerrado conditions (Figs. 3 & 4) are applied to the δO^{18} curve of the stacked LR04 record, it is possible to look back in time for when similar conditions are likely to have occurred (Fig. 5). Note that plant migrations during inception and termination of 100 k-world glaciations will follow the asymmetry of temperature, with slow cooling during inception allowing migration to occur, whereas the rapid warming of terminations may have skipped intermediate assemblages, i.e. the forested settings, as systems transitioned directly from savanna or cold cerrado to warm cerrado.

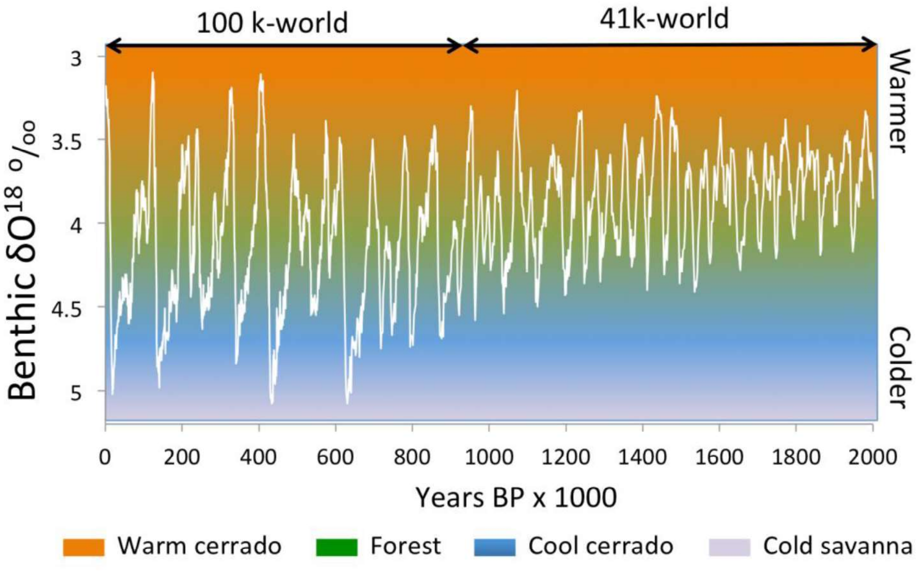

Fig. 4: Hypothesized vegetation for the Serra Negra region over the last 2,000,000 years. The stacked marine LR04 isotope record[27] provides an approximation of relative temperatures expected in southeastern Brazil.

Vegetation types evident in the fossil pollen spectra during the last glacial were extrapolated back through time. Colors follow those of Fig. 3. The 41 k-world is seen to have oscillated between forest and cerrado, whereas the larger glacial-interglacial variability of the 100 k-world led to colder cerrados and savanna expansions. This depiction raises the hypothesis that maximal forest connectivity between the Amazonian and Atlantic rainforest was in the early Pleistocene.

A major division within the Quaternary was the transition form glacial-interglacial cycles following a rhythm of 41,000 years, known as the ‘41 k-world’, to longer cycles approximating 100,000 years, and hence the ‘100 k-world’[45]. In the marine stacked record, the range of δO^{18} values that correspond to the forested period at Serra Negra between 114,000 and 70,000 years ago lie between 3.85 and 4.3 ^{o}/oo. If this range is projected back in time, it provides a first approximation of when the forest corridor may have existed. In the 41 k-world prior to c. 900,000 years ago, about 57% of time lay within the forested range, whereas in the 100 k -world this fell to c. 32% (Fig. 5). Similarly, the proportion of time in warm cerrado would have been c. 38% and 21% in the 41-k and 100 k -worlds, respectively (Table S2). It is also notable that the extreme conditions that resulted in savanna forming at Colônia and in a sedimentary hiatus at Serra Negra were restricted to the 100 k-world. Indeed, conditions for cool cerrado were rare in the 41-k world at just 5% compared with 30% of time in the 100 k-world. Thus the climatic transitions of the Quaternary not only produced novel assemblages but also novel biomes that would not have been filled with new species, but with species capable of adapting to those conditions, hence novel biogeographic distributions.

Forest expansion during wet interstadials provided connectivity between the systems, but those connections were not uniform in their suitability for species migration. While some species might freely migrate through any partially forested landscape (Fig. 6), for many other species forest structure and composition may have been important factors determining suitability. Indeed, the densest forest could act as a barrier to species that only thrive in lightly wooded habitats. Thus, the simple presence of forest does not immediately imply suitable habitat for all species to migrate.

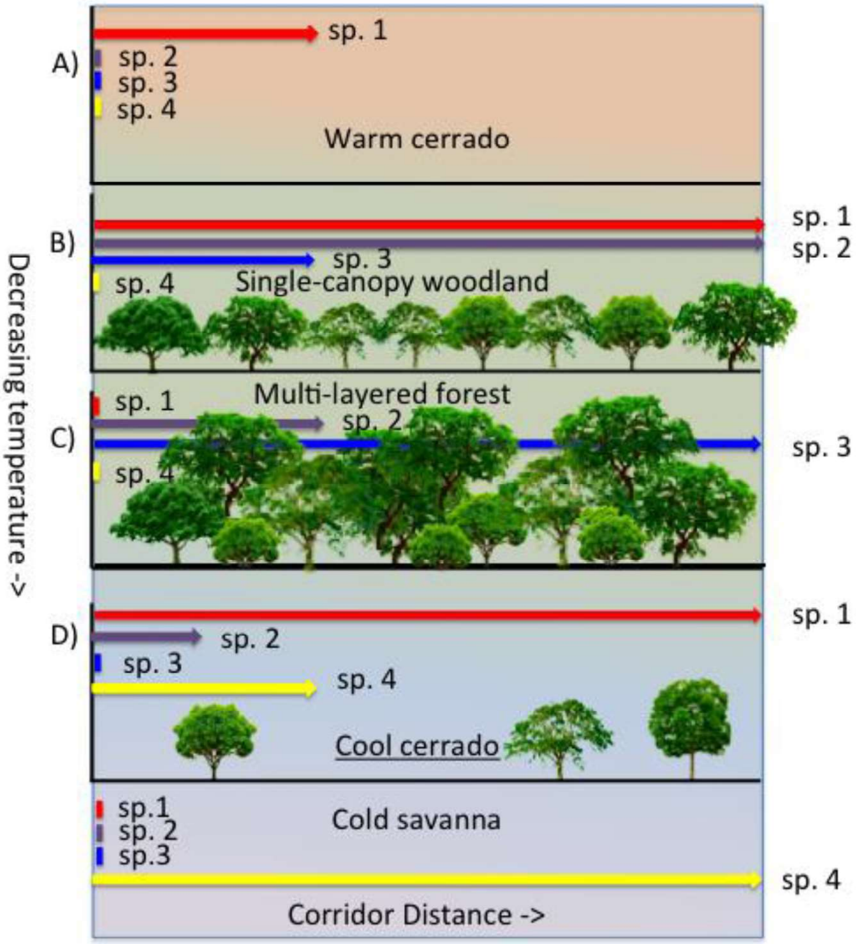

Figure 6. Schematic diagram showing individualistic migrations of taxa not belonging to warm cerrado and limitations under differing conditions. Three hypothetical forest species, and one savanna species illustrate varying tolerances to conditions in a migrational corridor. Arrows represent capacity to cross the region. A short arrow indicates that a microrefugium might be reached even if the entire distance cannot be crossed.

Another aspect of the migration is that the geographic spread of species may have originated from microrefugia[46,47]. Microrefugia are locations with anomalous local climates compared with the surrounding environment that are less hospitable [47]. Species that would otherwise go locally extinct due to climatic adversity can sustain populations in these settings. Population expansions from microrefugia are thought to have accounted for the rapid expansion of tree species in response to climate change in settings ranging from Central America to Europe[48-50]. The capacity of a microrefugium to sustain isolated populations is a function of the degree and duration of isolation, and the size of the population. All microrefugia have a finite chance of extinction due to happenstance, and so the shorter the isolation period the greater the probability of survival[51]. The period of isolation would have been strongly influenced by the magnitude and frequency of ice ages.

In the 41 k-world forest microrefugia suffered brief isolations compared with the longer glacial cycles of the 100 k-world (Fig. 7). Consequently, microrefugial populations would have been viable when cool conditions returned, promoting rapid forest expansion. Contrastingly, the 100 k-world would have offered possibilities for savanna expansions and grassland microrefugia.

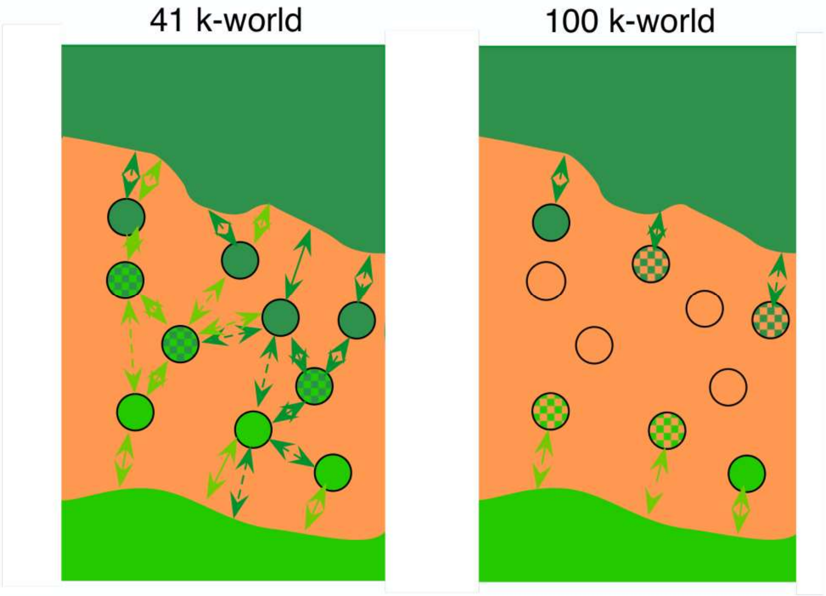

Fig. 7. Schematic diagram showing the influence of short versus long isolation of microrefugia. Microrefugia are color-coded to show the dominance of species from the nearest source area. Some connection

arrows are shown to illustrate stronger movement (solid arrows) from the source area, and weaker connectivity at increasing distance (dashed arrows). In the 41 k-world isolation times are short and microrefugial population persistence is high. Under the 100 k-world scenario there is a greater probability that microrefugia at great distance from the source areas would go locally extinct.

Microrefugia could also have offered genetic stepping stones. Even if species could not cross the entire distance between the Atlantic coastal forest and Amazonia, their populations may have spread to the nearest microrefugium. Such range expansions may have meant the addition of a new species to an existing biota or a genetic infusion to existing microrefugial populations, which would have increased the probability of population survival until the next opportunity for range expansion. Repeated opening and closing of genetic connectivity between the Atlantic and Amazonian rainforests provide an important long-term speciation pump and also, perhaps as importantly, influenced biogeographic distribiutions of species in southeastern Amazonia and the Atlantic rainforests of Brazil.

Methods

The crater lake of Serra Negra, also known locally as Lagoa do Chapadão (18°54’35’’S; 46°53’20’’W) occupies a shallow basin 2.5 x 4 km in diameter. No significant difference in lake level was observed in four site visits during both the dry and wet seasons between 1989 and 2014. Altitude of the inner crater rim varies from 1250-1273 m and elevation at the lake is 1200 m [52]. Lake depth in most of its area is 0.50-1.00 m, with a maximum depth of 6 m at the coring site.

Data from the nearest meteorological station in the town of Patrocínio (15 km from the crater) indicate that Serra Negra receives c. 1600 mm in annual precipitation, which is unevenly distributed throughout the year. Spring and summer months (September to February) account for 80% of rainfall. Mean annual temperature is 21.9°C, mean temperature of the coldest month (June) is 18.8°C, and of the warmest month (October) 24°C. Frontal incursions of Antarctic air can bring freezing temperatures in the winter months (JJA) to southern and southeastern Brazil [53].

Both cerrado and cerradão (tall forest-like savanna), are found as fragments of the original vegetation within the Serra Negra caldera. Typical elements of these vegetation types found at the edge of the lake are *Caryocar brasiliense* (Caryocaraceae), *Qualea grandiflora* (Vochysiaceae), *Kielmeyera coriacea* and *Kielmeyera* sp. (Clusiaceae). Members of Vochysiaceae, especially *Vochysia thyrsoidea*, are more common on the higher and drier soils. Cerrado elements also occurring in better-drained soils are *Jacaranda decurrens* (Bignoniaceae), *Lafoensia densiflora* (Lythraceae), *Palicourea rigida* (Rubiaceae), *Pouteria* spp. (Sapotaceae), *Psidium* spp. (Myrtaceae), *Solanum grandiflorum* (Solanaceae), *Stryphnodendron adstringens* (Mimosaceae) as well as many Asteraceae, herbs, and grasses (Poaceae).

Cold-tolerant elements such as *Podocarpus* and *Araucaria*, have more southerly distributions, primarily at latitudes > 24 °S, although isolated populations occur in highland areas at lower latitudes (Fig. 2a).

A modified Livingstone piston-corer from a platform supported by inflatable boats [54] was used to raise the 7.82 m-long core in 1989. Core sections were sealed in the field and returned to the laboratory for subsequent analyses at The Ohio State University, Columbus, Ohio, USA.

Before opening, cores were x-radiographed with a Norelco MG-150 X-ray unit on a 1:1 scale in order to confirm absence of disturbance of sedimentary layers by the coring process [54]. Sediment type and Munsell color were recorded as soon as the core was opened and subsampled. A total of 65, 1 cm^3 subsamples, were collected at 10 cm depth intervals along the sediment sequence. A chronology for the record was derived from ^{14}C bulk radiocarbon dating of 15 samples calibrated using the southern Hemisphere correction[55]. Radiocarbon infinity (> 43,500 years) was reached by 2.3 m core depth (Table 1S) and the chronology for the remainder of the core is a linear interpolation between 43,500 and 130,500 years ago, modified by a single tie point tuned against the EPICA ice-core record (Fig. S2) [30].

Standard palynological techniques were used: HF treatment, acetolysis [56] and spiking the sample with exotic *Lycopodium clavatum* spores, containing 11,300 ± 300 spores, to facilitate calculation of pollen concentrations [57]. The final residues were stained with 2% safranin solution and mounted in glycerol. Pollen was counted to a total of 300 terrestrial pollen grains.

Identification of palynomorphs was based on our reference collection of more than 7,000 neotropical pollen and the collections of M.L. Salgado-Labouriau, Universidade de Brasília and of M.L. Absy, INPA-Manaus, and published keys e.g. [58,59-62]. Modern reference materials for the flora of southern and southeastern Brazil were collected at the herbaria of the Field Museum of Natural History, New York Botanical Gardens and the Missouri Botanical Gardens. Pollen percentages, concentrations were calculated and plotted using C2 [63].

Data availability: Fossil pollen and radiocarbon data from Serra Negra will be made available on Neotoma <https://www.neotomadb.org>.

Acknowledgments

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CHAPTER 3

MANUSCRIPT 2 (unpublished)

THE BRAZILIAN ATLANTIC FOREST DURING THE LATE QUATERNARY: EXPANSION INDUCED BY TROPICAL INCURSION OF POLAR AIR MASSES

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Abstract

The origin of modern disjunct plant distributions in high elevations in Brazil with strong floristic affinities to distant montane rainforests of isolated mountain tops in northeast, northern Amazonia and the Guyana Shield remains unknown. To address this issue we mapped the presence/absence of taxa such as *Araucaria, Podocarpus, Drimys, Hedyosmum, Ilex, Myrsine, Symplocos, Weinmannia*, Myrtaceae and Ericaceae in paynological records and predicted potential distributions for each element during the Last Glacial Maximum and Heinrich Stadial 1, later combined each habitat suitability map into one single map of all montane rainforest taxa analysed. The data reveals two long distance patterns of plant migration connecting south/southeast to northeastern Brazil and to Amazonia suggesting a scenario of relative lower continental surface temperatures augmented by the effects of polar air incursions into the Brazilian Highlands. Total annual precipitation based on hourly rainfall estimates of modern distribution of *Araucaria angustifolia* and *Podocarpus lambertii* supports humid and cold conditions within those migration routes.

Keywords: Palynology, Late Pleistocene, montane forests, Brazil, highlands, migration

INTRODUCTION

The origin of disjunct vegetation types in mountainous landscapes of southeastern and central Brazil displaying strong affinity to humid montane floras of northern South America remains unknown. Earlier hypotheses[1] suggested ancient cold and humid migration corridors possibly in the Eocene or Miocene, later affected by Quaternary climatic, which could have allowed ancient contact between populations now isolated in mountain tops by inhospitable climate in the lowlands. In this work we investigate the impact of enhanced precipitation under lowered temperatures, ca. 5°C depression [2,3] during the Last Glacial Maximum (LGM), c. 25 – 17.5 K cal. Yrs BP, extendind into Heinrich Stadial 1 (H1) from 17.5 K – 14.6 K cal. yrs BP, on the distribution of cold-adapted montane tropical taxa belonging to the Atlantic Rainforest of southern/southeastern Brazil. We hypothesize that during the late glacial cycle intensified polar circulation with incursions of polar air masses, under a less intensified Hadley circulation over South America and relatively reduced insolation levels, promoted conditions suitable for the establishment of migration corridors for the expansion of montane forest niches. These former connections between southeast and central Brazil, 31° to 22 °S, and southeastern Amazonia could therefore explain much of the modern occurrence of disjunct humid and cold-adapted taxa in elevated areas of cerrado and semi-arid caatinga reaching 4 °S, with counterparts in the tepuis of the Guyana Shield, including those in Roraima and Venezuela[1]. In southern and southeastern Brazil large tracts of cold-adapted forests range from 1000 to 2000 m in elevation. These forests possess a typical architecture dominated by gymnospermous taxa forming a 35-50 m height emergent layer of *Araucaria angustifolia* and lower canopy of *Podocarpus lamberti* or *P.sellowii* reaching 20 to 30 m. At the northernmost edge of this distribution range, *Podocarpus* is found in relictual populations in orographically controlled humid islands within semi-arid climates, isolated in the Pleistocene, as indicated by genetic data (Dantas et al., 2014). Pollen data from a peatbog located within the semi-arid caatinga domain of Northeastern Brazil indicate the presence of rainforest vegetation during the Late Pleistocene/Holocene, thus reinforcing the hypothesis of former connections between Amazonia and the Atlantic Rainforest via a then humid Caatinga [4]. The discovery[5] of fossilized leaves of rainforest taxa found in the late glacial calcareous tuffs in a modern Caatinga region added more support for this mechanism.

We infer vegetational and correlated climatic changes by analyzing pollen abundance of 10 selected arboreal taxa. The selected cryophylic or cold-adapted genera or families are *Araucaria, Podocarpus, Drimys, Hedyosmum, Ilex, Myrsine, Symplocos, Weinmannia*, Myrtaceae and Ericaceae were chosen based on their common presence in glacial pollen signals of tropical America [6–12]. A detailed survey of Late Pleistocene palynological literature in Brazil reveal a total of 32 pollen profiles obtained from continental sedimentary records of the Brazilian Highlands (800 – 2600 m elevation) containing LGM age sediments (Figures 1 and 2), by number and name of the locality, corresponding to the locations numbered in Figures 1 through 6, showing the distribution of different indicator taxa.

1. Cambará do Sul (Behling et al., 2004); 2. São Francisco de Assis (Behling et al., 2005); 3. Serra da Boa Vista (Behling, 1995); 4. Serra do Tabuleiro (de Oliveira et al., 2012); 5. Pato Branco (Bertoldo et al., 2014); 6. Volta Velha (Behling and Negrelle, 2001); 7-8. Ilha do Cardoso (Pessenda et al., 2012; Vidotto, 2008); 9. Curucutu (Pessenda et al., 2009); 10. Rio Pardo (Bissa and de Toledo, 2015); 11. Lagoa de Itaipu (Bartholomeu, 2010); 12. Monte Verde (Siqueira, 2012); 13. Campos do Jordão (Behling, 1997); 14. Catas Altas (Behling and Lichte, 1997); 15. Lagoa dos Olhos (De Oliveira, 1992; Raczka et al., 2013); 16. Salitre (Ledru, 1993); 17. Serra Negra; 18. Serra do Espinhaço (Horák-Terra, 2013); 19. Buritizeiro (Lorente et al., 2013); 20-21. Crominia (Ferraz-Vicentini, 1993; Salgado-Labouriau et al., 1997); 22 and 23 Turfa de Inhumas (Ribeiro et al., 2003; Rubin, 2003); 24 Lagoa Bonita (Barberi, 2001); 25 Águas Emendadas (Barberi et al., 2000); 26 Chapada dos Veadeiros (Ferraz-Vicentini, 1999); 27 and 28 Serra dos Carajas (Absy et al., 1991; Hermanowski et al., 2012); 29 Lago Caçó (Ledru et al., 2006, 2001); 30 e 31 Lagoa da Pata (Colinvuax et al. 1996).

Migration routes during glacial conditions

Our data reveal constant presence of humid forest elements in montane corridors following two main distribution patterns along a general south-north route: 1. Southern-southeastern Brazil to southern Amazonia (SSA) Route, via Serra do Mar/Mantiqueira, Serra do Espinhaço, Central Brazilian Plateau:

Podocarpus, *Ilex*, *Myrsine*, *Hedyosmum*, Myrtaceae; 2. Southern-southeastern Brazil (SSB) Route, following the Serra do Mar/Mantiqueira and Serra do Espinhaço: *Araucaria*, *Drimys*, *Symplocos*, *Weinmannia* and Ericaceae. The presence of *Podocarpus* and *Araucaria* in LGM records, given as examples of the two proposed migration routes, is shown on Figs. 1 and 2, respectively.

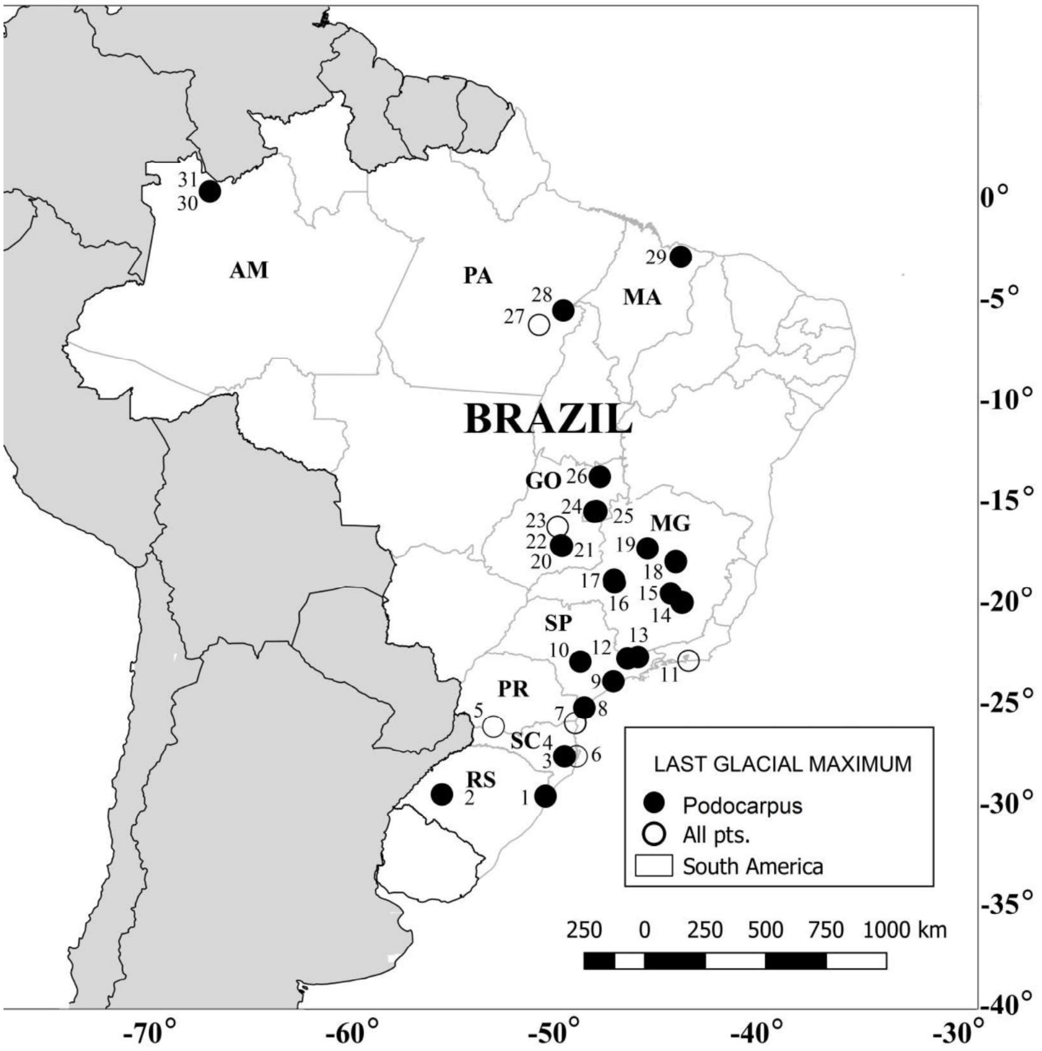

Fig 1. Presence (black circles) and absence (clear circles) of *Podocarpus* pollen in LGM records of Brazil.

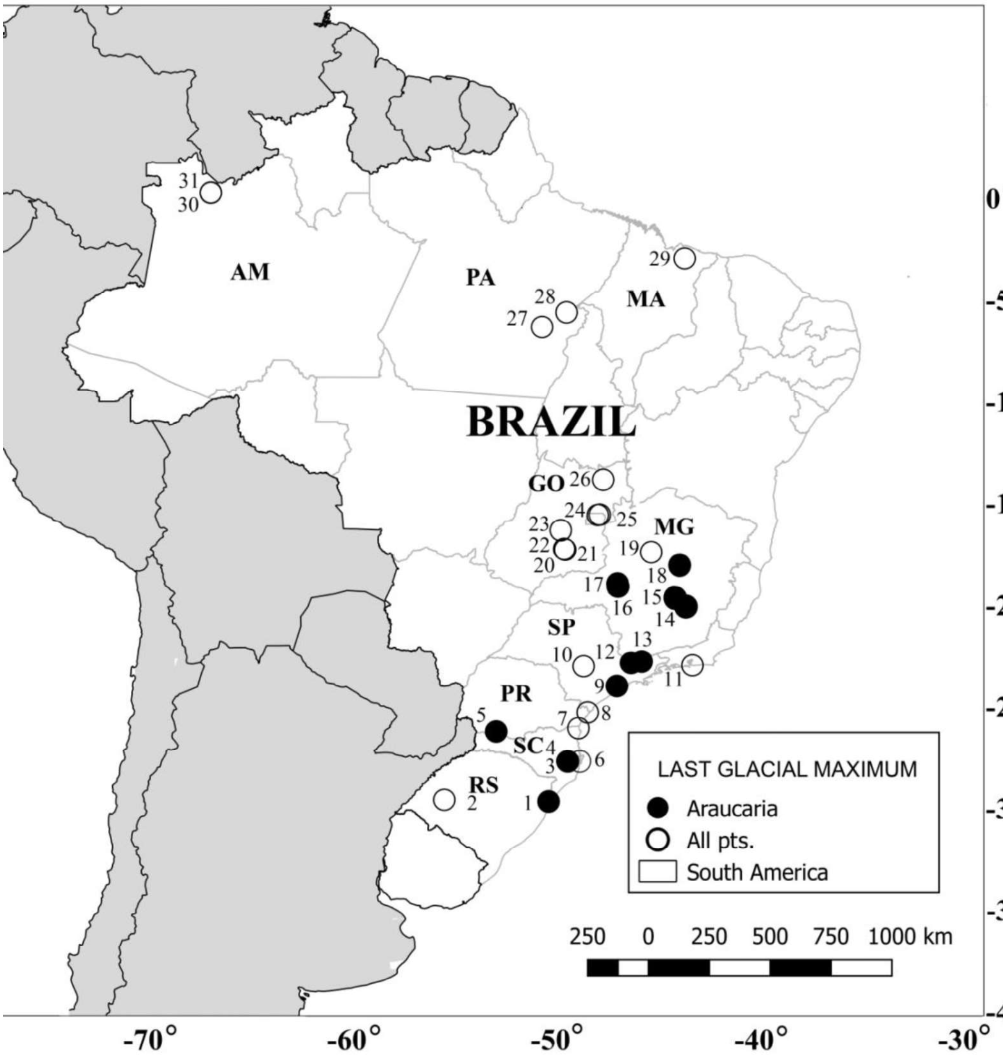

Fig 2. Presence (black circles) and absence (clear circles) of *Araucaria* pollen in LGM records of Brazil.

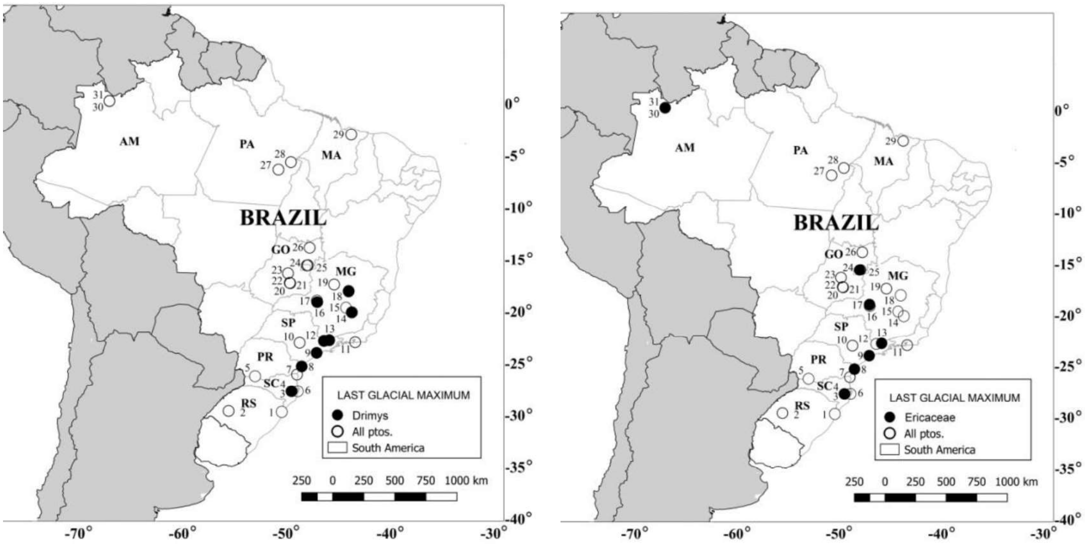

Fig 3. Presence (black circles) and absence (clear circles) of *Drimys* and Ericaceae pollen in LGM records of Brazil.

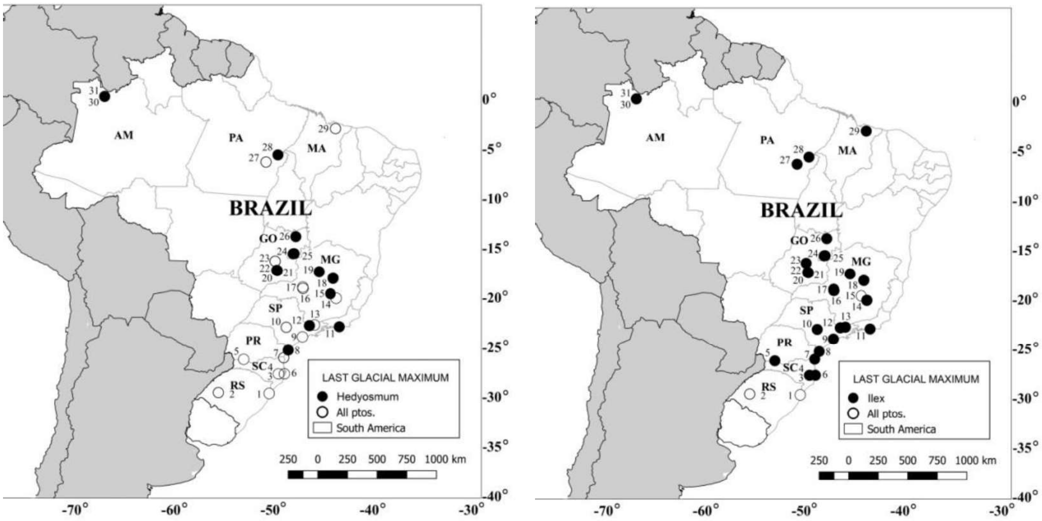

Fig 4. Presence (black circles) and absence (clear circles) of *Hedyosmum* and *Ilex* pollen in LGM records of Brazil.

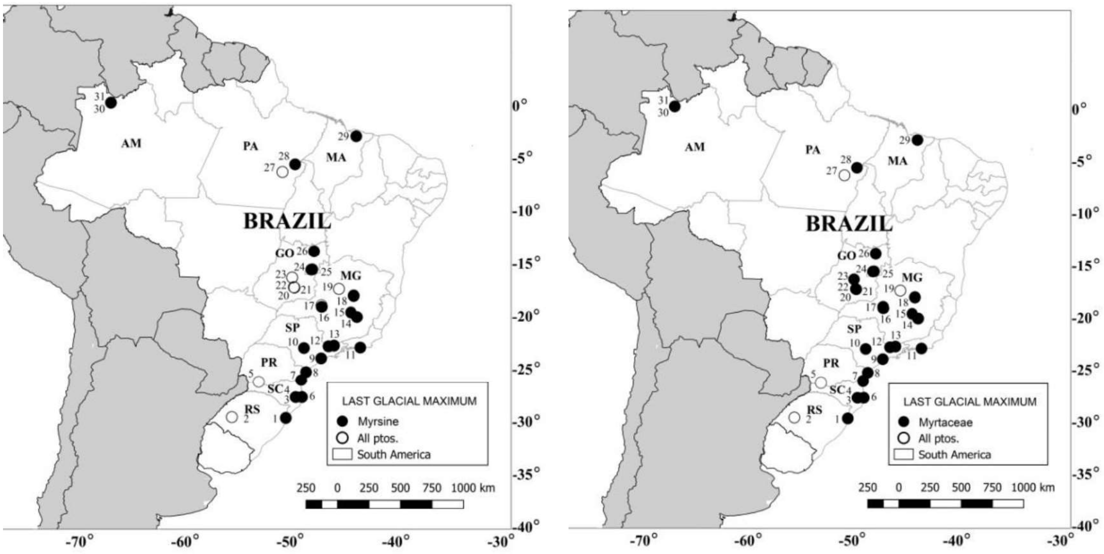

Fig 5. Presence (black circles) and absence (clear circles) of *Hedyosmum* and *Ilex* pollen in LGM records of Brazil.

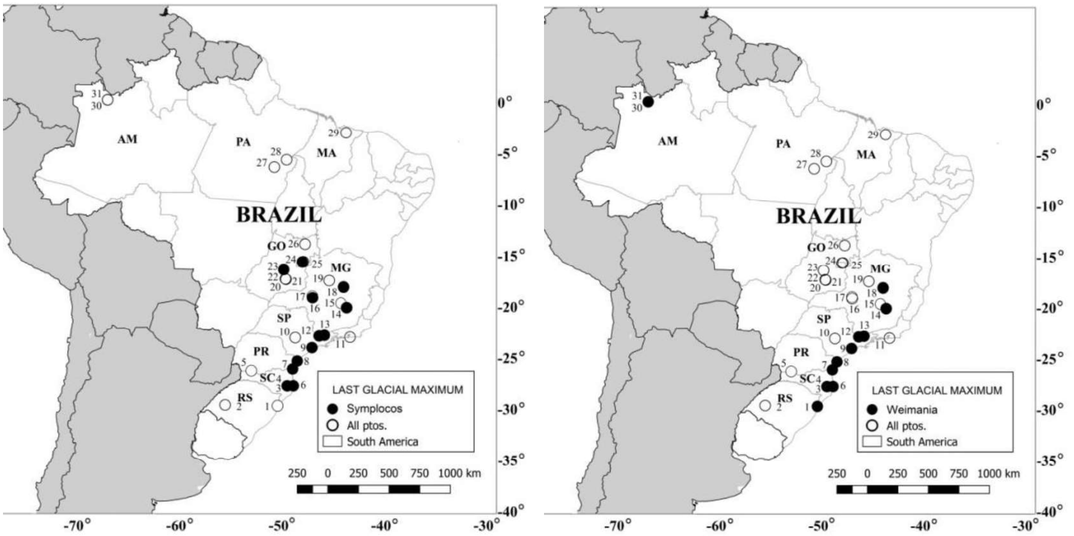

Fig 6. Presence (black circles) and absence (clear circles) of *Symplocos* and *Weinmannia* pollen in LGM records of Brazil.

Montane Niche Suitability during the LGM

From the habitat conditions at the sites where those taxa occur, it is possible to obtain a Species Distribution Model (SDM) for the Brazilian highlands. SDM link species distribution , observed in pollen fossil records, to environmental data (Elith et al., 2006). These models use spatial environmental data bioclimatics variables from Last glacial Maximum to make inferences on species range limits and habitat suitability (Hutchinson, 1957; Soberón and Nakamura, 2009; Peterson et al., 2011). A distribution map of average twenty bootstrap models for each taxa are produced with the MaxEnt modelling tool (Phillips et al., 2004; 2006; Elith et al., 2011), this map is an estimate of the potential distribution of the species for a given area, with values in a logistic scale from 0 to 1, where 1 is the maximum habitat adequability for the occurrence conditions of the species.

A Jacknife test was used to estimate the contribution and importance of each bioclimatc variable, estimating the gain when the variable is applied and the loss when the variable is omitted [Quenouille, 1956]. The AUC (Area Under the receiver operating characteristic Curve) is used to evaluate the predictive performance of those models, that is the measure of the model's ability to discriminate between omission and overlap of non-occupied areas (Elith et al., 2006)..

Niche suitability maps for *Araucaria* and *Podocarpus* are shown on Fig. 7, *Drimys* and *Hedyosmum* (Fig. 8), *Ilex* and *Myrsine* (Fig. 9), Myrtaceae and *Symplocos* (Fig. 10) and for Weinmannia (Fig. 11). Niche suitability for *Podocarpus* during most of the last glacial cycle closely matches the north/south two-forked orientation of the Brazilian highlands. This habitat was widened along a N-S axis and a W-E transect, specially in elevations above 600 m in contrast to current distribution above 1000 m elevation in southeastern Brazil. These taxa extended from southern/southeastern coast at 30°S, to the central elevated regions, thus reaching southern Amazonia at 4°S, describing an arch-like route. The suggested high niche suitability for these taxa, within this area, is also indicative of the geographical expansion of cold climates, notably in central Brazil.

During all the cold phases related to the LGM, *Araucaria*, *Drimys*, *Symplocos*, *Weinmannia* and Ericaceae maintained very definite ranges extending from coastal Santa Catarina to coastal São Paulo and Serra da Mantiqueira, reaching central Brazil latitudes in northern Minas Gerais. During the time of prevailing cold surges of the last glacial cycle the southernmost limit of *Araucaria* and *Weinmania* was reached in southern limit of the Brazilian Highlands in northern Rio Grande do Sul, in elevations around 1100 m. In contrast, the northern distribution limit of these cold-adapted taxa reached 18°S latitude as shown by the Serra Negra and Serra do Espinhaço records. One significant result is the general absence of *Araucaria* and other cryophyllic taxa during the LGM in areas where their presently abundant such as in the southern states of Parana, Santa Catarina and Rio Grande do Sul.

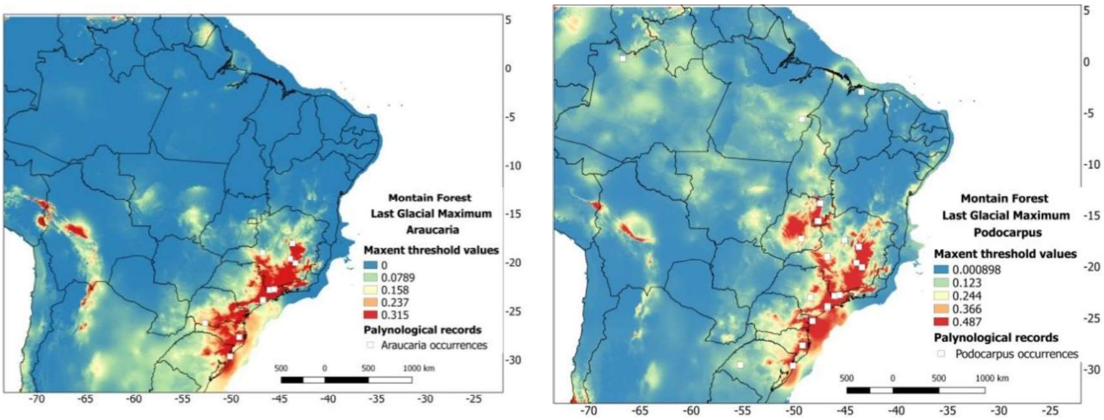

Fig 7. Niche suitability (MaxEnt) for *Araucaria* and *Podocarpus* in LGM records of Brazil.

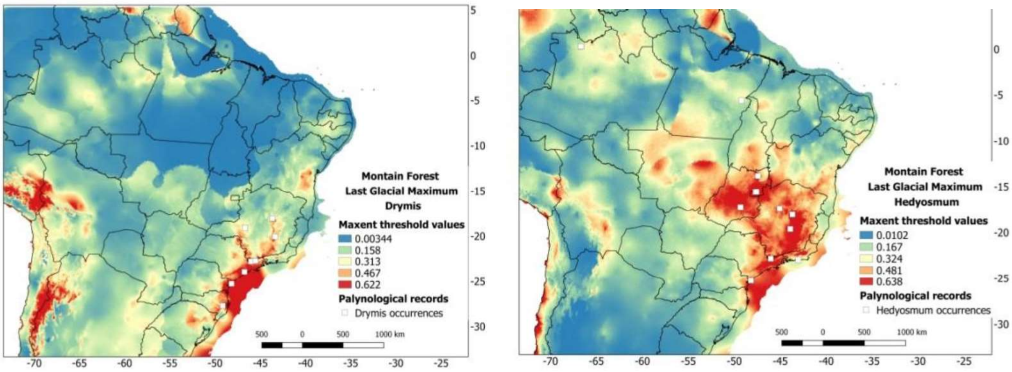

Fig 8. Niche suitability (MaxEnt) for *Drimys* and *Hedyosmum* in LGM records of Brazil.

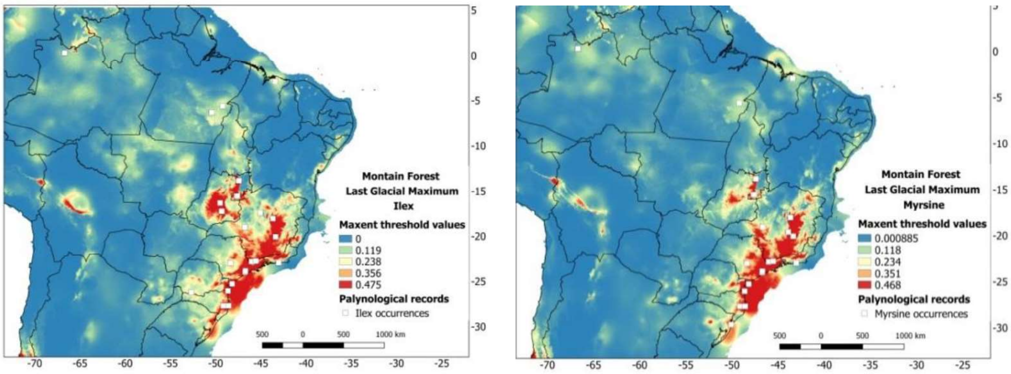

Fig 9. Niche suitability (MaxEnt) for *Ilex* and *Myrsine* in LGM records of Brazil.

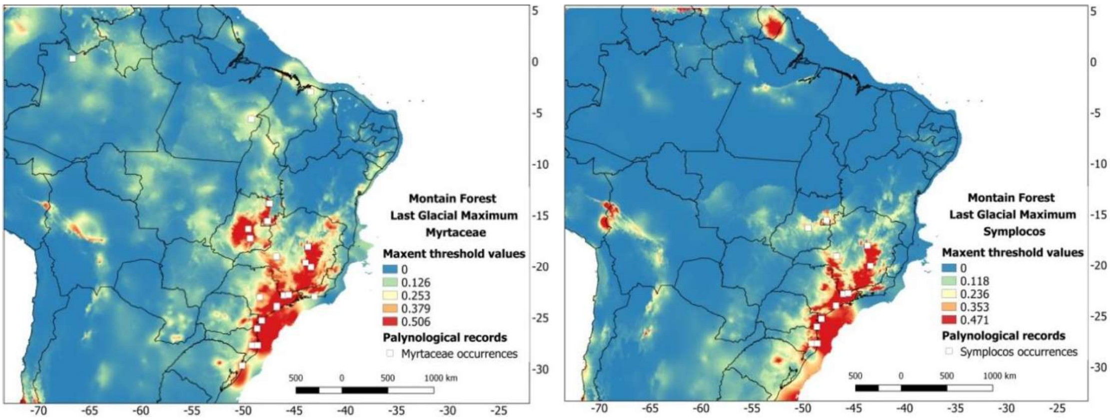

Fig 10. Niche suitability (MaxEnt) for Myrtaceae and *Symplocos* in LGM records of Brazil.

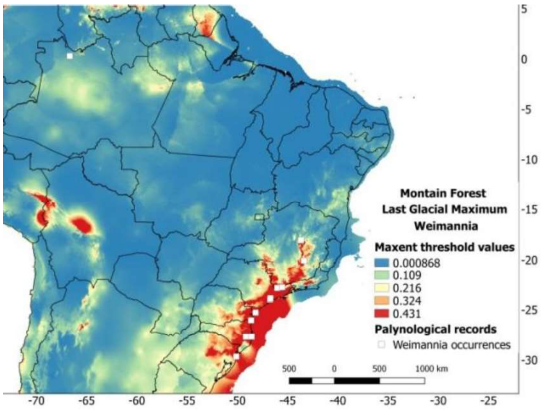

Fig. 11. Niche suitability (MaxEnt) for *Weinmannia* in LGM records of Brazil.

Considerations on route SSA and SSB and its relation to the modern floristics of NE Brazil must be made for *Podocarpus* and *Drimys*. Both taxa have species with modern distributions extending from southern to Northeastern Brazil, which are shown on Figs. 12 and 13, respectively. It is clear that both taxa have migrated northwards following both the SSA and SSB routes. *Podocarpus* reached Amazonia (Pará) during the LGM following route SSB and its absence in northeastern Brazil (Chapada Diamantina) by means of route SSA during the late glacial might be an artifact of the poor representation of LGM/H1 palynological records in northeastern Brazil. *Drimys*, on the other hand, has not been reported in palynological records of the late glacial in low latitudes (<15°S) and its presence in modern flora of high and humid mountain areas of northeastern Brazil such as the Chapada Diamantina mountain range cannot be proven to be a consequence of migration during the late glacial due to the lack of pollen records of dated to the LGM/H1 there.

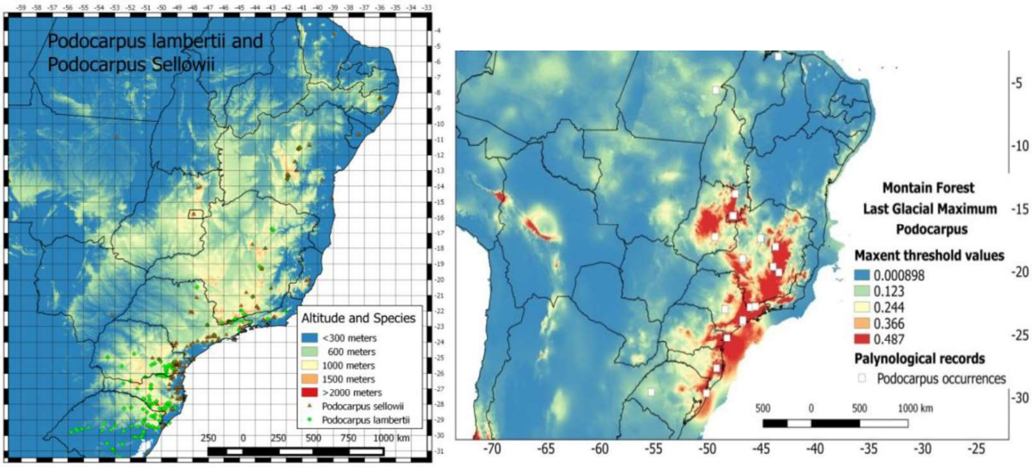

Fig.12. Modern distribution of *Podocarpus sellowii* and *Podocarpus lambertii* and *Podocarpus* niche suitability map for the LGM.

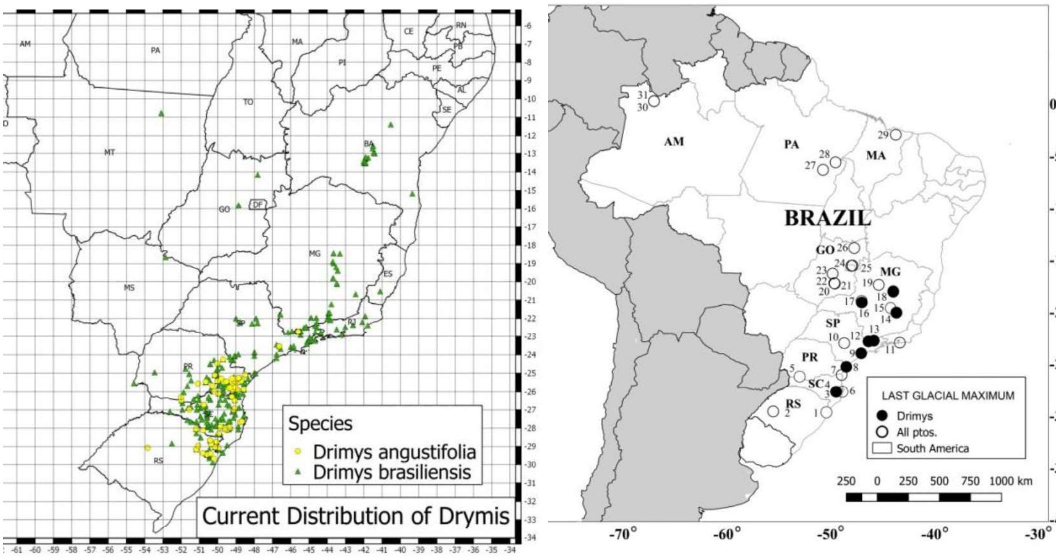

Fig.12. Modern distribution of *Drimys angustifolia* and *Drimys brasiliensis* and *Drimys* niche suitability map for the LGM.

Niche Suitability for combined montane taxa during the LGM

Based on the 31 palynological records a Species Distribution Model (SDM) was constructed by means of MaxEnt[18,19] algorithms for the LGM of the Brazilian Highlands, linking distribution records do environmental data (using 19 bioclimatic variables obtained from Max Planck Institute for Meteorology MPI-

ESM-P model for the Last Glacial Maximum, disponibilized to WorldClim 1.4 downscaled paleoclimate data[20]). The potential distribution maps (MaxEnt output used average of 20 bootstrap models) of each individual pollen taxa during the LGM were then combined into one single map denoting the potential distribution of montane forests in southern, southeastern and central Brazil (Fig. 13).

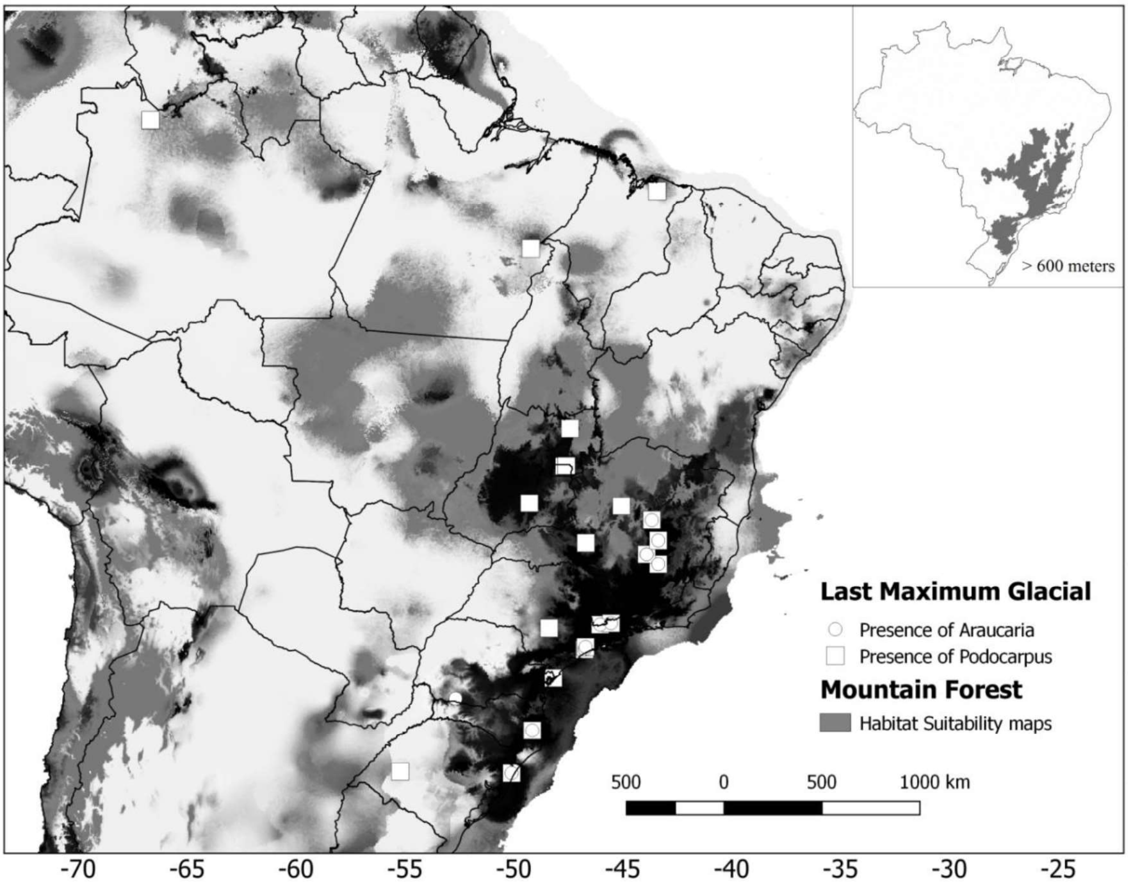

Figure 13. Potential Distribution Map based on ecological niche modelling of montane taxa for the LGM. Presence of *Araucaria* and *Podocarpus* based on pollen distributions is indicated by circles and squares, respectively. In detail the Brazilian Highlands (> 600 meters). Brazilian political division was used to indicate areas opened by the emergence of the continental platform due to reduced sea level during the LGM.

In order to investigate the factors controlling the modern occurrence of *Araucaria angustifolia* and *Podocarpus lambertii*, to strengthen our vegetation reconstructrion during the LGM-H1, we combined accumulated daily precipitation produced by CMORPH methodology[23,24] and adjusted by metorological stations from 2000 to 2015[22,22]. R-scripts were then elaborated to descriptive statistics, box plots and histograms, based in values of 1° grids of statistical mean of averaged year, four seasons, wet and dry periods (Fig. 14). Finally, a Principal Component Analysis (PCA) was carried out for each individual taxon as well as combined taxa, identifying the variables associated to different components in order simplify the interpretation of multivariate system into a two-dimensional plot (Figure 15).

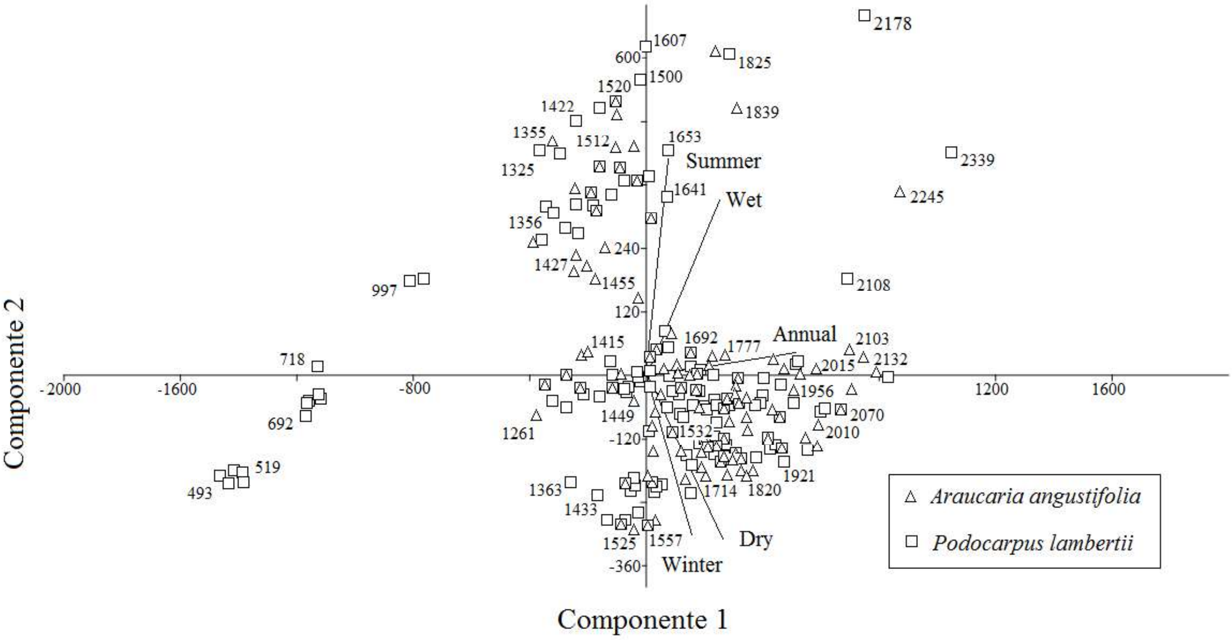

Figure 14. PCA biplot diagram of *Araucaria angustifolia* and *Podocarpus lambertii* modern distribution in relation to mean values of total annual precipitation based on hourly rainfall estimates with CMORPH51.

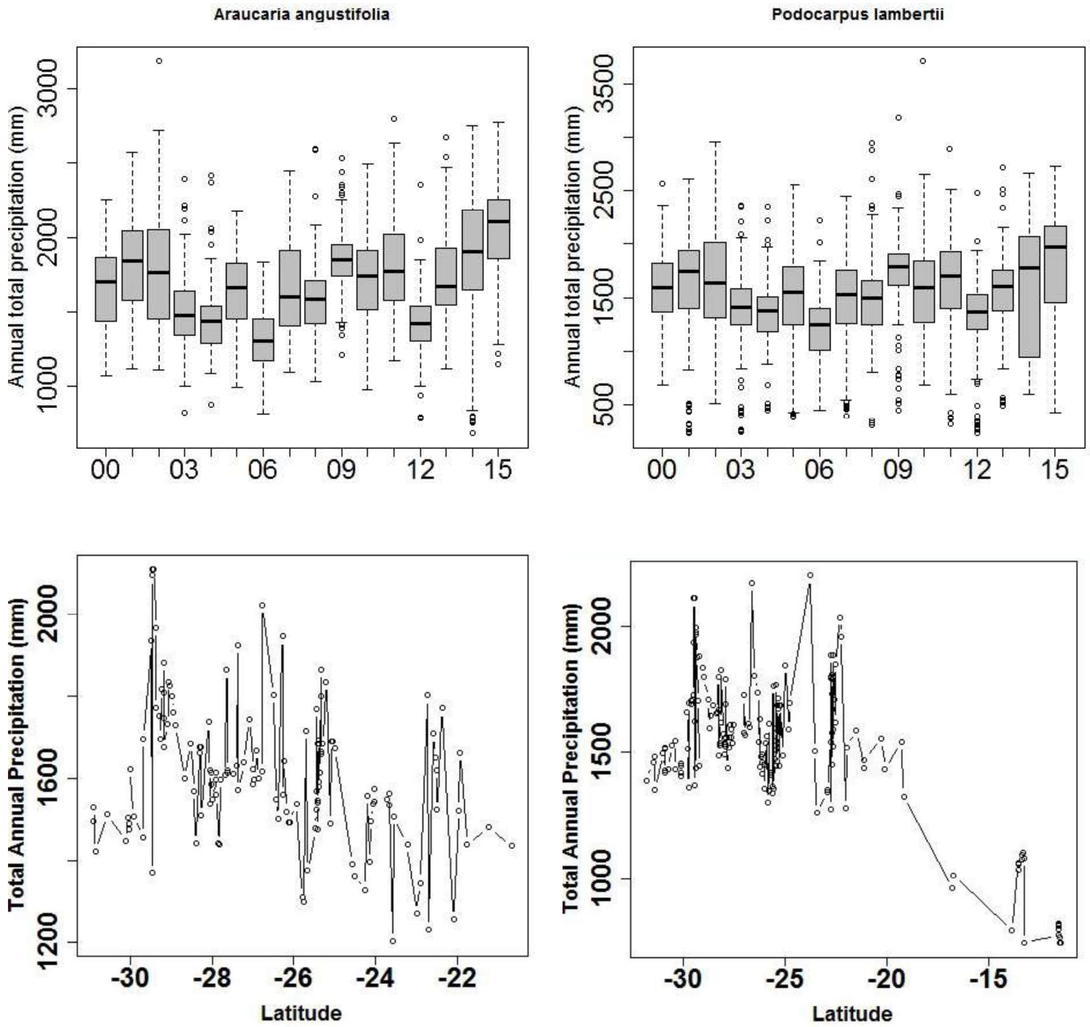

Figure15. Boxplot and dispersion of *Araucaria angustifolia* and *Podocarpus lambertii*. Annual total precipitation values representing the number of years since 2000 until 2015 for *Araucaria angustifolia* (1680 ±180 mm) and *Podocarpus lambertii* (1520 ± 220), in relation to mean values of total annual precipitation based on hourly rainfall estimates with CMORPH[23,24].

The PCA diagram of the combined distribution, with overlapping clusters, of both taxa shows that the ocurrence of *Araucaria angustifolia* and *Podocarpus lambertii* is controlled mainly by mean total anual precipitation of 1680 ±180 mm and 1520 ± 220 mm respectively based on a 15 year climatic series (2000-2015). These values range well within the classical temperature and precipitation values used in the literature for both taxa in Brazil[25] as well as in Koppen's climatic classification system for the brazilian highlands temperature range of -3°C to

18°C[26]. With these elements we assume that species reshuffling during the LGM were constrained by their physiological responses within these temperature and precipitation ranges.

The comparison of modern distribution of montane taxa, chosen to exemplify past of the montane forests of southeastern Brazil, with their suitability ranges, gives us subsidy to claim that both immigration routes may have taken place during the LGM/H1 stages under humid and cold climates.

Paleoclimatic conditions

The tilt of the Earth´s axis, the eccentricity of the orbit and the longitude of the perihelion affect the solar radiation at the top of the atmosphere, perceived as secular variations [27–29]. We therefore hypothesize that under a scenario of less intensified solar ration at the LGM, polar circulation became somewhat stronger while the Hadley circulation was weakened and that this mechanism is likely to have generated a larger displacement of polar air towards northern South America. Consequently, moist convergence could have been displaced northward over continental area where a weakened Intertropical Convergence Zone (ITCZ) prevailed [30–34].

During Last Glacial Maximum period, cold fronts were intensified and therefore could have dislocated further north than during present conditions, thus reaching northeastern Brazil. Because the resulting equator-pole temperature gradient was therefore larger, transients had probably higher intensity thus causing convergence of humidity precisely where the mean humidity zonal stream flow was high[30,31,35].

Oxygen isotopes in the Botuverá cave speleothems have indicated that humid phases have prevailed during the last glacial cycle in southern Brazil[36]. Additional support for this scenario comes from calcite deposits at lake margins within caves[37] and expansion of humid forests in the LGM of northern Bahia, currently covered by semi-arid vegetation (caatinga), suggested by abundant plant megafossils in calcerous tuffs, belonging to arboreal and herbaceous taxa presently found in the Atlantic and in the Amazon rainforests[5,38].

This humid pattern was probably not restricted to Brazil since climate during the LGM at middle and low latitudes in Andean region was apparently wetter than at present, as a consequence of more frequent occurrence of westlies equatorward compared with their concentration today at 50° S[83]. The effect of the Westlies in subtropical Chile (34° 30'S) during the last glaciation is found in the pollen record of a core from Tagua Tagua[39]. This author estimated for the last glacial an increase of 1200 mm to the modern value of 2000 mm annual precipitation, in contrast to its modern winter-wet, summer-dry climate. Additionally to the east in northwestern Argentina (20°-30°S), have amassed a long record of interbedded loess and palaeosols, for which Late Pleistocene displacements of the polar front / humid Westlies to lower latitudes are postulated[40].

Climatic changes and vegetation

Pollen records of arboreal taxa common in humid and cold forests of glacial age in Brazil[7,8,12,14,15,41,42] support the hypothesis of intensification of transient climatic systems under glacial regime and at the LGM due to the strong temperature contrast between the equatorial and polar regions. We suggest that continental lower surface temperatures down to 5°C in average in equatorial regions during the LGM[2,3,43,44] added by the effects of polar air incursions in South America acted as a significant forcing on modern plant biogeographical patterns by fostering long distance migration of montane elements within the Brazilian Highlands.

One of the best known indirect evidence for this hypothesis is given by the vegetation the Pico das Almas (13°34'S), at the Chapada Diamantina mountain range, northeastern Brazil is floristically more related to the Andean paramo and sub paramo forest with genera like *Podocarpus*, *Drimys*, *Symplocos*, *Weinmannia*, *Hedyosmum* (SSA pattern) and the flora of the tepuis of

Venezuela[1]. A second line of evidence is the pollen record of the Icatu site at 10°S, currently under semi-arid vegetation, which shows cold and humid-adapted taxa such as *Podocarpus*, *Ilex*, Myrtaceae and *Hedyosmum* coexisting with *Humiria*, an amazonian lowland arboreal taxon, at c. 11 K cal. yrs BP[4].

Although alternative and viable hypothesis for such biogeographical patterns may suggest that such connections could have been established during the cool phases of the Oligocene, following the tropical decline of the Eocene, Late Quaternary pollen data signal a powerful reorganization of ecosystems in South America during the terminal phases of the last glacial cycle. The enlargement of the montane niche in consortium with geographically more prevalent cold and humid climates must necessarily be accounted for by temperature depression and enhanced humidity brought about by cold fronts associated with more intensified polar air masses into the continent. Temperature depression in the neotropics during the last glaciation, in the order 5°C – 6°C in mean annual average, has long been derived from estimates yielded by pollen[6], underground water noble gas composition[44] and σ ^{18}O coral records[45]. The comparison of modern climates and the distribution of various tropical taxa, such as *Araucaria*, have suggested that specially in southern and southeastern Brazil, temperature depression during the height of the last glacial cycle, may have been as low as 12°C below current mean annual temperature[7,11].

SDM of this taxon´s distribution during the LGM, reveals habitat suitability is highest in coastal southern and southeastern Brazil (30°S to 18°S) suggesting temperature depression and increased humidity, a climatic scenario strongly supported by documented high precipitation levels during the LGM of northwestern Argentina at 25°S with enhanced landslide-dammed lake formation from 40 to 25 kyr BP[46] and by the paleolake Tauca wet periods[79,80]. The glacially-conditioned emersion of the Brazilian continental platform fostered by globally reduced sea-levels, down to 150 m in global average[77] offered ample niche opening for the Atlantic Rainforest, especially to cold and humid adapted taxa. Despite this probable niche opening, an unexplained fact relates to *Araucaria*, which despite the enlargement of apparent suitable environment, maintained its distribution centered in the Serra da Mantiqueira and Serra do Mar during the LGM[42,47] , and in central southeastern Brazil[7].

The ability of cold-adapted taxa to migrate considerable distances during periods of climatic change was the motor that triggered the appearance of novel plant communities with no modern analog. These new plant associations, revealed by various pollen analyses[6,48], corroborate to the ideas of the individualist concept[49,50] after analysis of glacial Late Quaternary pollen histories of eastern North America.

Consequences of cold air incursions can explain modern disjunctions

Combination of pollen occurrence of some montane forest taxa in Brazil with modelling of habitat suitability (MaxEnt) provides strong evidence of widespread migration of *Podocarpus, Ilex*, *Myrsine*, *Hedyosmum,* Myrtaceae from Southern-southeastern Brazil to southern Amazonia (SSA route) during the Late Pleistocene. When ensembled together (Fig. 13) these maps depict potential geographical links connecting areas of their then expanding fundamental niches. Our data indicate that during the LGM under intensified polar air incursions into the interior of South America a long chain of mountains, starting at the Serra do Mar, followed by the Serra da Mantiqueira and deriving into the Brazilian Central Plateau, and Serra Geral functioned as an efficient corridor for the migration of montane elements, thus supporting a previous hypothesis of such a corridor based on modern distribution data of plant species[81]. Therefore, *Podocarpus* and other SSA route taxa could then have reached southern and western Amazonia and possibly the Guyana Shield tepuis region bu using a Serra da Mantiqueira, Serra do Espinhaço and Serra Geral as a migration corridor.

It is interesting to note that the taxa that migrated further along the SSA route have wind-dispersed and are dioecious, two evolutionary traits that are linked to high dispersal potentials which renders them increased ecological amplitude and greater colonization ability[82]. On the other hand, taxa displaying the SSB route also migrated considerable long distances, and with the exception of *Araucaria*, all have their pollination syndromes controlled by insects and birds. However, it is possible that there might not be any slight disadvantage in long distance migration given by zoophily under a scenario of climatic change conducive to the opening of cool and moist habitats. This view is supported by a marine pollen record from the continental shelf off the coast of the State of Ceará[78], containing continental sediments generated in the region of modern semi-arid vegetation. This record shows a LGM pollen zone, characteristic of cold and humid adapted montane taxa with significan percentages of SSA route taxa such as *Hedyosmum*, *Ilex*, Myrtaceae, together with *Symplocos* (SSB route) and *Cyathea*. Furthermore, entomophilous and zoophilous pollination did not hinder the very long dispersal ability of *Drimys brasiliensis* whose modern distribution suggests that the SSB route could have extended well into northeastern Brazil, where it is found in the modern altitude of 1500 m in the Chapada Diamantina range. We therefore conclude that, although we do not devalue a possible scenario of early migration corridors during the Eocene/Miocene of Brazil, a significant imprint of the LGM in delineating modern disjunct distributions there is unquestionable.

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CHAPTER 4

MANUSCRIPT 3 (unpublished)

Late Pleistocene/Holocene Evolution of a Forest/Altitude Savana Mosaic in the southern Brazilian Atlantic Forest

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Abstract

We reconstruct the vegetational and climatic history of a locality in the southern section of the Brazilian Atlantic Rainforest, , at 900 m elevation, by means of pollen analysis of sediments deposited in the last 38,000 cal. yrs BP in an area covered by a vegetational mosaic of cloud forest tracts and high altitude grasslands.The objective was to bring light into the origin of this vegetation ecotone, previously hypothesized to be either a relict of drier climates during the Late Pleistocene or a consequence of former anthropogenic activities on the local landscape, conducive to exclusive rainforest cover. The results indicate that the modern grasslands has been present on the local landscape since the onset of sedimentation, however it represents a relict of an ecosystem that was more prevalent during the cool and wet phases of the Late Pleistocene. The pollen data of Curucutu provide no support for the hypothesis of drier climates during the Late Pleistocene. Although plant physiognomy had been constant through the Late Pleistocene, floristic composition revealed drastic changes, which are here interpreted under the light of modern paleoclimatic evidence of higher humidity brought about by enhanced monsoonal activities during times of glacial activities (Heinrich events) in the northern hemisphere. The predominance of cooler and humid climates during the Late Pleistocene is here interpreted as a consequence of intensified incursions of polar air masses, as suggested by variations in abundance of montane and exotic Andean pollen taxa (*Nothofagus*, *Alnus*).

Key words: Atlantic Forest, Pleistocene, Holocene, Brazil, palynology

Introduction

The history of the Brazilian Atlantic rainforest is central to the understanding the origin of its high biodiversity which rendered it a significant position among 25 areas around the Earth containing exceptional concentrations of endemic species which are threatened by habitat loss (Myers et al., 2000). According to these authors, the Brazilian Atlantic Forest contain ca. 20,000 plant species of which ca. 8,000 are endemics to this region, thus representing 2,7% of the total of ca. 300,000 species presently known in the world. The controversy on the causes controlling high diversity patterns found in the tropics has been lasting since the beginning of the discipline of Ecology but this debate generated various models of plant diversification scenarios involving long term maintenance of tropical ecosystems based on the Time Stability Hypothesis (Sanders 1968), speciation driven by vicariance/allopatry fostering speciation as shown by Hoorn et al.(2010) and Ribas et al. (2007) and by genetic fluxes triggered by climatic change (Colinvaux et al., 1999). Biological speciation is also a key element in another important issue of contention in the scientific literature concerning tropical ecosystems. According to the Refuge Hypothesis Model (Haffer, 1969; Ab´Saber, 1982; Haffer & Prance, 2001) large extensions of the tropical forest ecosystems had dwindled during the last glacial cycle, especially during the Last Glacial Maximum (LGM), ca. 20.000 cal. yrs BP and speciation was postulated to have generated species, thus generating disjunct biogeographical patterns. Despite a growing number of pollen records of sediments spanning the last 40 k yrs BP in the last decades showing humid and cold forests in many sites in southeastern Brazil and no evidence of caatinga ever reaching high southern latitudes, the Refuge Hypothesis is still prevalent in the Brazilian literature. One example is given by IBGE (1993) which maped ecotonal areas subjected to arid climates during the Quaternary.

After examining genetic diversity in frogs Carnaval et al. (2009) suggested that the high endemism found in the southern Bahian Atlantic Forest may be explained by ecosystem stability maintaining an undisturbed forest landscape throughout the Late Pleistocene. These results however may suggest that in other areas of coastal Brazil were not stable. Another tentative hypothesis is that high diversity in certain areas may also be a consequence of continuous climatic shifts forcing different taxa to migrate long distances to compensate for habitat change, thus enhancing genetic exchanges among populations over large areas, thus providinga a mechanism to speciation and formation of plant communities with no modern analogs.

In this contribution we present a Late Pleistocene/Holocene vegetational and climatic history of a forest/high altitude savanna mosaic in the southern section of the Atlantic Forest, in the State of São Paulo, which has been interpreted as a relict of past arid climates during the Late Pleistocene which favoured the retraction of forest ecosystem and expansion of savanna-like vegetation (Veloso et al., 1991; IBGE, 1993). Our study site provides an unique opportunity to test this and other hypothesis, specially the stability x unstability debate of tropical ecosystems and their relation to climatic shifts during the Late Quaternary. In this context, this analysis is presentend under the light of high temporal resolution paleoclimatic signals derived from $\delta^{18}O$ concentrations in cave speleothems of southern and southeastern Brazil (Cruz et al., 2005, 2006, 2009).

Study site: geographical, geological, vegetational and climatic settings

The Curucutu peatbog is located in southeastern Brazil, at 23°56'S, 46°39'W (Fig. 1), approximately 20 km northern of the cities of Itanhaém and Mongaguá in the southern coastal zone of São Paulo State, at an altitude ranging from 750 to 850m and mean annual precipitation in the range of 2000–3000 mm. The regional climate is subtropical with a defined seasonality (dry winters and humid summers), classified as Cfa according to the Köppen classification system (Serra, 1969). The study site region is under the influence of humid air masses from the Atlantic Ocean and is characterized by warm and rainy summers and dry winters with mild temperatures maintained by constant incursions of polar air masses, which become more intensified in the winter months of June, July and August. The annual average temperature is 19°C and the minimum and maximum annual average temperatures are 15°C and 24°C, respectively (Tarifa, 2001). The soil at the study site is classified as Dystropept, according to American Soil Taxonomy, USDA classification (Soil Survey Staff, 1999). The vegetation contains a mosaic of cloud rainforest and a subtropical grassland called Campos de Altitude (high elevation savannas), frequently covered by fog (Garcia, 2003; Garcia & Pirani, 2005). The landscape is formed by a mosaic of campos limpos ("clean" grasslands), constituted of herbs and very isolated trees, here denominated arboreal grasslands (*sensu* Goodland & Pollard,1973) and ombrophyllous cloud forest tracts (Fig. 2). The dominant plant species in the grassland vegetation are the sedge *Lagenocarpus rigidus* (C3 plant) and the C3 grass *Danthonia montana*; and the C3 arboreal taxa *Clusia criuva*, *Tibouchina sellowiana* and Asteraceae herbs are also abundant (Garcia & Pirani, 2005). The C4 grasses *Andropogon bicornis*, *Axonopus pressus*, *Paspalum polyphyllum*, and *Saccharum asperum* are also present in the landscape. Among the most abundant families in the local cloud forest and in the arboreal grasslands are Rubiaceae, Myrtaceae and Melastomataceae (Garcia & Pirani, 2005).

In the last four decades *Pinus elliottii*, an exotic gymnospermous taxon typical of reforested areas has become a common invasive species of the grassland, as well as of the more open forested areas.

The studied peatbog is located within a small depression basin of approximately 4000 m^2 with no influence of any modern drainage system. The forest/grassland mosaic vegetation is found in the surrounding area and around the coring site, located approximately in the center of the small basin. Due to the high annual precipitation, during the rainy season a water column can reach up to ~0.3 m.

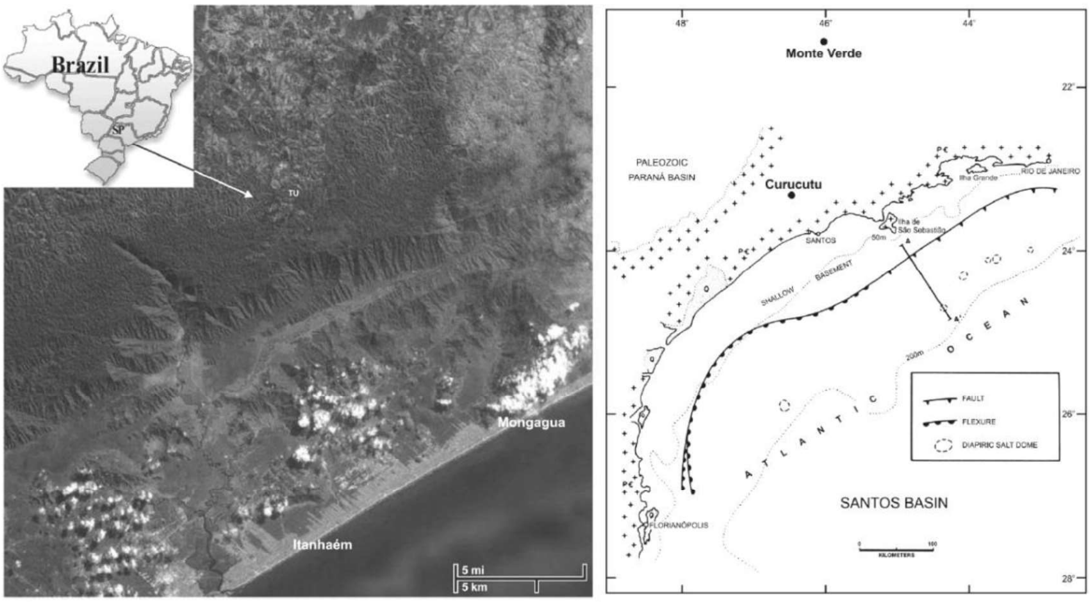

Figure 1. Map of Brazil showing the location of the Curucutu and the peatbog (turf = TU) sampling point and a structural map (right) displaying the Santos basin, São Paulo State and the Monte Verde peatbog location, in the State of Minas Gerais (From Pessenda et al., 2009).

Fig. 2. Satellite image of the Curucutu campos/Atlantic forest mosaic within the City of São Paulo Municipality, in southeastern Brazil (Google Earth 2018).

Sampling and laboratory methods

A 206 cm peat core was collected using a vibro-corer (Martin and Flexor, 1989) and sediment color was classified according to Rock-Color chart (Goddard et al., 1984). Sediment subsamples containing 1 cm^3 were collected in depth intervals that varied from 4 cm to 8 cm for pollen analyses with the exception of the first 8 cm which were sampled in 2 cm depth intervals to determine possible recent human interference on the landscape. A sampling depth interval of 2 cm was used for carbon isotopes analyses. Nine radiocarbon dates were obtained on peat samples by AMS and benzene synthesis liquid scintillation counting methods (Pessenda & Camargo, 1991).

Pollen analysis, conducted in intervals of 4 cm, followed the methodology described in Colinvaux et al. (1996), and included mineral removal with hot HF followed by acetolysis (9 parts acetic anhydride: 1 part sulphuric acid). Pollen sums and percentages were based on counts that contained at least 300 non Poaceae grains in each sample in order to reduce the bias produced by this over-represented taxon. Pollen concentrations (grains/cm^3) were determined by the addition of exotic Lycopodium clavatum spores (Stockmarr, 1971). All pollen and spore data were generated and represented graphically by the Tilia and TiliaGraph Software (Grimm, 1987, 1992). On the pollen diagrams, in order to facilitate the examination of the history of individual taxa, an exaggeration factor of 10X was applied to the aquatic and terrestrial and 5X for individual tree and shrubs elements.

Radiocarbon chronology

The 14C analyses were carried out by Accelerator Mass Spectrometry (AMS) at the Isotrace Laboratory of the University of Toronto, Canada. Radiocarbon ages are expressed as ^{14}C yr (1σ) BP (Before AD 1950) normalized to $\delta^{13}C$ of−25‰PDB and in cal yr BP (Reimer et al., 2004). Calibrated ^{14}C ages in cal yr BP (2σ) and Bchron age model for different depths of the Curucutu core are presented in Table 1.

Table 1. Radiocarbon dating of sediments from the Curucutu peatbog showing conventional age (yrs BP) and dates calibrated (cal. yrs BP) following Reimer et al. (2004) and Bchron age model according to Parnell (2015).

Sample	**Depth (cm)**	**Years BP**	**Cal. Yrs BP**	**Bchron Age Model (cal.yrs BP)**
I-Curu-1	6-8	900+-90	781	
	10			2120
I-Curu-2	14-16	2510+-110	2547	
	20			8436
I-Curu-3	24-26	8620+-120	9588	
	30			16117
I-Curu-4	30-32	13750+-160	16563	
I-Curu-5	33	15600+-260	18827	
I-Curu-6	34-36	19000+-280	22861	
	40			23349
	50			23722
I-Curu-7	50-52	19450+-150	23368	
	60			26399
	70			26975
I-Curu-8	74-76	22780+-170	27072	
	80			30246
	90			31172
	100			31717
	110			32216
	120			32846
I-Curu-9	121-123	28460+-280	32347	
	130			34714
	140			35494
	150			35857
	160			36240
	170			36678
II-Curu-10	178-180	32590+-280	36884	
	190			37557
II-Curu-11	204-206	34190+-310	38650	

Palynological results and interpretation

Three pollen zones were identified by the CONISS software: CUR 1 and 2, with two subzones each, and CUR 3. All taxa were grouped into the following categories: Trees and shrubs (Fig. 1-4), upland herbs (Fig. 5), aquatic herbs (Fig. 6), terrestrial cryptograms, *i.e.* ferns and bryophytes and algae (Fig. 7). Percent sums of all categories (trees and shrubs, upland herbs, aquatic plants, terrestrial cryptogams and algal cysts are shown on Figure 8. Figure 9 shows pollen concentration diagram (grains per cm^3) of montane taxa whereas Figure 10 depicts concentration of all pollen and spore categories expressed as number of grains per cm^3. Palynological zones are described based on the highest percentage values of each taxon, as follows:

Zone CUR 1A (206-178 cm; 41,856- 37,166 cal. yrs BP)

This zone marks the onset of peat accumulation on the local landscape and is characterized by ca. 20% arboreal pollen with Myrtaceae (2.7%), *Alchornea* (2.2%), *Symplocos* (2.4%), *Cybianthus* (1.4%), *Myrsine* (1.8%), Melastomateceae (1.5%), *Araucaria* (0.24%), *Cedrela* (0.3%), *Chrysophyllum* (0.2%) *Croton* (0.8%), *Drimys* (0.35%), Ericaceae (0.7%), *Euplassa* (0.3%), *Hedyosmum* (0.24%), *Ilex* (0.48%), *Roupala* (0.45%), *Vernonia* (0.3%) and *Weinmannia* (0.1%) suggestive of scattered mixed ombrophilous forest stands.

Terrestrial herbs range from 69% to 77% with the most representative taxa being Poaceae (53.5%) and Asteraceae (29%), followed by Begonia (1%), and Borreria (1.45%). Aquatic herbs do not exceed 5%, especially Cyperaceae (4%), Xyris (0.8%), Eriocaulon (0.4%) and *Eryngium* (0.4%). These taxa related to open and flooded swamp conditions, with low water column. Fern and bryophtytic spores range from 79% to 88%, represented mainly by monolete psilate grains (39%), *Cyathea* (from 19% to a minimum of 6%), *Anthoceros* (19%), *Cystopteris* (3%), *Lycopodiella cernua* (7.5%) and Selaginella (23%), an indicator of humid soils in forested habitats. All these latter taxa are commonly found at high elevation campos (campos de altitude). Algal cysts belonging to *Debarya* (12%), *Pseudoschizaea* (1.5%), *Botryococcus* (1.5%), oscillate between 6% and 17%.

The pollen and spore spectra, together with abundant *Debarya* algal cysts in this zone is suggestive of cold and somewhat humid open landscape with scattered *Araucaria* forest groves (mixed ombrophyllous rainforest) in the midst of herbaceous a landscape resembling the southern campos physiognomy characteristic of the highlands of modern southern Brazil. The presence of *Alnus* (0.1-0.2%), an anemophilopus taxon in this zone and the first occurrence of *Nothofagus* at the end CUR 1A is also suggestive of more intensified incursions of polar air masses, thus accounting for their long distance dispersal abilities.The climate of this zone is interpreted as cold and humid, possibly maintained by more intensified monsoonal circulation, during high insolation phase and enhanced polar air mass incursions into Brazil coincident with Heinrich Event 4 (*sensu* Hemming, 2004), with maximum cooling at 38,000 – 40,000 years AP in the northern hemisphere. Similar pollen spectra with predominance of herbs over arboreal elements found in this zone were reported by Ledru et al. (2009) at the nearby Colonia Crater. This zone together with CUR 1B fall within Pollen Zone COL 9 (40.2 to 28.8 cal kyrs BP) of the Colonia record (Ledru et al., 2005) dominated by herbaceous over arboreal pollen.

CUR 1 B (178 cm – 140 cm; 36,944 – 35,494 cal. yrs BP)

The initial phase of sediment deposition at Curucutu is characterized by an increase of arboreal elements (19%-29%) and pollen spectra of taxa belonging to montane forest such as *Araucaria* (0.17%), *Podocarpus* (1,5%), *Myrsine* (2.2%), Myrtaceae (3.3%), Symplocos (2.8%), *Drimys* (0.25%), Ericaceae (1.7%), *Hedyosmum* (0.24%), *Ilex* (0.86%) in synchrony with Melastomataceae (3.1%), *Alchornea* (2.5%), *Cecropia* (0.4%), Piperaceae (1%), Mimosa (0.22%), Sebastiania (1.0%), Tabebuia (1.1%), *Weinmannia* (0.6%), *Cordia* (0.5%), *Guapira* (0.5%), *Croton* (0.8%), *Hieronyma* (0.8%), *Erythroxylum* (0.4%), *Solanum* (1.4%), *Cassia*/*Senna* (2.5%) and *Roupala* (0.5%), among others. Terrestrial herbs vary from 61% to 70%, mainly composed of Poaceae (37%), Asteraceae (25%), Begonia (2.4%), Borreria (2%), Campanulaceae (0.8%) and Amaranthaceae (0.8%). This zone shows a marked increase in aquatics or plants that thrive in swampy soils (8% -10%), composed mainly by *Ludwigia* (22%), Cyperaceae (8.0%), Pontederiaceae (0.4%), Lentibulariaceae (0.15%), *Myriophyllum* (0.2%), *Eriocaulon* (0.6%), *Drosera* (0.2%), Xyris (1.15%) *Eryngium* (1%). Cryptogamic taxa (1.5% - 8.5%) are represented by *Isoëtes* (4.25%), *Riccia* (3.75%), *Sphagnum* (2.85%), indicating cold and shallow water. Fern spores (77%-87.5%), mainly monolete psilate (40%) and verrucate grains (20%) cooccur with the tree ferns *Cyathea* (11%), and *Dicksonia* (4%) and with *Hymenophyllum* (2.7%) and *Selaginella* (23%). It is noteworthty the marked increase in taxa typically found in altitude campos (campos de altitude) such as *Anthoceros* (11%), *Phaeoceros* (3.8%), *Blechnum* (11%) and *Jamesonia* (2.75%). The latter taxon currently presents a geographical distribution restricted to the Itatiaia massifs, at elevations ranging from 2000 m to 2500 m. Algal cysts (4% - 20%) of *Debarya* (10%), *Mougeotia* (4.5%), *Pseudoschizae* (2.9%) and *Zygnema* (5%) are a further indication of humidity and cold climates.

The pollen, spore and algal signals within this zone are highly suggestive of increase moisture levels when compared to CUR 1A, under continuing cool climates which allowed the maintenance of a humid herbaceous vegetations interdispersed with forest groves containing cold and humid adapted taxa commonly found in high altitude habitats of the modern Atlantic Forests.

This zone falls partially within Colonia Pollen COL 9 (40.2 to 28.8 cal kyrs BP), characterized by a more reduced arboreal component and loss of *Araucaria*, which maintains itself in very low percentages at Curucutu, which can be attributed to wind dispersal from other sources on higher elevations.

CUR 2 A (140 cm -116 cm; 35,494 - 32,505 cal. yrs BP)

This pollen zone is characterized by stable arboreal/shrub component (14.5%-18%) composed of *Alchornea* (0.9 %), *Araucaria* (0.6%), *Podocarpus* (0.8 %), *Myrsine* (1,8%), Myrtaceae (3.7%), *Symplocos* (1.2%), *Drimys* (0.15%), Ericaceae (0.6%), *Ilex* (0.92%), Melastomataceae/Combretaceae (2.7%), *Hedyosmum* (0.13%), *Cordia* (1.4%), *Mimosa* (0.19%), *Sebastiania* (0.9%), *Tabebuia* (0.6%), *Weinmannia* (0.3%), *Roupala* (0.19%), *Cybianthus* (0.32%), *Guapira* (0.29%), *Vernonia* (0.19%), *Croton* (0,39%), *Hieronyma* (0.33%), *Sapium* (0.98%), *Solanum* (0.19%), *Cassia/Senna* (0.53%)., among others. The predominating herbaceous component (68%-80%) has the terrestrial herbs Poaceae (60%), Asteraceae (14%), Iridaceae (1.35%) and *Borreria* (1%) while among the aquatic herbs, which appear reduced when compared to the previous zone, stand Cyperaceae (9.7%), *Xyris* (1.16%) and *Eriocaulon* (1.17%). Fern and bryophytic spores vary from 41% to 73%, composed mainly of taxa typically found in high elevation campos such as *Blechnum* (15.6%), *Cystopteris* (1.75%), *Jamesonia* (2.3%) and *Lycopodiella cernua* (12.3%), which maintain reasonable stability and times of increase in abundance. There´s a clear decrease in aquatic taxa simultaneously with an increase in the algal component given by *Debarya* (up to 32%), *Botryococcus* (3.1%), *Pseudoschizaea* (0.8%), *Mougeotia* (7%) and *Zygnema*, reaching up to 47%. The exotic Andean taxa *Alnus* and *Nothofagus* reappear in this zone with low percentages coincidentally within a chronological period of high summer insolation driving the South American Monsoonal System (*sensu* Cruz et al., 2006, 2007).

CUR 2 B (116 cm - 64 cm; 32,505 – 26,657 cal. yrs BP)

The pollen spectra of CUR 2B show the continuing trend of open landscape given by maintenance of terrestrial herbs as the main category (57%-78%) with trees and shrubs accounting for 16.5% to 27.5% of the total pollen counts. The arboreal component is made up of *Alchornea* (2.3%), *Araucaria* (1.4%), *Podocarpus* (0.9%), *Myrsine* (2.8%), *Drimys* (1%), *Hedyosmum* (1.3%), *Ilex* (0.98%), *Symplocos* (1.3%), *Weinmannia* (1.3%), Melastomataceae / Combretaceae (4.9%), *Mimosa* (0.43%), Myrtaceae (6%), *Sebastiania* (1.3%), *Tabebuia* (1.4%), *Copaifera* (0.75%), *Cordia* (0.7%), *Sloanea* (1.0%), *Croton* (0.32%), *Hieronyma* (0.33%), *Daphnopsis* (0.5%), *Cassia*/*Senna* (0.8%), *Luehea* (0.31%), *Roupala* (0.43%). Piperaceae (0.5%) and *Cecropia* (0.5%), among others.

The slight decrease in herbs is given by Poaceae (52%) and Asteraceae (12%) counterbalanced by an increase of aquatic herbs such as Cyperaceae (16%), within pollen spectra also containing *Eriocaulon* (1%), *Eryngium* (1.2%), Pontederiaceae (0.4%) and *Sagittaria*/*Echinodorus* (0.3%). This increase in humidity is also signaled by Bromeliaceae, a family commonly associated with humid conditions and by the more widely represented fern taxa in high elevation habitats such as *Cyathea* (21%), *Dicksonia* (6%), *Hymenophyllum* (1.8%), together with abundant monelete psilate and verrucate spores.

Among bryophytes common in altitude rupestrian fields are *Blechnum* (3.2%) and *Cystopteris* (2.8%) whereas Jamesonia disappears from the record. A relative increase occur in some aquatic cryptogamous taxa such as *Isoëtes* (2.8%), *Riccia* (1.7%) and *Sphagnum* (5.2%) concomitantly with disappearance of *Pseudoschizeae* and *Botryococcus* and maximum percentage increases in *Debarya* (25%), *Mougeotia* (22%) and *Zygnema* (40%).

The pollen and spore assemblages of this zone suggest increased relative humidity levels in association with cold climates, which are further supported by the occurrence of *Alnus* and *Nothofagus*, reaching their highest percentage values within this zone, suggestive of a period with more intensified polar air incursions. The chronology of this zone falls within Heinrich event 3, under high insolation, and intensified humidity brought about strengthened monsoonal circulation, as supported by a strong negative anomaly in $\Delta^{18}O$ variation in speleotherms in southeastern Brazil analysed by Cruz et al. (2005, 2006). According to these authors the increase in humidity was a consequence of a southward displacement of the Intertropical Convergence Zone (ITCZ) brought about by glacial conditions in the northern hemispheres (Heinrich events).

CUR 2 C (64 cm - 30 cm; 26,546 – 16,117 cal. yrs BP)

This zone contains fluctuating values of montane forest elements within the arboreal category, reaching in average 37% of the pollen counts. This subset is composed of *Araucaria* (1.2%), *Alchornea* (2.3%), *Cecropia* (3.2%), *Podocarpus* (1,4%), Myrsine (3.8%), Myrtaceae (3%), *Drimys* (0,4%), Ericaceae (0.45%), *Hedyosmum* (0.8%), Ilex (3.1%), *Symplocos* (1.3%), Melastomataceae/Combretaceae (8.5%), *Mimosa* (0.64%), Sebastiania (1.9%), *Tabebuia* (2.0%), *Weinmannia* (0.9%), among others. As in previous zone the herbaceous layer is dominated by prolific pollen producers like Poaceae (31%) and Asteraceae (11%), which probably masks the pollen signature of arboreal taxa.

A clear increase in aquatic herbs is noted. Cyperaceae reaches up to 19% of the pollen counts, accompanied by other macrophytes in low percentages such as *Eriocaulon*, Lentibulariaceae, Pontederiaceae, *Xyris* and Nymphaeaceae a reasonable water column, sustaining *Isoëtes* (12.5%) and *Sphagnum* (4%). The tree ferns assemblage made up by *Cyathea* (13%), *Dicksonia* (4%) contains *Blechnum* (4%), *Cystopteris* (2,8) and the bryophyte *Selaginella* (8%) and other taxa, mainly of the Polypodiaceae, represented by monolete psilate and verrucate spores (30%). The interpretation of this zone as a very humid phase is also supported by the substantial increase in algal cysts belonging to the cold-adapted *Debarya* (25%) as well as in *Coelastrum* (13.4%), *Mougeotia* (11%) and *Zygnema* (43%).

According to the chronology model, this zone encompasses the final cold phases of the last glaciation, including the LGM and Heinrich 1 and 2 events, which could explain this zone as the last occurrence of cold-adapted montane forest taxa like *Araucaria* under humid conditions associated with more intensified southern monsoonal system as described by Cruz et al. 2005, 2006, 2009) coupled with more frequent polar air incursions into the southeastern Brazil. This interpretation is conducive with the highest concentration of Andean

Alnus pollen, which in the final stage of this zone that reaches ca. 1500 grains/cm^3.

A sharp increase in the arboreal component (50%-89%) is reported at Colonia from 28.5 and 23.5 k cal yrs BP is somewhat similar to the pollen spectra of CUR 2C where a sharp increase in arboreal occurs at 23 K cal. yrs BP.

CUR 3 (30 cm - 0 cm; 15,033 cal yrs AP – Present)

This zone contains the most dissimilar pollen assemblage in the entire record due to the disappearance of *Araucaria* during the Holocene and the predominance of forest containing some montane taxa reaching 66% of the pollen counts. The disappearance of *Araucaria* is well established at the Colonia record at 9.9K cal. yrs BP and is not as clear in the Curucutu record due probably to the low resolution of the latter.

The dense arboreal vegetation signal reported in CUR 3 contains *Cybianthus* (15%), Myrtaceae (8.2%), *Illex* (7.8%), *Vernonia* (6.2%), *Symplocos* (6%), *Maytenus* (5%), *Drimys* (3%), *Didymopanax* (3%) and *Myrsine* (3%), among many others. Some of these montane taxa can be possibly interpreted in this zone as indicators of taxa migrating to higher altitudes due to a significant warming trend in the lowlands during the Holocene.

The forest pollen spectra of CUR 3 contrasts with a more reduced open altitude savanna signature of herbaceous elements (30%) containing the lowest Poaceae (13%) and Asteraceae (11%) representations in the entire record. Tree ferns prospered during this time with significant increases of *Cyathea* (up to 33%), *Dicksonia* (6%) and *Hymenophyllum* (12%), an epiphyte in dense tropical forests. Like *Araucaria*, many of the high altitude indicators such as the alga *Debarya* and the ferns *Blechnum* and *Jamesonia* disappear from the record and are now more prevalent in altitudes reaching above 2000 meters in southeastern Brazil (Tryon & Tryon, 1982; Sánchez-Bacaraldo, 2004).

The modern pollen signal of surface samples at the Curucutu site contains clear signs of human manipulation of the vegetation possibly the main factor affecting the reduction in arboreal pollen. In addition to the loss of forest, the appearance of *Cannabis sativa* pollen (5%), introduced exotic *Pinus* (1.3%) and a substantial increase in *Cecropia* (9%), an indicator of recent successional vegetation, strongly support this interpretation. The interpretation of the present vegetation, somewhat anthropogenically affected, is also supported by the overwhelming presence of carbonized micro- and macroparticules in the modern soils of the Curucutu landscape.

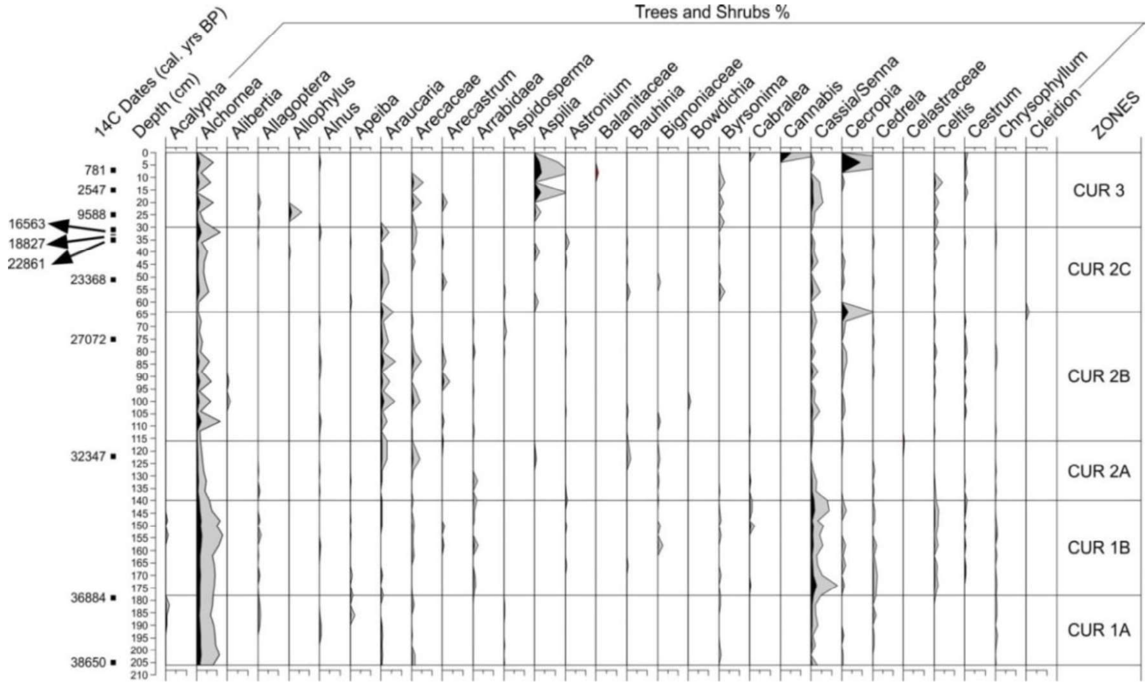

Fig. 1. Percent ollen diagram of trees and shrubs, from *Acalypha* to *Cleidion*.

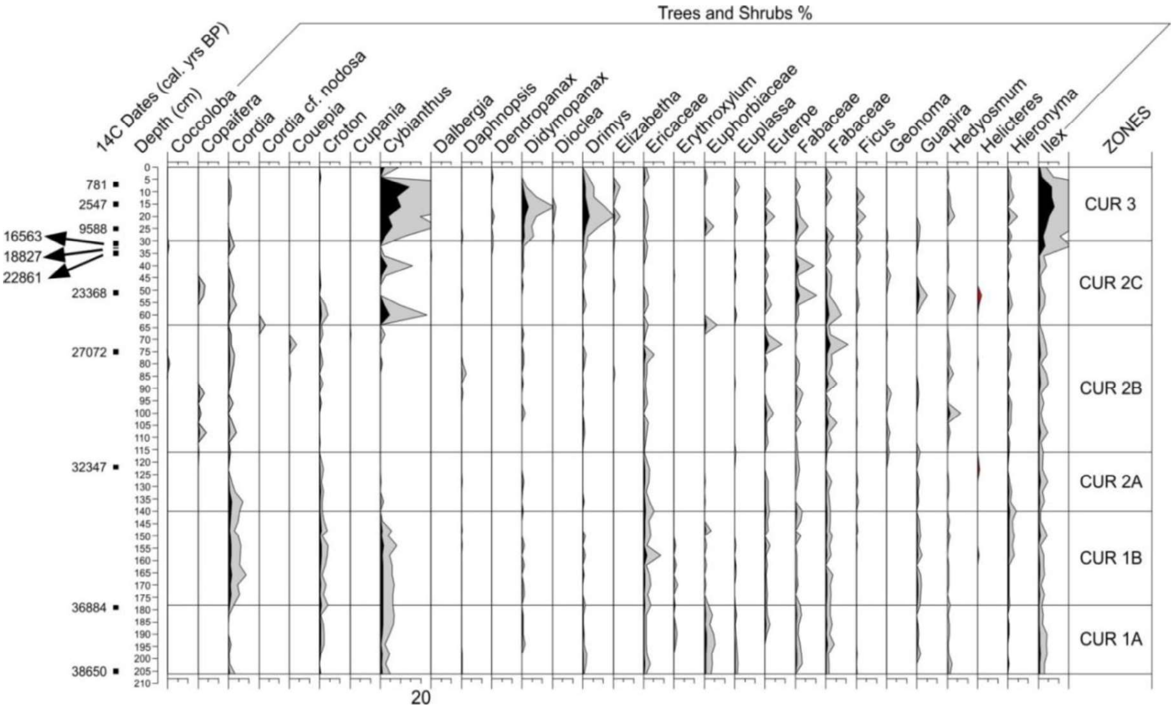

Fig. 2. Percent pollen diagram of trees and shrubs, from *Coccoloba* to *Ilex*.

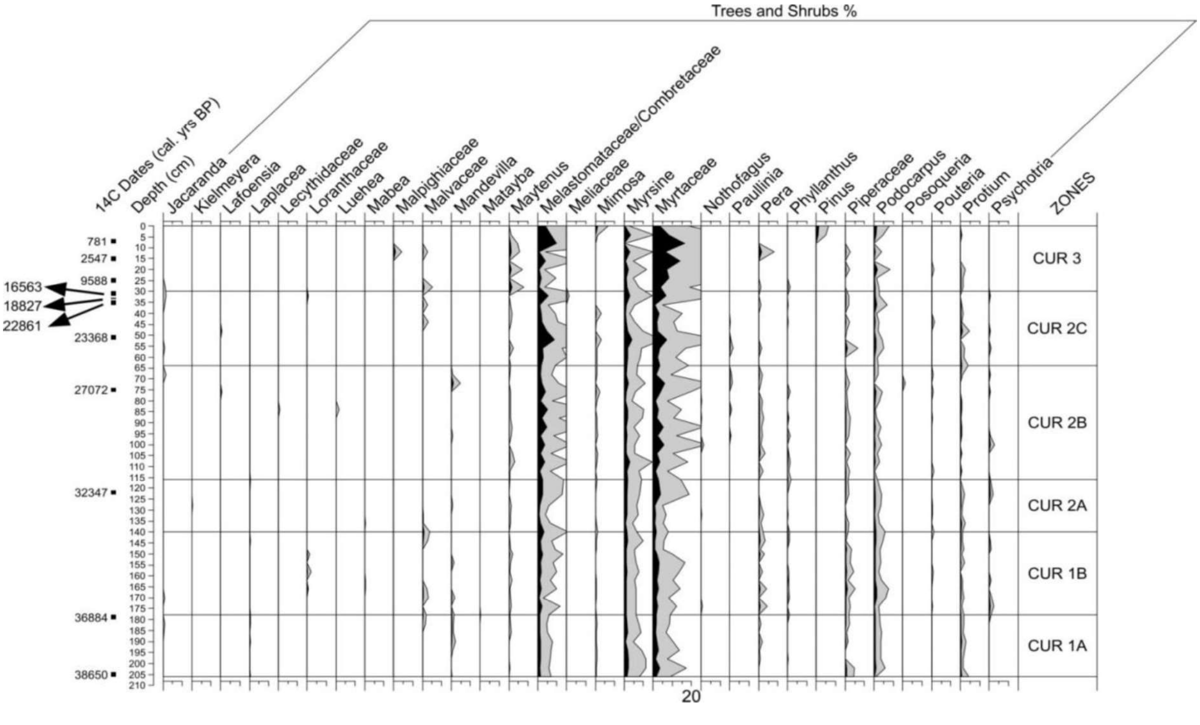

Fig. 3.Percent pollen diagram of trees and shrubs, from *Jacaranda* to *Psychotria.*

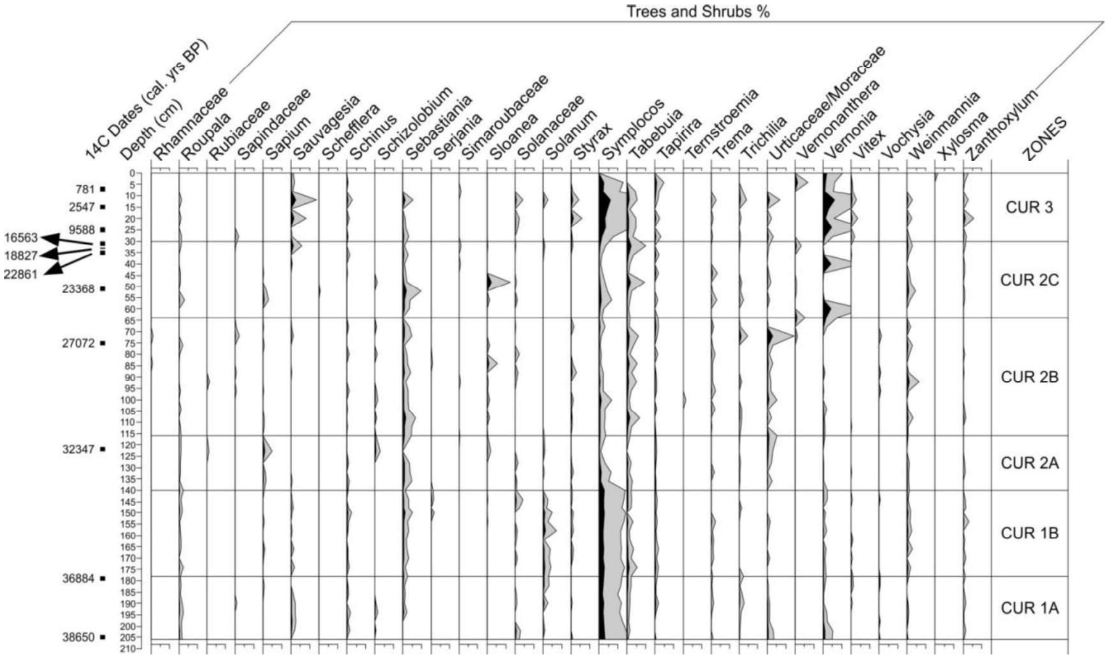

Fig. 4. Percent pollen diagram of trees and shrubs, from Rhamnaceae to *Zanthyoxylum.*

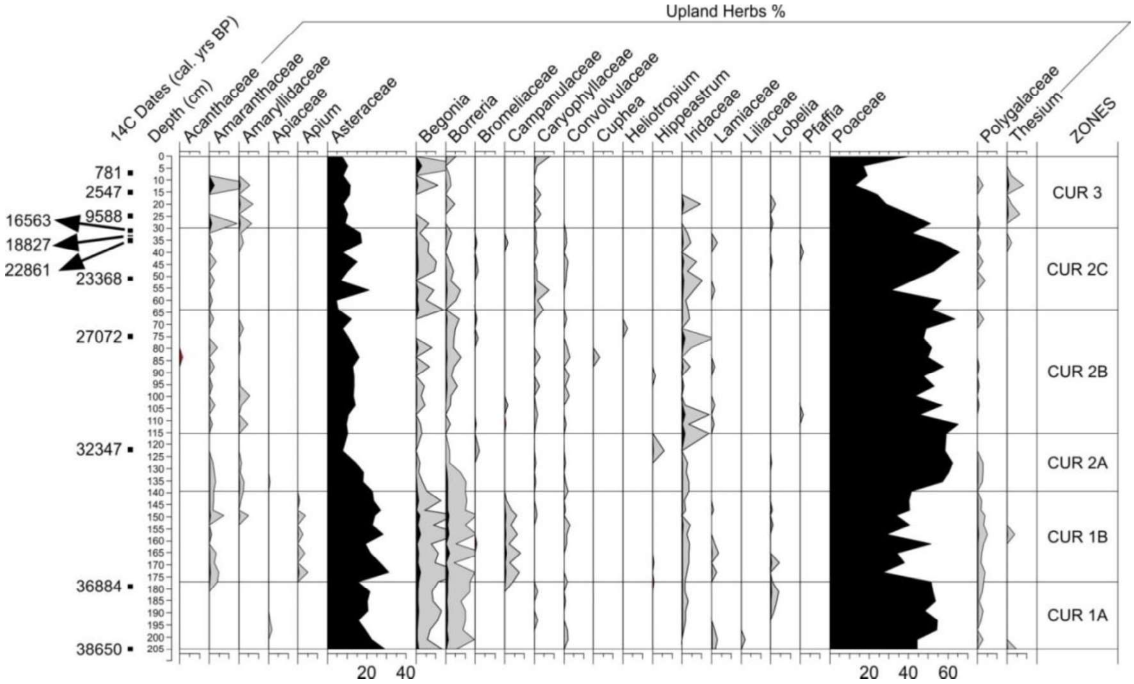

Fig. 5. Percent pollen diagram of upland herbs.

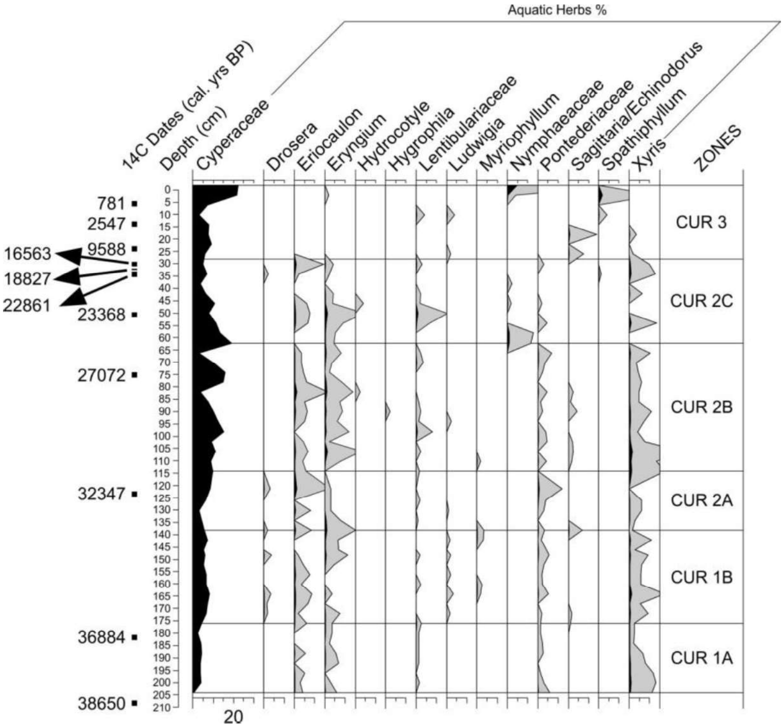

Fig. 6. Pollen diagram of aquatic plants (*Drosera* to *Xyris*).

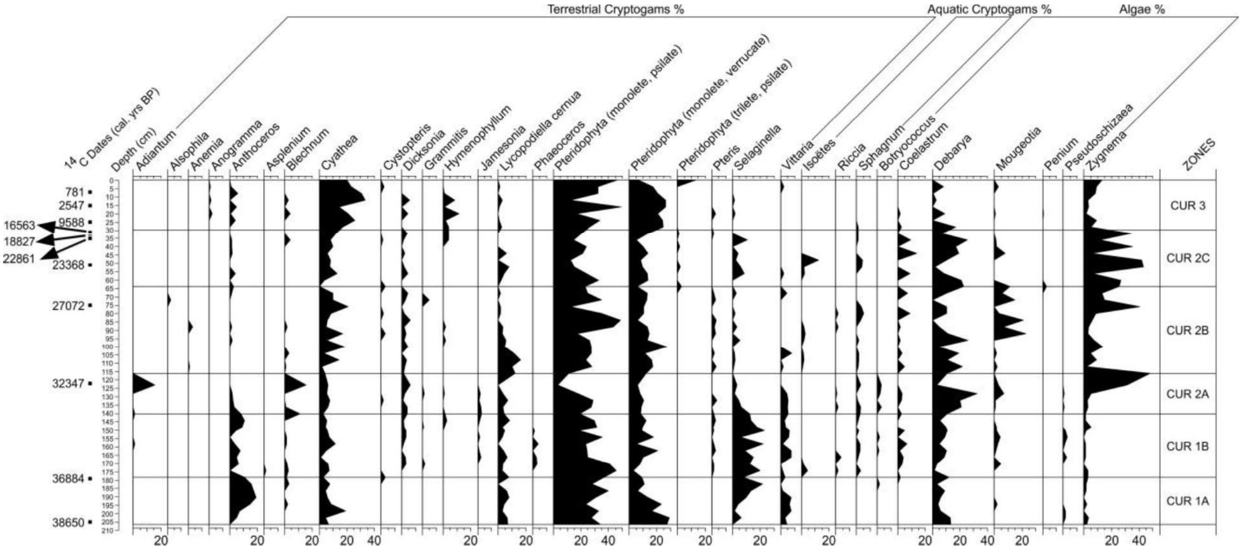

Fig. 7. Pollen and spore diagram of terrestrial and aquatic cryptogams and algal cysts.

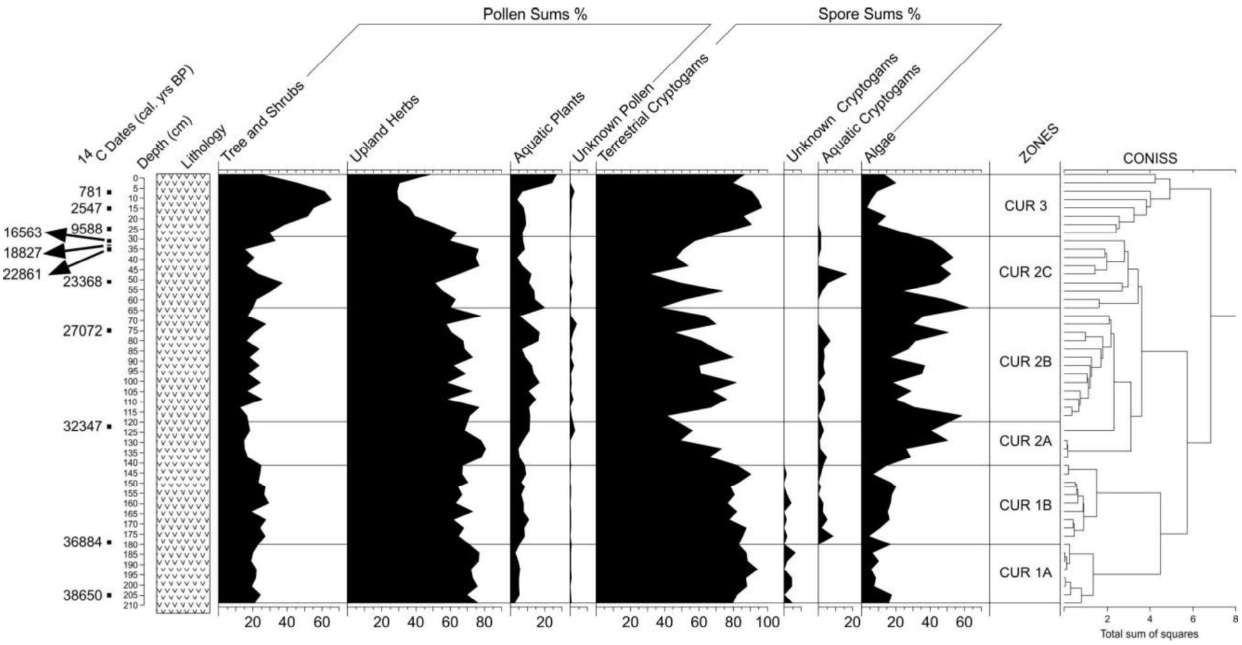

Fig. 8. Pollen diagram of percent sums of all categories (trees and shrubs, upland herbs, aquatic plants, terrestrial cryptogams and algal cysts.)

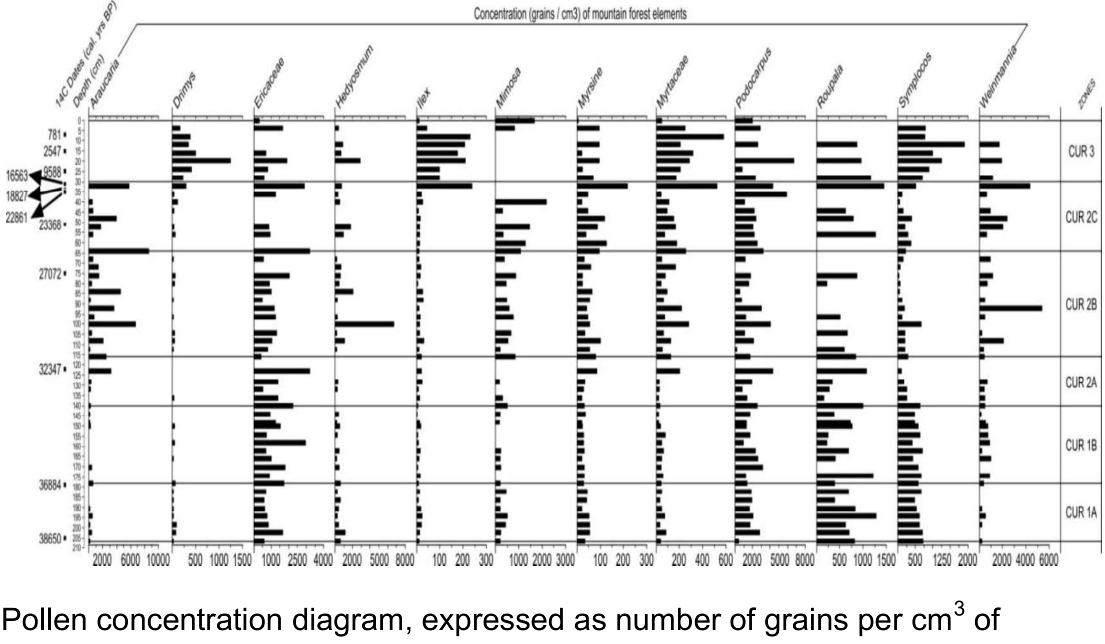

Fig.9. Pollen concentration diagram, expressed as number of grains per cm^3 of montane taxa.

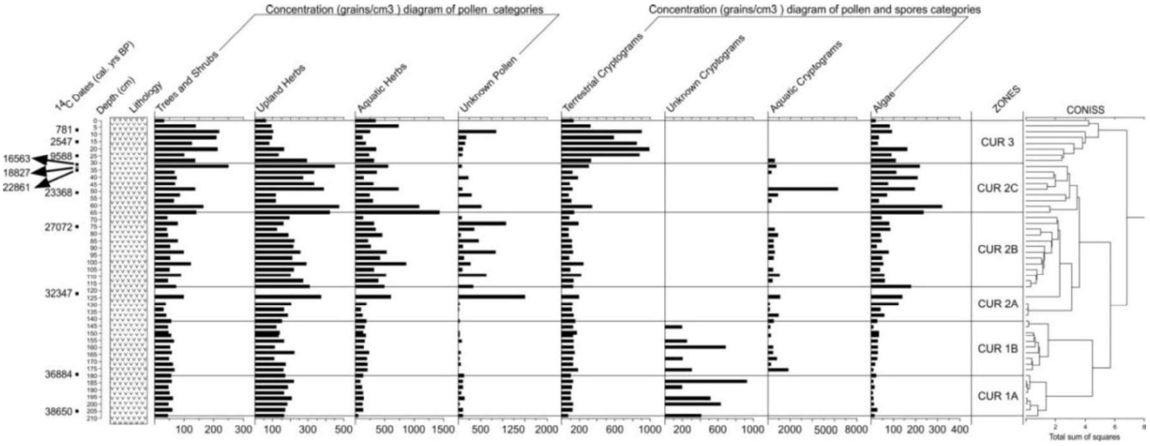

Fig. 10. Pollen concentration diagram of all categories, expressed as number of grains per cm^3 of all categories.

Origin of the modern Forest/High Altitude Savanna mosaic at Curucutu

The present forest/savanna mosaic at the Curucutu region of the southern Atlantic Rainforest is an ancient physiognomy extending at least the 40,000 years and cannot be thought of as a consequence of either modern human interference on the landscape nor a relict of Pleistocene rainforest contraction brought about dry Pleistocene climates as suggested by the Forest Refuge Hypothesis (*sensu* Haffer, 1969; Ab´Saber, 1982; Prance, 1982; Haffer & Prance, 2001). Indeed, the grasslands appear more widespread during the Late Pleistocene at Curucutu, but under moist and cold conditions, similar to those found at its core distribution presently at ca. 2000 m elevation. Nevertheless, Poaceae and Asteraceae profiles together with the constant signature of montane forest elements indicate a long history of co-existance of these two contrasting ecosystem for at least the last 40,000 years, well beyond the time frame of the Refuge Hypothesis and the arrival of humans in the early Holocene. One alternative hypothesis is that the forest/high altitude savanna mosaic is constrained more by the interplay of edaphic and geomorphological conditions than by climate alone. This idea is more conducive to the observation of the mosaic maintenance during the Holocene, which under moister conditions is not alone sufficient for the replacement of the altitude savanna by forest vegetation.

The different patterns of sedimentation rate and different temporal zonation displayed by the Curucutu and by the Colonia (Ledru et al., 2005) records, both of low temporal resolution, do not permit a clear comparison between their pollen spectra. However, similar trends in arboreal and herbaceous categories are clear in the two sites. For example, the striking low frequency of arboreal at Colonia from 40 – 30 k cal yrs BP corresponds to the same trend at Curucutu from 38 k cal. yrs BP to 27 k cal yrs BP as well as the substantial increase in arboreal taxa after 10k cal yrs BP. Although some pollen spectra are not completely the same in both sites at the same time, this can be easily explained by the typical heterogeneity found in tropical forests, and may be caused by local geomorphological characteristics. In the case of Curucutu, the hilly landscape may present differential accumulation of nutrients in valleys due to erosion and particular runoff characteristics. On the other hand the Colonia Crater is characterized by a large flat landscape reminiscent of a large and ancient impact crater within wich a marsh of considerable dimensions is more likely to contain a more regional signal of the vegetation as opposed to the rather small sedimentary basin in Curucutu, registering a very local pollen signal.

One of the most important conclusionsof this work, regarding the mosaic of high altitude grasslands and forests, is that the modern landscape is the result of warm and humid climates of the Holocene in contrast to a more spread out high altitude grasslands with pockets of forests during the cool and wet phases of the Late Pleistocene. With increasingly warm climates at md elevations, this ecosystem migrated uplands in other areas of the Serra do Mar and that the present landscape con be thougt of as a relict stage of a once more abundant ecosystem at elevations near 1000 m. The modern tree line at Campos do Jordão (SP) and at the Itatiaia mountain range, in Southeatern Brazil, is located at ca. 2000 m.

***Alnus*, *Nothofagus* and montane forests in relation to climatic forcing**

Two Andean taxa appear in the pollen record of the Curucutu region. These are *Alnus* (Family Betulaceae) and *Nothofagus* (Family Fagaceae), two genera of trees and shrubs in high altitude moist Andean forests. *Alnus* extends from the northern Andes in Peru, Colombia, Venezuela and Ecuador, reaching Chile and Argentina (Markgraf & D´Antoni, 1978) whereas *Nothofagus* is a genus, exclusive to the southern Andes of Chile and Argentina. These two anemophilous pollen types (Weng et al., 2004; Markgraf & D´Antoni 1978) have been reported for the LGM of Brazil in various palynological studies in low percentages, usually <4% (De Oliveira, 1992; Colinvaux et al., 1996; Haberle, 1997; Behling et al. 2004). However, Cohen et al. (2014) reported values reaching 26% during the LGM of Western Brazilian Amazonia, implying expansion of this tree species in the amazonian lowlands during glacial times. In the Curucutu site, the presence of these two taxa can hypothesized as a result of long distance transport by means of intensified cold polar air masses, especially during the end of the last glacial cycle (Fig. 11)

The largest concentration of *Alnus* at Curucutu occurs at 32 cm depth, with an age of ca. 18, 000 cal. yrs BP at the final stage of the LGM (c. 25 – 17,5 K cal. yrs BP) with concentration of ca. 1500 grains/cm^3 and 0.2%, a value indicative of long dispersal by air masses. *Nothofagus*, on the other hand, is not as common on the record as its counterpart but its presence is also registered also during the LGM and Heinrich events (Fig.12).

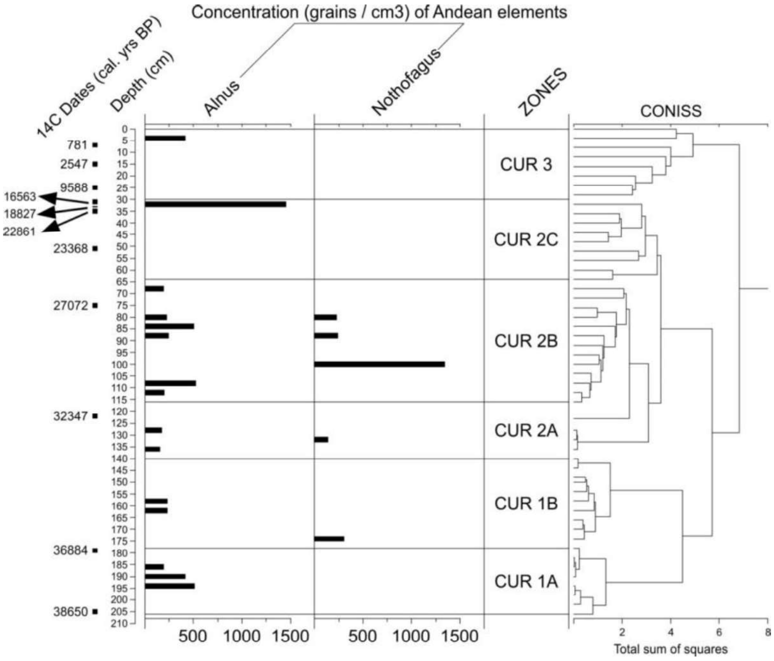

Fig. 11. Late Pleistocene and Holocene occurrence of *Alnus* and *Nothofagus* pollen in the Curucutu core.

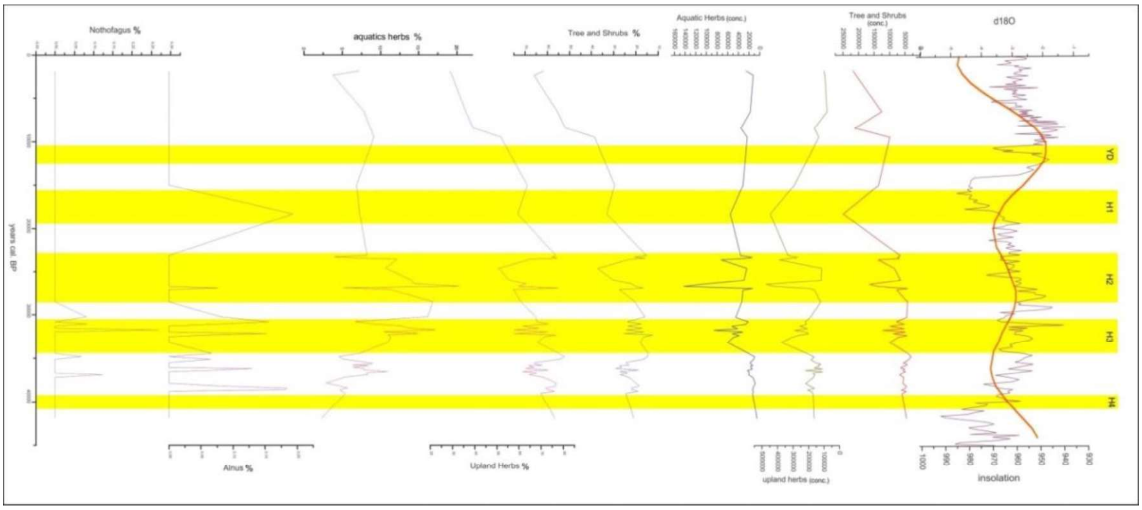

Fig. 12. Percentage and concentration values of different pollen categories and of Alnus and Nothofagus along the Curucutu sediment core in relation to Heinrich events, summer insolation at 30°S and Δ^{18}O variation in the Botuverá speleothem (Cruz et al., 2005, 2006).

The presence of these two Andean pollen taxa in the Curucutu sedimentary sequence appears to be correlated either with Heinrich events (H1, H2 and H3), synchronously or not with high summer insolation and enhanced monsoonal in the southern hemisphere as indicated in Figure 10. Both climatic forcing are conducive to more active polar air incursions into South America, forming the South Atlantic Convergence Zone (Cruz et al., 2005, 2006, 2009). It´s noteworthy the presence of *Alnus*, although in very low percentages, in modern sediments at the Curucutu site. A possible explanation for this occurrence can be found in the recent abnormally cold incursions of polar air into southeastern Brazil in the winters of 1895, 1928, 1955, 1985 and 1975, with snow precipitation in the Serra do Mar in São Paulo (1928, 1955) and in all of those events in the high terrains of the Brazilian Highlands, specially the Itatiaia Massif in the Mantiqueira Mountains, ca. 300 km from the Curucutu site.

Although these two taxa may be used as proxy for paleoclimatic studies in South America, especially for those interested in determining routes of polar incursions, such analyses must take into account the 100 – 150 m reduction in sea level during the last glacial, which in turn allowed the subaerial exposition of the Brazilian continental shelf, distancing the coast line by at least 150 km eastwards. Such new geomorphological configuration is likely to have affected at least the maritime route of polar air masses and might explain why both taxa are always synchronous in the sedimentary record.

Although climatic change does not appear to have a major role in the establishment of the physiognomy of the modern forest/high altitude savanna mosaic, drastic floristic changes occurred within these plant communities. Along the history of the Curucutu sector of the southern Atlantic Rainforest, the distribution of montane forest taxa such as *Araucaria* and *Podocarpus* appears to be strongly correlated with periods of intense cooling and humidity during the LGM and Heinrich events in the northern hemisphere. Likewise, in other areas of Brazil, various palynological studies suggest that more frequent and more intensified polar air masses altered the vegetational composition of different ecosystems during the Late Quaternary concomitant with the expansion of

Podocarpus and other montane elements into the lowlands (De Oliveira, 1992; Ledru, 1993; Ledru et al., 1996; 2001; Colinvaux et al., 1996; Haberle, 1997; Haberle & Maslin, 1999; Colinvaux et al., 2001). Cooling and high humidity in Curucutu during the late glacial phase, including the LGM and Heinrich events 1 and 2 is in full agreement with pollen analyses in central Brazil (Barberi, 2001; Ledru et al., 1998; Salgado-Labouriau et al., 1998) where the landscape underwent major environmental changes leading to the replacement of cerrado by a *Podocarpus* forest with various other montane tree taxa.

The disappearance of *Araucaria* in the Curucutu record at ca. 10,000 years BP can be hypothesized to be a consequence of climatic and physiological barriers detrimental to its full development brought about by the predominatly warm climates of the Holocene. It is hypothesized that this major vgegetational change might also be related to the migration of this taxon to higher elevations after the onset of the Holocene. If this is correct, this event would mark the emergence of the present day distribution of this taxon in elevations higher than 1000 m in southeastern Brazil. On the other hand, other members of montane forests such as *Podocarpus*, *Ilex*, *Symplocos*, *Drymis*, Ericacae, *Weinmania*, and the large Myrtaceae family, with its pollen possessing only one morphological type that prevents identification of different genera, appear either more resilient to warming climates or have different species not recognizable by the palynological tool, with broader fundamental niches (*sensu* Kearney & Porter, 2004) conferring them the genetic plasticity to tolerate climatic change.

Despite the consensus that *Alnus* pollen reaching continental Brazil is linked to air masses moving eastwards, an alternative hypothesis is that the South American Monsoon system, which brings humidity from the northern South America, during the austral summer, could be invoked as the a possible mechanism for dispersing this taxon thousands of kilometers of its source areas.

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CHAPTER 5

MANUSCRIPT 4 (published in 2014)

PALEOCLIMATES OF AMAZONIA: AN ICE-AGE VIEW

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Abstract

This chapter brings a point view regarding the Ice Age period in Amazonia under the light of palynological data and their relation to other proxies in order to provide a general overview of the vegetational changes in the equatorial tropical rainforest domain of South America during times of highly variable temperature and precipitation regimes. This point of view is divided into topics such as an overview of the objectives of paleoecology, long temperature and precipitation records, asynchrony and synchrony of climatic events, fire and finally the future of Amazonian paleocology. In the last topic we state what we believe are the necessary steps to be taken by Amazonian paleoecologists. We believe this is the time when our science is needed and we have the opportunity to elevate the status of our science. To have the impact that is needed, we need to produce more sophisticated records and interpretations of past systems, and then display them in a way that other scientists and policy makers find readily understandable.
Keywords: *Amazonia, ice age, paleoclimates, palynology, LGM*

1. Introduction

Lowland Amazonia is over half the size of the continental United States, and yet all too often it is discussed as a climatic and biological monolith. One of the most important understandings to have come from the last half century of paleoecological research is that the history of Amazonia is characterized by tremendous spatial and temporal variability. We cannot make simple assertions about the past climate of ‘Amazonia’, as there is no such uniformity. Indeed, the closer we look at the patterns of variability, the more we begin to understand past climatic processes.

Recent droughts that struck Amazonia, including the megadroughts of 2005 and 2010, have taught us a lot about the potential effects of climate change on the vast Amazonian ecosystem. Six basic observations are: First, even the most severe droughts were not uniform in their impact across the basin. The 2005 megadrought was centered on western Brazil, while the 2010 drought had its epicenter further south and east (Lewis *et al.*, 2011). Second, the causes of the droughts were different, there have been El Niño Southern Oscillation (ENSO)-related droughts and these have their strongest impact on eastern Amazonia while droughts derived from sea-surface temperature anomalies in the tropical and subtropical Atlantic have the strongest effect on southwestern Amazonia (Lewis *et al.*, 2011; Marengo *et al.*, 2011). Third, the effects of a given drought are exacerbated by forest fragmentation and human presence (Shukla *et al.*, 1990). Fourth, large canopy trees are disproportionately impacted by drought, showing higher than average mortality rates (Laurance & Williamson, 2001). Fifth, even with severe drought, fire is almost uniquely associated with human actions (Cochrane & Barber, 2009). And sixth, when fire does occur, it changes forest composition markedly (Barlow & Peres, 2008). Repeated burns within a few decades can result in the complete species turnover among ground nesting birds as mature forest is replaced by regrowth rich in bamboos and vines (Barlow & Peres, 2008).

Taking these observations together, the critical message is that vegetation in Amazonia is not a single lump that will be molded uniformly by a given event. Climate forcing across the Amazon Basin will be heterogeneous. The response of vegetation to climatic forcing will also be heterogeneous across the basin and will reflect variability in the source and intensity of the forcing. Within the forest, responses will also be heterogeneous with the forest biome overall appearing to be very resilient, while individuals or functional types (not individual species necessarily) may be more vulnerable. The great changer of Amazonian ecosystems is fire.

Paleoecology is at its most relevant when it can provide insights that affect policy. Current climate change projections for what may or may not occur in Amazonia in the next century should be tested through what Flenley referred to as our ‘time-machine’ (Flenley, 1979). While we cannot leap forward we can certainly leap backward in time to estimate how ecosystems (vegetation) and climate forcing have changed. The projection that Amazonia will suffer enormous drought and lose 80% of its forest cover by 2100 AD in a catastrophic climatically-driven, die-off (Cox *et al.*, 2004; Malhi *et al.*, 2008) has gained a lot of attention. While the HadCM3LC model that makes this prediction is very sophisticated, it may be equally flawed (Cochrane & Barber, 2009; Cox *et al.*, 2013). Of the 8 major climate models used for IPCC projections, they are about equally divided as to whether the Amazon will become wetter or drier going into the future. Precipitation has always been harder for climatologists to predict than temperature, and the same is true for paleoclimatologists. From an ecological standpoint, however, the annual precipitation amount is secondary to the seasonality of that precipitation. The statistic for the duration and intensity of soil moisture deficit is far more important than total precipitation. For example, so long as the system is relatively aseasonal a precipitation of c. 1600 mm is sufficient to maintain diverse rain forest, e.g. Pucallpa, Peru (1587 mm pa), whereas the same rainfall in a strongly seasonal setting could support savanna (Eiten, 1982; Salo *et al.*, 1986). Determining this patterning of precipitation is an area where fusion of palynology with isotopic records could reveal new insights.

In this chapter we will lay out some of the challenges and opportunities in front of us, while at the same time attempting a synthesis of Late Pleistocene climate change in Greater Amazonia.

2. Long temperature records

In the lowlands there are a handful of climate records that span one or more full glacial cycles. All of these records are valuable, none of them is perfect. Amazonia has few ancient lakes because the processes that provide the ancient rift lakes of Africa, glacially gouged lakes or large solution basin and impact craters, are simply not present in Amazonia (Colinvaux, 1989). Rather, there are lakes associated with inselbergs that rise above the Amazon plain at Carajas (Absy *et al.*, 1991; Hermanowski *et al.*, 2012), the Hill of Six Lakes (Colinvaux *et al.*, 1996; Bush *et al.*, 2004) and Maicuru (Colinvaux *et al.*, 2001). In greater Amazonia, there are some ancient lakes on the flanks of the Andes (Mourguiart & Ledru, 2003; Bush *et al.*, 2004; Urrego *et al.*, 2010), and in the Altiplano (Baker *et al.*, 2005; Chepstow-Lusty *et al.,* 2005; Fritz *et al.*, 2007; Hanselman *et al.*, 2011). To the south of Amazonia there are solution basins in Central and southern Brazil (Salgado-Labouriau, 1997; De Oliveira *et al.*, 2005; Whitney *et al.*, 2011) that provide records spanning the last 50 ka and the c. 130 ka record from Colônia, São Paulo (Ledru *et al.*, 2005). A common theme of the records from the lowland Amazonian lakes of Hill of Six Lakes, Carajas, and Maicuru is that forest dominated the landscape for much of the Pleistocene. A commonality among these records is that they all show increased abundances of species that are today associated with moist uplands, i.e. *Podocarpus, Hedyosmum, Myrsine,* becoming more abundant in lowland forest (Bush *et al.*, 2011).

Converting an altered range to a temperature difference was first achieved by van der Hammen in his analysis of cores from the High Plains of Bogota (Van der Hammen & González, 1960; Van der Hammen, 1974). He observed that the vertical distance of migration could be equated to temperature via the moist air adiabatic lapse rate. Air masses lose temperature predictably as elevation increases, with the only variable being humidity. On the flanks of the Andes today the lapse rate is close to 5.2 ^{o}C per 1000 m of ascent (Bush & Silman, 2004). So if plants occur at the glacial maximum 1000 m below their modern range, they indicate a cooling of about 5 ^{o}C. If the taxa are clearly mesic species then, humidity has not changed much, and the modern lapse rate can be applied to the past. Even though this is a simple way of estimating paleotemperatures it produces results consistent with more complex transfer functions (Correa-Metrio *et al.*, 2010), and also with mapped changes in ice limits and estimates of equilibrium line altitudes *(*ELAs) of glaciers (Rodbell *et al.*, 2008; Smith *et al.*, 2008).

The presence of taxa such as *Podocarpus, Myrsine, Hedyosmum, Alnus, Ilex* and *Drimys*in lowland settings is generally indicative of about a 5°C cooling. One of the most detailed temperature reconstructions from the edge of the Amazon basin comes from Lake Consuelo at 1380 m elevation in Peru on the eastern flank of the Andes (Urrego *et al.*, 2010). The Consuelo record shows a downslope migration of taxa consistent with a c. 5-7 °C cooling, and that this 'cool' forest was remarkably constant in terms of projected temperature between c. 42 and 22 ka (ka = thousand calibrated radiocarbon years before present). It was notable from this record that the peak of northern hemispheric glaciation, defined as 26-18 ka, was not especially cold in southern Peru. Smith et al. (Smith *et al.*, 2005; Smith *et al.*, 2008) mapped glacial moraines and erratics in Peru's Cordillera Blanca and found that the greatest glacial descent occurred c. 34 ka, notably earlier than the maximum ice extent in the northern hemisphere. Glaciers respond both to cold and moisture availability and so it is possible that precipitation in the Peruvian Andes was exceptionally heavy around 34 ka. Note the close temporal proximity of this major ice advance (within radiocarbon error occurring just prior to the drier period observed in some lowland records between c. 35 ka and 15 ka (below)). The period between c. 70 ka and 30 ka was strongly influenced by wet events associated with northern Hemispheric Heinrich events (Kanner *et al.*, 2012). The wet event that induced the surge of glaciers in eastern Peru at c. 34 ka may have been associated with a Heinrich event.

Between 22 and 16 ka there were some temperature oscillations, with a steady warming evident between 16 and 11 ka (Urrego *et al.*, 2010). Contrastingly in the lowlands, although the overall temperature depression is usually quoted as c. 5 °C, the pattern of cooling appears to be different. The 'cool' indicator taxa are present throughout much of the last 40,000 years but in some records the absolute peak abundance of these taxa was at 14 ka rather than during the peak of the ice age (Bush *et al.*, 2004; Ledru *et al.*, 2007). A possible explanation for the late peak in ‘cool’ taxa demonstrates the inter-relatedness of niche, precipitation and temperature. It is possible that though cold enough to support *Podocarpus* and other mesic forest taxa throughout the last 50 ka, the glacial maximum was seasonally dry, exhibited greater seasonality or was at least precipitationally sub-optimal compared with the period at 14 ka. Again, it needs to be emphasized that different regions within Amazonia may have been more or less strongly influenced by any or all of these climatic factors.

3. Long precipitation records

While temperature caused the invasion of some cool-adapted species into the lowlands, and their ecology provides evidence of overall mesic conditions, there is no doubt that precipitation was also an important factorwith likely high spatial variability. At issue has been the extent to which forest cover disappeared or became more open between c. 35 ka and 15 ka due to reduced precipitation across the basin (Ledru *et al.*, 1998). Initial discussions centered around whether forest was replaced by savanna (Haffer, 1969; Colinvaux *et al.*, 2001; Haffer & Prance, 2001; Bush & De Oliveira, 2006), but the impetus behind this debate – to explain speciation patterns in terms of ice age climate change – became less relevant as molecular and phylogenetic data indicated that a few large drought episodes could not account for Amazonian speciation patterns (Cheviron *et al.*, 2005; Hawkins *et al.*, 2006; Miller *et al.*, 2008; Rull, 2008; Colwell & Rangel, 2010). The discussion has since become more nuanced and more realistic. There is little doubt that past climates, and particularly changes in precipitation regime, shaped the forest boundaries and altered canopy composition and density. The question now becomes one of assessing the response of different plant functional types or taxa, the geographic and temporal variation in those changes, and the consequences for ecosystem function.

In the last few years, isotopic records from speleothems have begun to provide insights into Amazonian paleoprecipitation (Wang *et al.*, 2004; Cruz *et* *al.*, 2005; Cruz *et al.*, 2009; Mosblech *et al.*, 2012; Cheng *et al.*, 2013). Speleothems do not provide a direct record of the amount of precipitation, as the source of the precipitation can influence the isotopic record. Nevertheless, most of the speleothem records are interpreted as indicating 'wet' versus dry' phases.

The speleothems reveal that Amazonian precipitation was forced primarily either by local changes in convection or by shifts in the meridional overturning circulation (MOC) of the Atlantic (Cruz *et al.*, 2005; Kanner *et al.*, 2012; Mosblech *et al.*, 2012). During the period between about 70 and 30 ka the growing Laurentide ice mass went through cycles of expansion and partial collapse that induced the Dansgaard-Oeschger cycles that lasted 3000-7000 years (Dansgaard *et al.*, 1993). The most extreme of these events was usually initiated by a Heinrich event in which rafts of icebergs were released into the North Atlantic (Heinrich, 1988). At high latitudes the Dansgaard-Oeschger and Heinrich events are primarily recorded as abrupt changes in temperature. In the tropics, these events are now evident in many records, but they are manifested differently through space. In Guatemala and Colombia, Heinrich events are cold, dry events, whereas in Peru they are wet events and lack a strong temperature signal (Fritz *et al.*, 2010; Groot *et al.*, 2011; Correa-Metrio *et al.*, 2012). This spatial heterogeneity mirrors regional differences to a common stimulus (*i.e.* a La Niña event) seen under modern conditions. Although the current number of study sites is insufficient for assessing the full variability of responses to Heinrich eventsand other millennial-scale forcings in Amazonia, some signal of these fluctuations in Atlantic sea-surface temperature could reasonably be expected to be evident at most Amazonian locations.

The influence of these events on the tropics was to cause a southward displacement of the inter-tropical convergence zone (ITCZ), with wet events in northeastern Brazil, butprevented summer rains from reaching Guatemala. The ITCZ, however, was not the cause of climate change in the interior of the Amazon Basin and the Andes (Bush & Metcalfe, 2012). As the MOC strengthened (weakened) the tropical north Atlantic cooled (warmed), which in turn led to less (more) moisture being entrained into the South American Low-

Level Jet (SALLJ). It was the strength of the SALLJ that caused changes over much of Amazonia (Figure 1).

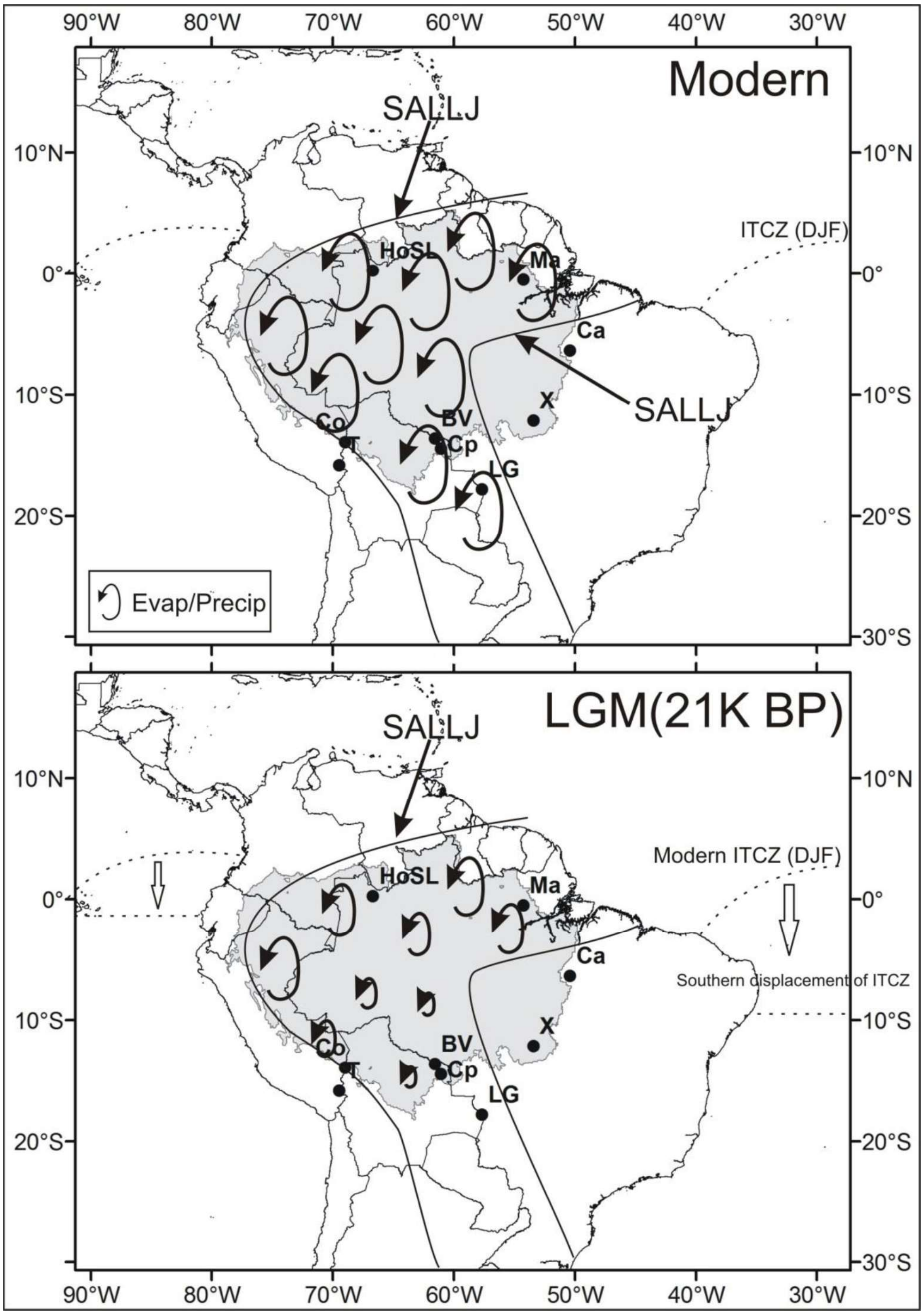

Figure 1: Differences in austral summer (Dec-Jan-Feb) ITCZ positions and convective cell strength between the Holocene (top) and Pleistocene (bottom). Amazonia is shown in light grey. The size of the Evap/Precip arrows represent the convection strength. SALLJ = South American low level jet; Sites mentioned

in the text (see text for references): Ma = Maicuru, HoSL = Hill of Six Lakes, Ca = Carajas, X = Xingu, LG = La Gaiba, BV = Bella Vista; Cp = Chaplin, Co = Consuelo.

It is important to note here that a number of paleoecological papers perpetuate a fallacy that the ITCZ exists over South America; it does not (Hastenrath, 1997). The ITCZ is a maritime phenomenon, and it migrated (annually and millennially) over the ocean not over land. On land, peak annual insolation establishes strong convective cells and these cells migrate with (though lagging behind) the solar equator. Consequently, northern South America has a summer convective peak in July-Sept, whereas south of the equator the peak convection occurs Jan-Mar. It is this convection that establishes the timing of the wet season (Garreaud *et al.*, 2009). As insolation has varied at these latitudes, so too has the strength of convection, and the strength and length of the rainy season. The other variable that is independent of the position of the ITCZ (or nearly so) is the amount of moisture evaporated from the Atlantic warm pool and carried onshore in the SALLJ. Thus, the precipitation arriving to South America is not simply a product of the position of the ITCZ, but is determined by the amount of moisture entrained in the SALLJ in the path of that system, and the strength of convection. This basic observation leads to an expectation of different spatial responses across Amazonia to even the longest climatic forcings.

Given this mechanism, it becomes clear that locations in the path of the SALLJ would be expected to be wet when the tropical Atlantic warms, and that is during northern hemispheric stadials. Conversely, interstadials will favor drier conditions in the path of the SALLJ. Again it is important to note that the SALLJ only covers a portion of South America, whereas northeastern Brazil, southeastern Amazonia, and the Bolivian Chaco, for example, lie outside its strong influence and therefore will be responding to other forcings.

The Pleistocene fluctuations in rainfall and the ecological consequences were large, but whereas Haffer regarded the modern state as being at the wet extreme with glacials being much drier, we may now turn this around to state that within the area influenced by the SALLJ, modern conditions are neutral or dry compared with long term norms (Mosblech *et al.*, 2012). Evidence for the modern climate being a neutral or drier phase than the glacial-interglacial average comes from persistent evidence of wetter than modern conditions in the past. Combinations of reduced evaporation as a result of lower temperatures coupled with strong precipitational inputs linked to the SALLJ induced the formation of vast paleolakes in the Altiplano during the last ice age. Under modern evaporitic conditions those same areas support the largest saltpans in the world. Have there been drier times than now? Absolutely, there have been, though not the arid landscapes predicted by Haffer. Outside the sphere of influence of the SALLJ it was a somewhat different story with local convection being driven by insolation. There has yet to be a long continuous lake record or speleothem record from eastern Amazonia that can reveal whether Dansgaard-Oeschger events were dry there rather than wet, but that would be the prediction. In southern Amazonia unpublished data from the Xingu points to cool mesic conditions about 35 ka, but possibly a dry LGM (Bush, n.d.) and this is consistent with data from Bolivia and geomorphological data from the southern Amazon Basin (Iriondo & Latrubesse, 1994; Latrubesse & Rossi, 2000; Valente & Latrubesse, 2012).

The precipitation data from speleothems support the importance of an Atlantic sea-surface temperature influence on Amazonian paleoprecipitation patterns. Isotopic records from nordeste are broadly out-of-phase with records that lie within the path of the SALLJ (Cruz *et al.*, 2009). Lake level-records directly influenced by the SALLJ, e.g. Lake Titicaca, and the Hill of Six Lakes are broadly coherent in showing highstands (lowstands) during times predicted to have strong (weak) moisture transport by the SALLJ. Areas away from the SALLJ show opposite fluctuations, e.g. the High Plains of Bogotá (Hooghiemstra & van der Hammen, 2004), Carajás (Sifeddine *et al.,* 2001) and the Chaco (Burbridge *et al.*, 2004; Mayle, 2004). Such a simple explanation of events can only provide a default expectation and is bound to predict the wrong outcome for some locations. An example of such a misfit is the low lake levels seen at the glacial maximum, rather than the predicted highstand, in northeastern Bolivia

(Mayle *et al.*, 2000). Here the climatic modifiers may be the position of the Bolivian High, which can bring drought to an area(Lenters & Cook, 1997), or a decrease in dry season cloudiness that causes shallow lakes to evaporate more readily.

These wet and dry events occurred at the rapid pacing of Dansgaard-Oeschgerfluctuations. Consequently, records with large overt or covert uncertainties, i.e. those relying on ^{14}C at the limit of its measurable range or on assumptions relating to thermoluminescence or optically stimulated luminescence, could easily be misplaced relative to a wet or dry event. One of the great strengths of the speleothem records is that they provide uranium/thorium ages that are more exact than those attainable from other forms of dating. As the number of speleothem records increases, so does the potential for having a stacked continental record against which other records can be compared.The speleothem records support the various apparently contradictory assertions made by different research groups regarding whether the glacial maximum was wet or dry, and show that there was immense local, though predictable variability across the continent.

The impact of the wet and dry oscillations on vegetation was probably most apparent in the central 'dry corridor' that runs northwest-southeast across central Amazonia, much of it lying outside the strongest influence of the SALLJ (Bush, 1994) (Figure 1). In this dry corridor there may have been substantial change in forest composition and coverage during the driest times. Although a lot of attention has been focused on the last glacial maximum as the time of maximum aridity, it is more likely that the driest times were interglacials (especially marine isotope stages 5e and 9) rather than glacial periods (Hanselman *et al.*, 2011). Biogeographic analyses point to pathways that would have allowed snakes and plants to migrate through what is now dense Amazonian forest (Gosling & Bush, 2005; Wüster *et al.*, 2005). This dry corridor seems the most likely route with interglacials as the most likely times. As we learn more of these dry events another prediction is that the 'dry corridor' may have been more marked in the east, and that it may not have been synchronously from dry north to south within the corridor, i.e. the corridor may have offered sequential opportunities for migration rather than a simple connection. Another caution is warranted here regarding climate models. The current generations of models of LGM and interglacial conditions (i.e. the PMIP2 reconstructions) tend to be biased toward overly dry conditions, because they are based on the CCSM3 models that underestimate modern precipitation in Amazonia (Cochrane, 2011). While these models provide some valuable insights and hypotheses to test, they do not perform well as the basis for bioclimatic envelope modeling.

One of the problems with models is that they adopt 'normal' conditions, and in the case of the last interglacial, this is sometimes identified as a permanent ENSO state, i.e. permanent El Niño or La Niña. Empirical data for El Niño during MIS 5e is scanty but, to the extent that they exist, they indicate ENSO patterns similar to those of today (Tudhope *et al.*, 2001; Bush *et al.*, 2011). In other words, there was not a permanent state favoring El Niño or La Niña. While assigning a permanent state may make sense to modelers it makes no ecological sense. A single drought such as 2005 and 2010 did not lead to catastrophic tree mortality, because in the following year there were rains that replenished soil moisture reservoirs. Thus, though stressed by the drought, the plants could recover. If there had been sustained drought lasting decades or even millennia as some models project (Cox *et al.,* 2004) then the trees would undoubtedly be replaced by savanna. But, again, the empirical data refute that argument, and so the projections of a permanent state for ENSO are almost certainly misleading. It is precisely this permanent El Niño state that induces the Amazon dieback suggested by the HadCM3LC model, and it is why we as paleoecologists should become engaged in testing its assertions.

4. Synchrony and asynchrony

The relationship between temperature and precipitation during the last ice age is complex and it caused aspects of the paleoclimatic record to vary synchronously with that of the North Atlantic, while other aspects (or locations) have clearly asymmetric responses (Cruz *et al*., 2005, Mosblech *et al*., 2012).

Even where both temperature and precipitation responses are both recorded in the same record they are temporally asynchronous, leading to many permutations of dry, wet, warm or cold conditions, e.g. the La Gaiba record from Bolivia (Whitney *et al.*, 2011).

The broad pattern of glacial activity reflects insolation, i.e. the Milankovitch Cycles of eccentricity (c. 100k years), obliquity (c. 40 k years), and precession (19 and 23 k years), are all evidentin long paleoecological records. In general, temperature follows the eccentricity cycle, while precipitation is forced by precession (Hooghiemstra *et al.*, 1993). Note, however, that the largely ignored role of obliquity was recently emphasized as an important climatic driver in the 2.5 million year record from Lake Fuquene, Bogotá (Groot *et al*., 2011). Local conditions will determine which month(s) are critically influenced by precession. So while different authors find a common c. 20,000-year cycle apparently influencing their record the peaks and troughs will not necessarily be aligned. For example the precessional signatures in the Botuverá Cave and Hill of Six Lakes records are strong with wet peaks predicted by December-February insolation (Bush *et al.*, 2002; Cruz *et al.*, 2005), whereas in Nordeste the wet peaks are February –May (Wang *et al*., 2004). A 3-month difference in the season that is forced by the precessionalcycle, is a quarter (3 of 12 months) cycle change in the location of the peak, i.e. c. 5k years. The north to south differences will also be pronounced. For example, sites north of the equator, such as the Cariaco Basin and the High Plains of Bogota, would respond to northern hemispheric summer, i.e. June-August, while São Paulo would respond to December-February.

The Milankovitch Cycles thereby establish what we can think of as default expectations for climate. But it must be remembered that these are relatively weak forcings and can be modified if not totally overwhelmed by local signatures. Consequently, we find that there can be a strengthening or weakening of precessional signals at a given location. For example, prior to c. 70 ka the precessional signal is weak in Altiplano records (Fritz *et al.*, 2007), but it, and a superimposed North Atlantic signature of rapid climate fluctuations, become increasingly apparent between 70 and 15 ka. Contrastingly, close to the Atlantic

Ocean, the Botuverá Cave sequence shows a precessional signal throughout the last 120 ka (Cruz *et al*., 2005). In Panama, Guatemala, and the Altiplano, it has been suggested that the entrainment of climate with North Atlantic variability reflects the progressive influence of the growing Laurentide ice mass (Bush & Metcalfe, 2012).

At Santiago Cave in Ecuador, the record looks remarkably similar to that of Botuverá Cave until c. 35 ka (Mosblech *et al*., 2012). Between 35 and 17 ka, the Santiago data do not reflect strong correlation with either Atlantic or Andean records. It is possible that this record is aberrant and as new records emerge this portion of the record will be seen to reflect cave specific conditions. Before rejecting this record as an anomaly, however, it is important to note that where the decoupling occurs, between 35 and 17 ka, coincides with what appears to be the time of lowest lake levels in much of Amazonia. Santiago cave is still receiving abundant moisture at this time, and so it is not the driest time in the record, but it may be that the seasonality became markedly different.

The idea that, through time, sites couple and decouple from larger climate patterns is an important realization that is emerging as we obtain higher quality records from across South and Central America. Investigating the underlying mechanisms and the consequences of these shifts will be a profitable avenue for further research.

5. Fire

Fire is a hugely important variable in Amazonian systems and yet its Pleistocene history remains almost completely unknown. Fire is known to have been a natural part of high Andean ecosystems (Hanselman *et al*., 2011), but its occurrence and periodicity in mesic lowland settings is far from certain. In the highly seasonal setting of northeastern Bolivia, charcoal is seen in most samples from periods where sediment was accumulating, suggesting a regular presence of fire in this system. From more humid areas of the Amazon Basin, there is either a lack of charcoal (Bush *et al.,*2004; Urrego *et al*., 2010), or a lack of data. Ten samples spanning the last 70 ka from the Amazon fan (Piperno, 1997) contained charcoal. All of the fossil samples had charcoal concentrations within the range of 6 modern charcoal samples collected from the surface of the Amazon fan. The altering flow pattern of local currents and eddies as sea-level fell and then rose could easily account for the observed variability. The fan data tell us that somewhere in the catchment fires were producing charcoal throughout the glacial period, but that is all that can be said. Detailed analyses of charcoal needs to be done on all long Amazonian records.

6. The future of Amazonian paleoecology

For the first time we have a skeletal understanding of past climatic changes in portions of Amazonia. Our hypothesis of the importance of the tropical North Atlantic as a driver of the SALLJ needs to be tested rigorously. Much remains to be discovered regarding local manifestations of these climate events, and whether the interglacial forcing mechanisms of MIS 5e were similar to those of today.

In the past 30 years there has been an exponential growth in the detail of Amazonian paleoecological and paleoclimatic records. We have more records, with finer temporal resolution than ever before. The next step for palynologists is to refine our taxonomic identifications so that we can provide genus or species level paleoecological records and these in turn will facilitate improved transfer functions for both temperature and precipitation. Research areas that seem suitable for further exploration include establishing transfer functions or ecological interpretations for chironomids (Williams *et al.*, 2011), phytoliths (Piperno, 1990; McMichael *et al.*, 2012), non-pollen palynomorphs (Montoya *et al.*, 2010) and wood (Bush *et al.*, 1990; Di Pasquale *et al.*, 2008) as these are all potentially highly sensitive ecosystem indicators.

The speleothem records have provided a new opportunity for us to assess the resilience of Amazonian systems. The isotopic records provide an independent assessment of climatic change through time. What they do not tell us is the extent of ecological change. Improved pollen taxonomy applied to high-resolution lake core records will allow us to determine whether a climatic oscillation was ecologically important or not. As our understanding of Amazonian habitat and climate heterogeneity increases, so too may be the apparent role that such lack of uniformity has played in maintaining species diversity through time. From these observations we may be able to ascertain what events are needed to cause basin wide state change in Amazonian ecosystems and thereby identify the vulnerability of Amazonia to ongoing climate change.

Clearly this is the time when our science is needed and we have the opportunity to elevate the status of our science. To have the impact that is needed, we need to produce more sophisticated records and interpretations of past systems, and then display them in a way that other scientists and policy makers find readily understandable.

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CHAPTER 6

MANUSCRIPT 5 (published in 2014)

THE HOLOCENE OF THE AMAZON

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Abstract

The Holocene is unique within the Quaternary. The Pleistocene-Holocene transition was not a time of simple forest expansion, but primarily involved reshuffling of dry- and cold-indicator forest taxa with rainforest taxa. Within the Holocene, we focus on two phenomena: drought and the influence of humans on the ecosystem. Paleoecological evidence suggests that Holocene drought in Amazonia was not uniform in space or in time, and the period may have just been more climatically dynamic. Thus, the term 'the mid-Holocene dry event' is something of a misnomer. Human signatures, including evidence of fire and changes in vegetation, become more frequent in paleoecological records during the last 2000 years. The imprint of human activity on Amazonian systems appears to have been heterogeneous across space and episodic through time.

Keywords: Amazon, Holocene, paleoecology, Quaternary, palynology, human interference

1. Introduction

To understand the Holocene ecology of Amazonia it is important to place it in the context of the preceding ice age, and also within prior interglacial cycles. The majority of time in the last 3 million years has been spent in glacial conditions and only in the last 500,000 years have there been five interglacials similar in intensity and duration to those of modern times. Even within these periods the Holocene stands out as being climatically unusual and ecologically unique. Only one of the four other major interglacials had orbital patterns – which set the seasonality of climate – similar to those of the Holocene (Imbrie *et al.,* 1984). Only the Holocene had Amazonian landscapes without 50 genera of megafauna that could disperse large seeded trees (Janzen & Martin, 1982). And of those interglacials only the Holocene had a human presence in South America (Roosevelt *et al.,* 2002).

The old idea that ice ages were dry and interglacials were wet (Haffer, 1969) has been thoroughly refuted by paleoclimatic and paleoecological data (Colinvaux *et al.,* 2001b;Cruz *et al.*, 2005;Bush, 2006). Consequently, the belief that forests were fragmented by ice age drying is similarly defunct. As ecologists, we can breathe a sigh of relief that we do not have to explain the inexplicable: How could tens of thousands of plant taxa have migrated so far and so fast to form a diverse forest in the earliest Holocene (*sensu* McLachlan & Clark, 2005)? It is now evident that great expanses of Amazonian rain forests persisted throughout the last ice age and that for many species, while local distributions changed, their regional presence continued. This view does not argue for a static and unchanging set of communities, rather it predicts that novel communities would have been assembling and disassembling continuously. Dry events may have led to some dry forest expansion especially between 35,000 and 15,000 BP (all ages are expressed in calibrated years before present; BP) in the driest areas of Amazonia (Absy *et al.,* 1991;Bush & De Oliveira, 2006).

Importantly, it is likely that even in these areas of apparent change, at the biome level the forests had the openness, understory and productivity characteristics of drier settings, but at the species level the turnover may have been limited. Local extinction may have been common, but regional extinction much less so. The rainforest taxa would have become less abundant in those assemblages, and in the most extreme settings may have been restricted to riparian corridors or microrefugia. In the same way that cool-tolerant taxa were added to the Amazonian flora during the ice age, so too it is likely that dry forest taxa were added to rainforest taxa in these settings. Clearly, the outcome was a suite of forests without modern analog, but the changes were more additive in terms of species diversity than subtractive. Only in northeastern (Mayle *et al.,* 2000; Burbridge*et al*., 2004) and eastern (Whitney *et al.,* 2011) Bolivia is there direct evidence of the replacement of forest with savanna. Thus, the terminal Pleistocene and early Holocene were not marked by a rapid expansion of rainforest as per the refugial hypothesis. In most settings, one version of tropical rainforest replaced another as CO_2 levels and temperature rose. In the dry areas local population expansions took place as competitive balances shifted. Biogeographically, the most interesting changes may have been the contraction and isolation of populations of some dry and cold-indicator taxa, leaving them as modern microrefugial populations. The persistence of some of those populations such as low-lying populations of *Podocarpus* and *Hedyosmum*, and '*dry*' taxa surrounded by wet forest *Aristidatincta, Byrsonima crassifolia* and *Curatella americana* (Eden, 1974) may provide exciting genetic data that help to confirm (or refute) this version of the transition to Holocene landscapes. This rather stable view of biome histories within Amazonia at the continental scale does not deny profound changes taking place as the ice age gave way to the Holocene at ecological or individual scales.

In the high northern latitudes, the onset of the Holocene is marked by a rapid temperature rise at the end of the *Younger Dryas cold event*. This transition from the last gasp of the ice age to Holocene warmth occurred in a few decades, i.e. is a sharp and consistent boundary in regional records. In the Colombian Amazon it may be that this was the climatic pattern, but for most of Amazonia the transition from glacial to interglacial looked rather different. In central and southern Amazonia, over about five thousand years (16,000-11,000 BP), there was gradual warming, some rapid – though not always synchronous – changes in precipitation, a faunal extinction event, and the arrival of humans. The relative importance, timing and relatedness of these events are open to discussion (Hubbe *et al.,* 2007; Pinter *et al.,* 2011). From the Arctic south into Colombia, evidence of this rapid warming begins about 11,500 BP and is a natural boundary between glacial and interglacial conditions. For most of Amazonia and the central and southern Andes, however, the *Younger Dryas* was at best a weak event in which precipitation increased slightly. Certainly major ecological changes occurred in Amazonia between 15,000 and 10,000 BP, but they are not dominated by the abrupt warming and cooling characteristic of high northern latitudes. Consequently, the boundary between glacial and interglacial, if defined as 11,500 BP, seems artificial for most of Amazonia.

2. Holocene warming and human occupation

The warming of South America may have begun as early as 22,000 BP, and was clearly taking place by 19,000 BP, a period that was still within the classic glacial maximum of northern latitudes (24,000 - 18,000 BP). Between 19,000 and 11,000 years ago taxa were migrating upslope (Urrego *et al.,* 2010) and expanding their ranges southward (Whitney *et al.,* 2011) as temperatures rose. Within this period, humans first arrived in South America, with the earliest widely accepted occupation being that of Monte Verde at c. 14,500 BP. The first evidence of humans in Amazonia came from the rock shelter at Monte Alegre, where paintings were dated to c. 13,200 - 12,400 BP (Roosevelt *et al.,* 1996a). If the number of occupation sites in South America discovered so far paralleled the actual number of people, a surge of human occupation took place between 11,000 and 10,000 BP (Dillehay, 2008). In Amazonia, however, clear evidence of human activity is scarce until there is marked increase in occupation evident c. 2000 BP (Neves & Petersen, 2006) (Figure 1).

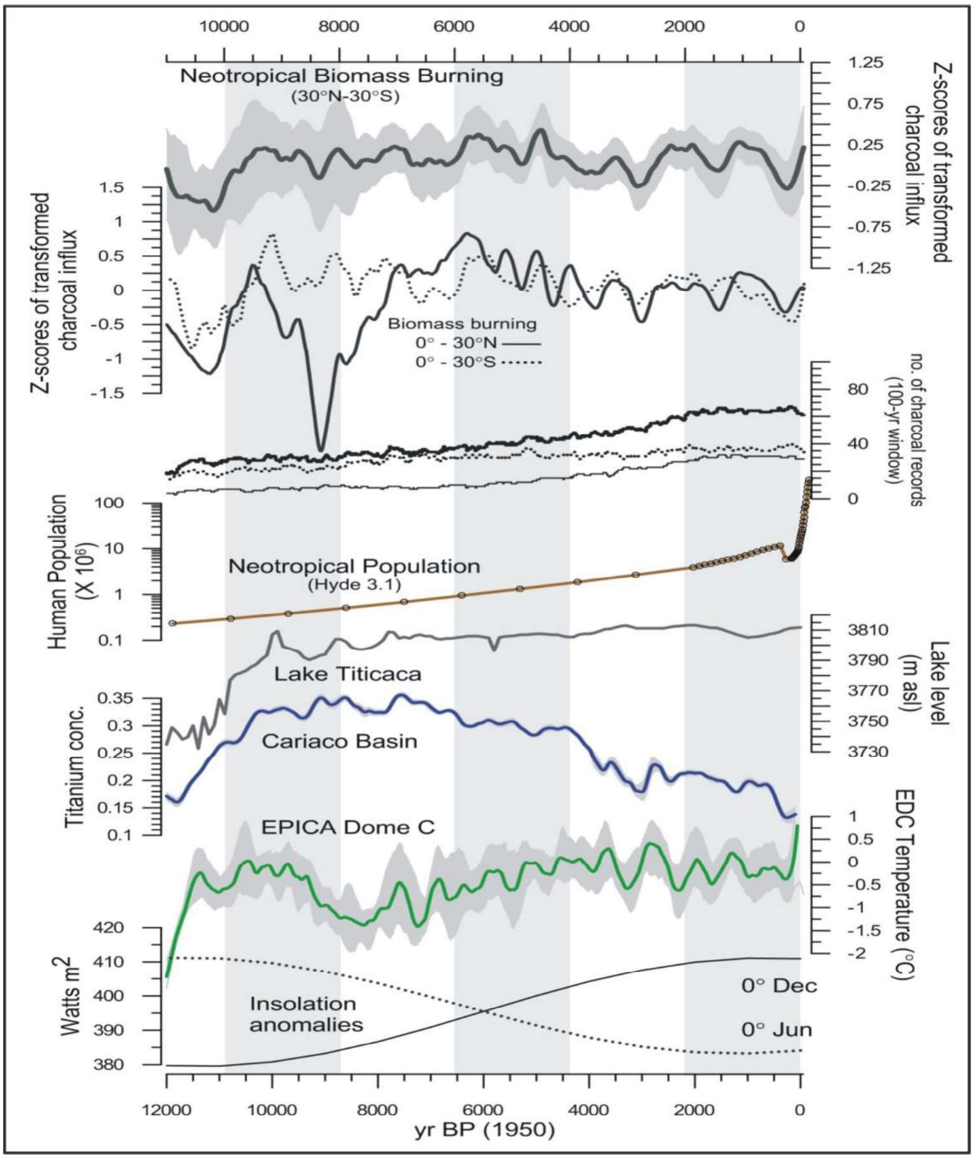

Figure 1: **A**) 12,000 BP composite time series of biomass burning from all Neotropical records between 30°N and 30°S (N=56), shown as smoothed Z-score charcoal anomalies (thick black line). The upper and lower 95% confidence limits from bootstrap analysis are shown in light gray. **B**) Biomass burning in the Holocene for the northern Neotropics (0°-30°N; thin black line), and southern Neotropics (0°-30°S; dashed line). **C**) The number of charcoal records contributing to the composite record, the northern Neotropics curve, and the southern Neotropics curve (line symbology is the same as in A and B. **D**) Lake level reconstructions for Lake Titicaca inferred from δ13C (Abbott *et al.*, 2003). **E**) Neotropical population estimates through the Holocene Paleomoisture and paleotemperature proxies are shown from selected tropical records, including (**F**) Cariaco Basin (Haug *et al.,* 2001), and (**G**) Epica Dome C ice cores (Delmonte *et al.,* 2002). **H**) Mid-month insolation anomalies for June and January at 0° latitude (Berger & Loutre, 1991). Grey vertical bars represent 2 ka intervals.

Between 8000 and 5000 BP many lakes in the Andes reach their lowest level of the Holocene (Baker *et al.,* 2005; Bush *et al.*, 2005; Hillyer *et al*., 2009). Because the lowstands are not synchronous, appearing earliest in sites closest to the equator, it was suggested that the timing fitted a nadir in wet season insolation, which would also exhibit this spatial pattern (Abbott *et al.,*1997). While this forcing may be part of the story, it does not appear to be a complete explanation. The detailed nature and cause of this event or events remain(s) unclear. After c. 4400 BP the signature of human land-use becomes more abundant in many Andean records, with a parallel increase in Amazonian land-use after c. 2200 BP (Figure 1). The scale of human alteration of pre-Columbian forests is a topic of active discussion. Some see Amazonia as a landscape so modified by human activity that the majority of it can be described as a parkland, whereas others acknowledge that humans altered the landscape locally, but consider the majority of forests to be largely unchanged by human presence. In this short chapter we will select two themes to follow that are linked by fire: the lake lowstands of the mid-Holocene and the scale of human impact on ecosystems.

3. Were lake mid-Holocene lowstands caused by a drought?

While Pleistocene records from the Amazon are rare (Chapter crossref), records covering the period between 11,500 and 9000 BP are only slightly more common and are shown on figure 2. At the risk of generalization, lakes in southern Amazonia show a relatively dry start to the Holocene, whereas in northern Amazonia the forested landscapes appear to approximate what would be expected in the absence of human activity. Even this simple comparison reveals that Amazonia does not undergo uniform changes in climate across timescales.

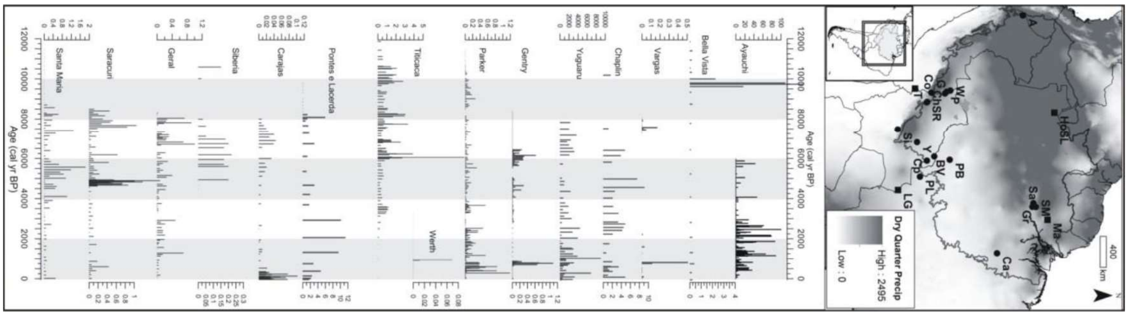

Figure 2: (Top) Site map for paleoecological reconstructions in and around Amazonia, shown in the context of dry quarter precipitation – or the driest 3 months of the year – in mm (Hijmans *et al.,* 2005); HoSL = Hill of Six Lakes (Colinvaux *et al.,* 1996), Ma = Maicuru (Colinvaux *et al.,* 2001a), SM = Santa Maria (Bush *et al*., 2007), Sa = Saracuri (Bush *et al.*, 2007), Gr = Geral (Bush *et al.*, 2007), Ca = Carajas (Cordeiro *et al.*, 2011), PB = Pimenta Bueno (Pessenda *et al.*, 1998), BV = Bella Vista (Mayle *et al.,* 2000, Burbridge *et al.*, 2004), PL = Pontes e Lacerda (Gouveia *et al*., 2002), LG = La Gaiba (Whitney *et al.*, 2011), Cp = Chaplin (Mayle *et al*., 2000; Burbridge *et al*., 2004), Y = Yaguaru (Taylor *et al*., 2010), Si = Siberia (Mourguiart & Ledru, 2003), T = Titicaca (Hanselman *et al*., 2011), Ch = Chalalan (Urrego *et al.*, 2012), SR = Santa Rosa (Urrego *et al.,* 2012), Co = Consuelo (Bush *et al*., 2004), G = Gentry (Bush *et al.*, 2007), P = Parker (Bush *et al.*, 2007), W = Werth (Bush *et al.*, 2007), V = Vargas (Bush *et al.,* 2007), A = Ayauchi (Bush *et al.*, 1989; McMichael *et al.,* 2012) (circles = sites with Holocene charcoal reconstructions; squares = other sites mentioned in text) (Lower) Holocene charcoal concentrations for sites shown on top panel.

As records become more abundant in the mid Holocene (between 9000 and 4000 BP) it is apparent that individual sites or proxies will reflect the same event in subtly different ways. For example, if diatoms are being used to monitor lake depth, they may be relatively insensitive to change in a shallow lake until the lake dries out, and then they have no sensitivity. In contrast, the same drying event impacting a deeper lake may show a substantial change only when the depth of the lake decreases to the point where it no longer stratifies. This could appear as an abrupt change in the diatom community that is not synchronous with the drying of the shallow lake. Furthermore, tropical tree taxa are far more sensitive to the seasonal distribution of precipitation (i.e. the length and severity of the dry season) rather than the total annual precipitation. Consequently, a profound vegetation change (e.g. forest-savanna biome turnover) caused by increased drought may not necessarily be manifested as a change in lake level (i.e. diatom community). Thus a drier dry season but wetter rainy season with no overall change in annual precipitation could produce rather different effects depending on the starting limnological and vegetational conditions.

Spatially, it is apparent that Amazonia does not respond uniformly to extreme events, i.e. the megadroughts of 2005 and 2010 left some areas virtually unchanged in precipitation while other areas parched (Aragão *et al.,* 2007). Between the events there were also strong regional differences in the strength of the drought. If those droughts are scaled up temporally, it is likely that results of those forcings would be heterogeneous within and between episodes.

Long-term variability in Andean and Amazonian precipitation for much of the last ice age appears to have varied in phase with December-February insolation. Speleothem records from the Andes and also southeastern Brazil show a long-term relationship between moisture source and precession. In each of these cycles, December-February (wet season) insolation minima were associated with dry events. Isotopic records from lakes are broadly concordant with this pattern, showing the 'driest' signature at c. 10 ka (Seltzer *et al.,* 2000). The precessional minimum of *c.* 10,000 to 9000 BP according to latitude, is reflected in falling lake levels across much of Ecuador, Peru and Bolivia (Bush & Metcalfe, 2012). By 8000 BP, the peak of the event had passed, but the peak of the observed *'dry event'* was between 8000 and 5000 BP in most areas. As the insolation minimum and the dry event were not aligned, either the peak of wet season insolation was not particularly relevant, or there was a substantial lag effect (Figure 1). A further parallel to the Pleistocene is that just as abrupt climate changes associated with Dansgaard-Oschger events were superimposed on the December-February precessional pattern, so too was the mid-Holocene drought of the Amazon and Andes.

Explanations of the dry event have included a lack of El Nino Southern Oscillation (ENSO) activity, although some of the areas most affected by ENSO variability, such as the eastern Amazon, were strongly impacted by the event. What is missing is an explanation of why this period of the Holocene should have especially stable Pacific Ocean temperatures. In light of recent megadroughts, we should also look to the temperature anomalies of the northern tropical Atlantic as a potential source of drought, especially in southwestern Amazonia (Aragão *et al.,* 2007). Here again there is no obvious link between the timing of the drought and insolation patterns. Although we do not know the immediate cause of the dry event, we are continually gaining more insight into the nature of the event.

Probably the first important realization is that this drought was not a time of uniform aridity (Figure 2). Indeed, many Amazonian lakes formed during this period. Rising sea-level may have influenced the coastal region, but could not have accounted for lakes filling in the lowlands of the central and western Amazon. Consequently, we can conclude that wet periods, which allowed lake formation, alternated with dry events that induced drought-impacted forests and falling lake levels. Interestingly, the strongest evidence of marked lowering of lake level came from the high Andes rather than the Amazon lowlands. At Lake Titicaca, lake level dropped 90 m between 9,000 and 5,000 BP, and many other Andean lakes were shallow or ephemeral at this time (Figure 1). Contrast this massive loss of water from a lake in the Altiplano with the persistence of shallow lakes in NE Bolivia or the Central Amazon where, despite lakes being only a few meters deep, they deposited continuously throughout the event. The difference between the Andes and the Amazon was that the evaporation rates in the low humidity Altiplano and Andean valleys were much higher and the precipitation much lower than in the humid lowlands. Lakes that were very finely hydrologically balanced by evaporation: precipitation (e.g. the Altiplano of Peru/Bolivia) or leakage:precipitation ratios (e.g. The Hill of Six Lakes in northern Brazil) exhibited relatively strong responses, whereas systems that were not vulnerable in that way (e.g. Chalalan in Bolivia), showed almost no response to the drying.

More direct evidence that SW Amazonia (lowland eastern Bolivia) experienced drier mid-Holocene conditions compared with present comes from several different lines of geomorphological data from the Andean piedmont and foreland basin. Increased fluvial-aeolian sedimentation and aggradation, parabolic palaeodune systems, large-scale river channel shifts, as well as palaeosol-sediment changes, have all been interpreted as evidence of drier climatic conditions with more episodic rainfall and increased aeolian activity due to reduced vegetation cover (May, 2006; May *et al.,* 2008, May &Veit, 2009; Servant *et al.,* 1981; Valente & Latrubesse, 2012).

While most of the inference regarding the dry event came from observations of hydrology and geology, ecological cues also indicated a stressed system. The Amazonian record with the strongest apparent signature of the mid-Holocene dry event on its vegetation was that of Carajas. In two separate records from this region, the proportion of savanna indicators was higher in the mid-Holocene than at any time in the preceding 60,000 years. These hilltop wetlands were probably similar to the Hill of Six lakes in that they were imperfectly sealed and lost water through leakage. Under such circumstances, as leakage persisted, but precipitation became erratic the lake dried down and became replaced by a grassy marsh. Clearly Holocene warmth would tip the balance by adding increased evaporative loss to the equation compared with the cooler Pleistocene. Another central Amazonian site with low rainfall, high seasonality, and a leaky basin was the inselberg of Maicuru. A sedimentary hiatus between 9,000 and 5,000 BP, suggests that this swamp was in a predominantly oxidative state during the mid Holocene. This does not mean that it was permanently dry, just that there was no net accumulation of new organic material. That other central Amazonian sites near Prainha and in the drainages of the Tapajos do not show such an extreme response suggests that local hydrological balance amplified the response at Carajas and Maicuru.

Signs of increasing canopy gap formation and fire activity are evident in most records during this period. *Cecropia*, the classic colonist of canopy gaps more than doubles in abundance in central Amazonian records. *Cecropia* is the classic successional species that exploits treefall gaps in Amazonian forests. *Cecropia* can certainly flourish in the aftermath of fire, and it can also increase in abundance just because large trees die during drought episodes and create openings in the forest. Consequently, although fire and increased *Cecropia* representation in pollen records can both be symptomatic of drought, they are not necessarily directly related.

Under modern conditions fire is rare in the western Amazon unless set by people. It is interesting, therefore, to see that during the period from 9000 to 5000 BP several major fire events often occur within records, with an event at 6 ka evident in records from southern Peru, Bolivia and central Amazonia (Figure 2). It is entirely possible that these 'events' are not synchronous, also that they are an artifact of sampling and taphonomy, i.e. there could be many more events that are blurred into one by taphonomic processes or sampling protocols. Nevertheless, it is also apparent from all records that charcoal during this period was not uniformly increased in abundance, suggesting that fire was distinctly episodic (Figure 2). The possibility that there were distinct megadroughts that rendered even portions of western Amazonia flammable prior to 5000 BP is crucially important to understanding the fate of the Amazon forests under climate change. Note, that fully-coupled climate models predicting Amazonia's future state do not include fire probability within their feedback mechanisms.

A mid-Holocene marked by strong droughts, high insolation and marked wet events is consistent with an emerging view of intense mid-Holocene climate variability in southern Brazil (Cruz *et al.,* 2005; Raczka *et al.,*2013) (Figure 1). If we accept that the mid-Holocene was more climatically dynamic than modern, rather than simply drought prone, the term 'the mid-Holocene dry event' is something of a misnomer. Humans are said to have abandoned marginal habitats, i.e. those where climatic volatility would make the area inhospitable, in the Andes and southeastern Brazil during this period. In the Andes, this period was described as the "zone of archaeological silence", but whether the same was true of Amazonia remains to be seen. Abandonment cannot be demonstrated when there is an almost complete lack of archaeological data, with the exception of the Monte Alegre rock shelters, for occupation of Amazonia prior to 9000 BP.

4. Human occupation and modification of Amazonia

The extent to which humans occupied and modified the lowland Amazon Basin prior to European arrival has recently become a hot-button issue among archaeologists, anthropologists and ecologists. In the past this discussion centered on whether sophisticated Amazonian cultures ever developed and whether they influenced the system in which they lived. There is no longer any real doubt that such cultures emerged, as they built causeways, earthworks, and fish weirs, and overcame the challenges of infertile soils through the formation of enriched soils known as *terra preta*. The issue that is now discussed is the spatial extent, temporal continuity, and overall effect of these alterations of Amazonian ecosystems.

So let us start with where there is no strong disagreement. On major river channels in eastern Amazonia and around the periphery of Amazonia there is abundant evidence supporting substantial, permanently-settled, human populations that formed complex societies (Figure 3). Additionally, over 300 geometrical earthworks, termed geoglyphs, scatter the landscape to the north of the Beni and were formed mostly between 2000 and 1200 BP. Artifact density in these structures is lower than other major Amazonian archaeological sites, but the sheer size of the geoglyphs (up to 300 m diameter and ditches up to 5 m deep) (Schaan*et al.,* 2012), indicate a direct transformation of the immediate landscape. *Terras pretas* indicate long-term trash accumulation or deliberate soil improvement, either of which suggest some permanent occupation of a given site. These soils are also the most common archaeological feature in Amazonia, and with few exceptions these modified soils are located close to major waterways in central and eastern Amazonia (Figure 3). For most of western Amazonia, there is little evidence of the complex settlements that characterize these eastern and southern regions of Amazonia.

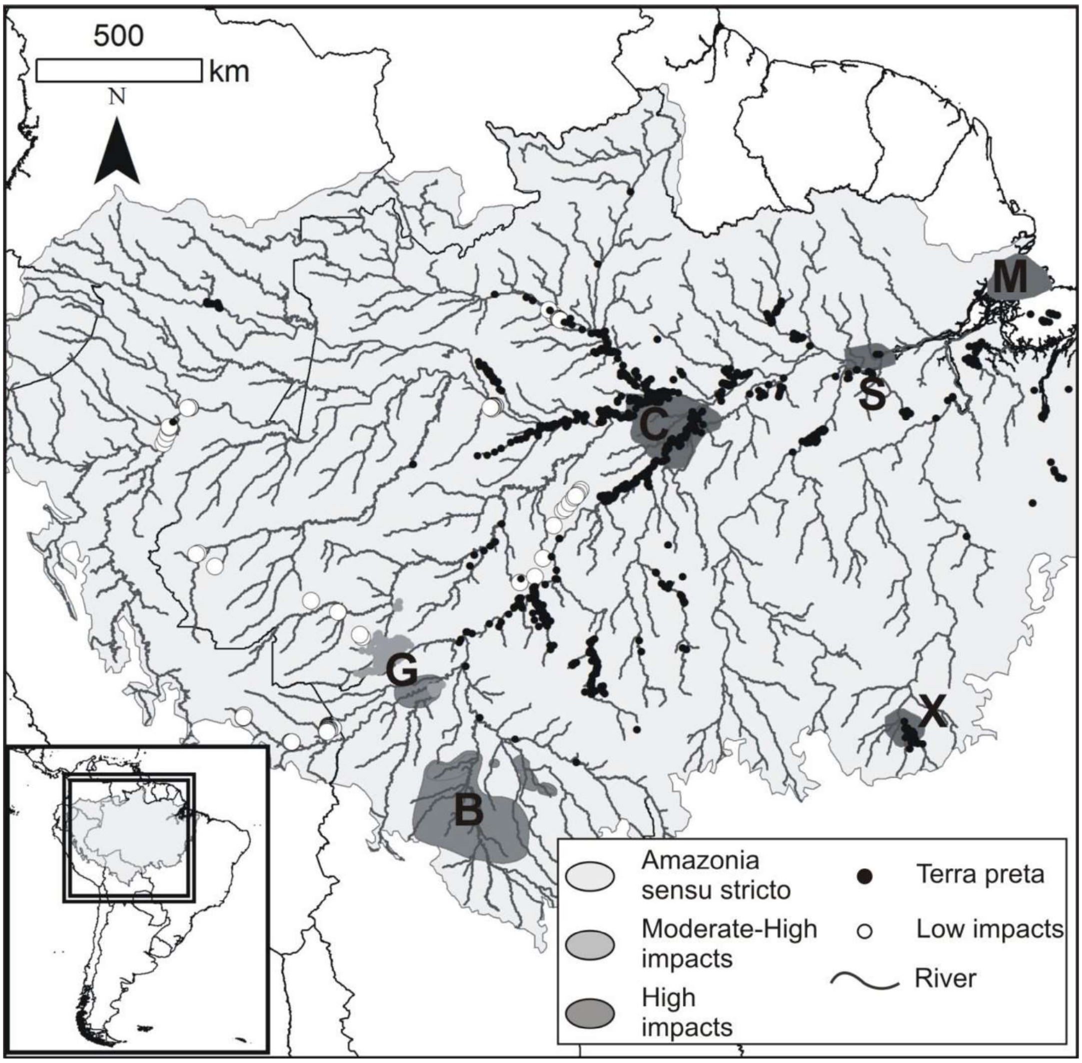

Figure 3: Locations of major archaeological sites and soil survey sites in Amazonia. M=Marajo (Meggers & Evans, 1957; Roosevelt, 1991), S=Santarem/Monte Alegre (Roosevelt *et al.,* 1991, Roosevelt *et al.,* 1996b), C=Central Amazon Project (Neves *et al.*, 2004; Neves & Petersen, 2006), X=Upper Xingu (Heckenberger *et al.,* 2003, 2008), B=Beni (Erickson, 2000, 2006), G=Geoglyphs (Pärssinen *et al.,* 2009; Schaan *et al.*, 2012).

The overall degree of disturbance ubiquity across the landscape is where there appears to be substantial disagreement. It has been proposed that human impacts were widespread and common across most of Amazonia, and that the forests became an anthropogenic landscape either through forest clearing or enhancing the populations of 'useful' forest species. The alternate view is that most of the forests, particularly the interfluvial areas and westernmost forests, were for the most part, sporadically or lightly used by people who did not exert sufficient influence that can be characterized as ‘major habitat alteration’. The Upper Xingu region of southeastern Amazonia is one of two regions containing direct evidence of anthropogenic landscape modification (i.e. earthworks and roads) in the interfluvial forests. The second is the geoglyph-rich region, as geoglyphs tend to be located in interfluvial settings on topographically high positions overlooking river floodplains. Additional evidence for human footprints in interfluvial forests relies on determining the proportion of ‘useful’ species in the forest, but as any presence is counted as significant evidence of human influence despite them being native to the forest, this quickly becomes a circular argument. Paleoecological records from other sites in interfluvial settings contain limited human activity. In southern Peru, only two of four lake records located within the same interfluvial region contained any evidence of prehistoric human activity. A similar pattern was seen in the Prainha district in central/eastern Amazonia. In a recent study that sampled > 400 soil pits in western lowland Amazonia, no *terra preta* was found, no pot sherd was found, but there was evidence of fires in some sites at some times. Fire is almost uniquely associated with human activity in modern times, and thus in the post *‘dry event’* history of Amazonia if fire is found it is a fairly strong indication of human activity. The spatial arrangement of these data was consistent with a very light use of the interfluve and westernmost settings.

Lightning can hit emergent canopy trees in the Amazon and occasionally cause them to burn. Such fires, however, do not spread and die out almost immediately. Consequently, modern western Amazonian systems are not fire-adapted as fire is essentially missing from the ecology. At Lake Werth in southern Peru there is a continuous 4000-year record of forest that shows no human activity and in over 50 samples analyzed it contained just one very small fragment of charcoal (Figure 2). In the drier areas of central Amazonia the probability of occasional natural fire must be higher. Experimental data from precipitation reduction experiments showed that ten days of dry season drought could render forests in the Santarem region flammable. On that basis, fire might be expected to be a regular component of the ecology of this section of the Amazon Basin. Other empirical studies, however, indicate that while this is possible it must be vanishingly rare under modern conditions. When humans set fires in these forests the impacts are devastating, with large changes in biomass and faunal and floral community composition. The data indicate that the forests have not burned within the lifetimes of the trees, and that fire is so rare that there are no adaptations to it.

To some extent the researchers engaged in the debate over the pre-Columbian land use of Amazonia are ‘talking past’ each other. Fires that escaped from human control to become wildfires would have influenced forest structure, though these were probably drought-driven accidents rather than attempts at cultivation. Evidence for the accidental nature of such fires is that the charcoal found in soil pits was not associated with cultivars or repeated burning in most cases. So the extremes of ubiquitous use vs non-use are untenable. In the middle there is a gray area of what constitutes ‘significant’ habitat alteration and what the spatial and temporal consequence of human activities were. Humans were in the landscape in the late Holocene, and they would have exerted some influence on large mammal populations, such as tapir, through hunting, thereby affecting seed dispersal. This division over human impacts should not become an entrenched battle as there is really very little substantive disagreement, and where it exists, it is fueled by lack of data rather than genuinely conflicting data.

Proponents of both views are concerned that a misuse of data will create social problems. The advocates of histories that invoke minimal human alteration of the interfluve areas are concerned that irreversible outcomes may follow bad policy decisions. For example, if these forests have not been disturbed previously on the modern scale, the confidence that they will re-grow is unfounded, and short-term exploitation could lead to a very substantial loss of biodiversity. Also, if the modern forests are really only 500 years old, then by being overly conservative and limiting exploitation, near term profits are denied, but the potential for long-term profits remains until further data become available.

Those who advocate that human actions shaped the landscape use this as an argument that native people were active managers of a resource and therefore have vested rights in the land. The fear on this side is that if large areas were essentially unused in the past, the claims of indigenous people to land rights are weakened. Clearly scientists should be aware of the consequences of their research findings, but to maintain legitimacy we must approach this research without a desire to influence larger social issues. The vesting of indigenous rights should be independent of the kind of stewardship or use of a landscape.

5. Conclusions

The Holocene of Amazonia was a time of subtle but important natural changes in climate, and was also the time of human arrival and ensuing landscape modification. As with most emerging scientific fields, as data become available the initial questions are replaced by more sophisticated ones that demand a great understanding of the system and higher quality data sets. New fusions of geographic mapping and databasing techniques with molecular biology and paleoecology offer exciting prospects for generating data that will be important for historians, anthropologists, biologists and policy makers, alike.

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CHAPTER 7

Manuscript 6 (published in 2017)

The collapse of megafaunal populations in southeastern Brazil

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Abstract

Whether humans or climate change caused the extinction of Pleistocene megafaunal populations is actively debated. Caves in the Lagoa Santa region provide mixed assemblages of megafauna and human remains, however, it remains uncertain the extent to which humans and these large mammals interacted or overlapped temporally. Here we present the first paleoecological record from lowland South America that tracks the decline of megafauna and its ecological implications. We provide paleoecological records for pollen, microscopic particles of charcoal, and *Sporormiella,* from two lakes in the Lagoa Santa region that span the last ca. 23,000 years. The data showed reduced abundances of *Sporormiella* and an inferred megafaunal population decline that began more than 18,000 years ago, with the functional extinction occurring between ca. 12,000 and 11,500 years ago. Population declines coincided with wet events. The age of the final megafaunal decline is within the range of the first human occupation of the Lagoa Santa region. Our data are consistent with climate causing the population collapse, with humans preventing population recovery and inducing extinction. We did not observe some of the ecological repercussions documented at other sites and attributed to the megafaunal extinction. Habitat-specific ecological consequences of the extinction add to the heterogeneity of late-Pleistocene and early-Holocene landscapes.

Keywords: Charcoal, Climate Change, Human, Megafauna, Pleistocene, Pollen, Precipitation, *Sporormiella*

Introduction

The deglacial period, ca. 22,000 – 12,500 before present, was a period of rapid change in composition and structure of terrestrial environments that coincided with a major extinction of large mammals (Alroy, 2001; Barnosky et al., 2004; Barnosky and Lindsey, 2010; Fiedel, 2009; Koch and Barnosky, 2006; Villavicencio et al., 2016). At the end of the Pleistocene, ca. 59 species of megafauna, accounting for 79.6% of animals weighing > 44 kilograms went extinct in South America (Barnosky et al., 2004; Wroe et al., 2004). In fact, the only large herbivore in Brazil that survived this mass extinction event was the tapir (Steadman et al., 2005). The proportion of megafauna lost from the South America fauna was higher than on any other continent (Bartlett et al., 2015), and the loss of grazers and browsers may have contributed to changes in vegetation cover (Doughty et al., 2016). Representatives of megafauna were major ecosystem engineers crucial for ecosystem functions such as seed dispersal (Giombini et al., 2016; Janzen and Martin, 1982; Sridhara et al., 2016), reduction of fuel load (Knapp et al., 1999), and nutrient cycling (Doughty et al., 2013; Feeley and Terborgh, 2005). The loss of these animals may have induced transformations in the landscape, including the formation of no-analog communities (Gill et al., 2009), and had repercussions that are still felt today (Doughty et al., 2013; Owen-Smith, 1987).

The cause of the megafaunal extinction has been debated for many decades (e.g Barnosky et al., 2004; Cione et al., 2009; Feranec et al., 2011; Martin, 1973). Multiple conflicting hypotheses have been proposed ranging from widespread auto-immune diseases (Stevens, 1997) to a meteorite impact that triggered abrupt climatic changes such as the rapid cooling of the Young Dryas Event ca.12,500 calibrated ^{14}C years before present (hereafter cal. BP) (Firestone et al., 2007). The two most widely cited hypotheses are that humans induced the extinction (Brook and Bowman, 2004; Koch and Barnosky, 2006; Martin, 1973; Mosimann and Martin, 1975) or that it was caused by climatic changes (Cione et al., 2003; Coltorti et al., 1998). Of these causes, extraterrestrial impact (Firestone et al., 2007) seems the least likely (Kerr, 2007), while the other three need not be mutually exclusive. A modern analog to megafaunal loss is perhaps found in the decline of amphibians that results from the effects of human-induced habitat loss (Stuart et al., 2004), climate change and chytridiomycosis (Kilpatrick et al., 2010). While it can be argued that all three of these agents of population decline are the product of human activity, it is the synergy of these different forces that is detrimental to a wide range of amphibian species. Such ecological synergy weighing on the megafaunal populations was suggested by Diamond (1989). More recently, a multiproxy approach study carried out in the southwestern Chile, also identified warm wet conditions coincident with human presence as synergistic causes for the extinction of the Pleistocene megafauna (Metcalf et al., 2016; Villavicencio et al., 2016).

Although the extinction of the megafauna is well-documented globally, most studies conducted in South America have been limited to descriptions of undated fossil remains (Lima-Ribeiro et al., 2013; Villavicencio et al., 2016; Weinstock et al., 2009;Cartelle and Hartwig, 1996; Dantas et al., 2011, 2005; Ghilardi et al., 2011; Hubbe et al., 2007; Lopes et al., 2005). Despite the importance of the investigations carried out in Brazil, most studies have focused on the latest survival of taxa, rather than on the ecological aspects and geographic patterns of the extinction. Although well-dated remains are very limited, at least nine species are thought to have survived into the early Holocene, such as *Catonyx cuvieri*, *Smilodon populator*, *Megatherium americanum*, and various edentates (Borrero et al., 1998; Hubbe et al., 2007; Long et al., 1998; Neves and Pilo, 2003).

Paleoecological archives are a powerful tool for understanding ecological change. Fossil pollen data can be used to evaluate whether a given community or population underwent compositional or structural changes. Glacial-age sediment records from lakes in southeastern Brazil suggest that cool and humid forest, rich in *Podocarpus*, *Myrsine* and *Araucaria* dominated this area (Behling, 2002, 1997a, 1997b, 1995; De Oliveira, 1992; Ledru, 1993; Ledru et al., 2015). Toward the end of the Pleistocene, warming caused glacial retreat as early as 21,000 cal. BP in the Andes (Seltzer et al., 2002). In southern Brazil, however, the deglacial was marked by the replacement of cold forest indicator species with those of warmer systems, a transition that began ca. 16,000 cal. BP and was largely complete by 11,000 cal. BP (De Oliveira, 1992; Ledru et al., 2002, 1996). The presence of cold-tolerant taxa at numerous palynological settings in SE Brazil suggested a ca. 5^{o} C cooling during the Late Glacial relative to modern (Barberi et al., 2000; Pessenda et al., 2009); observations consistent with temperature estimates based on noble gas concentrations (Stute et al., 1995). Isotopic data from speleothems collected in Botuverá cave provided the first detailed reconstruction of precipitation change from SE Brazil. These data demonstrated the long-term precessional control of summer (DJF) insolation over precipitation in southern Brazil (Bernal et al., 2016; Cruz et al., 2007, 2006) and suggested that the Late Glacial was a relatively wet period, with the early Holocene being drier.

During the termination of the last ice-age, no-analog floras were reported from North America, the Andes, and the Amazon Basin (Bush et al., 2005; Cárdenas et al., 2011; Colinvaux et al., 1996; Hermanowski et al., 2012; Hooghiemstra and Van der Hammen, 2004; Overpeck et al., 1992; Velásquez-R. and Hooghiemstra, 2013). These combinations of currently allopatric taxa living in sympatry during glacial stages may have reflected no-analog climates (Williams and Jackson, 2007), differential migration rates (Gill et al., 2012), or a general disequilibrium of climate and vegetation change in response to rapid warming (Correa-Metrio et al., 2012; Harrison and Sanchez Goni, 2010).

Sporormiella and megafauna

Ascospores of *Sporormiella,* a coprophilous fungus that grows and reproduces in the dung of herbivorous animals (Bell, 1983), has been used to assess changes in megafaunal abundance through time (Davis, 1987; Davis and Shafer, 2006; Gill et al., 2009; Robinson et al., 2005; van der Kaars et al., 2017). In modern settings, *Sporormiella* has been shown to be a reliable proxy for the presence, and to some extent the abundance, of large herbivores (Gill et al., 2013; Raper and Bush, 2009). Comparison among lakes with different levels of usage by livestock activities demonstrated that *Sporormiella* was a consistent component of surface sediments at locations frequently visited by livestock (Raczka et al., 2016). On longer timescales (>1000 years), *Sporormiella* became an important tool for detecting the past presence of large herbivores (Davis, 1987; Davis and Shafer, 2006; Gill et al., 2009). Similarly, extinction events were identified through falling values of *Sporormiella* (Burney et al., 2003; Gill et al., 2009; Wood and Wilmshurst, 2012). The extinction identified using *Sporormiella* data is a functional extinction, which is when the animals become so rare as to cease imposing a signal on the landscape, as opposed to a final extinction, which is the death of the last individual. In North America, the consensus was that the *Sporormiella* decline coincided with the onset of the Bølling-Allerød warm period at ca.14,000 cal. BP (Gill et al., 2009), but in the high Andes, researchers found a much earlier decline, first occurring at ca. 21,000 cal. BP, with local extinction occurring as early as ca. 15,800 cal. BP (Rozas-Dávila et al., 2016). The two step decline of megafauna in the high Andes was attributed primarily to ecological changes in the environment (Rozas-Dávila et al., 2016).

The collapse of megafaunal populations was linked to the formation of no-analog plant communities (Gill et al., 2012, 2009). Those changes may have come about as a result of altered seed dispersal, fire regimes, or invasions (Giombini et al., 2016; Jansen et al., 2012; Janzen and Martin, 1982).

Here we investigate the megafaunal decline through analysis of fossil *Sporormiella*, pollen, and microscopic particles of charcoal recovered from ancient lake sediments that spanned the time of megafaunal extinction and human arrival in SE Brazil. We seek to answer three questions: (1) Did Climate change cause the megafaunal extinction? (2) Was the decline of *Sporormiella* spores coincident with the formation of no-modern analog assemblages in the pollen spectra? (3) Did the decline in *Sporormiella* abundance occur before the arrival of humans to the Lagoa Santa region?

Study area

The Lagoa Santa region is a karstic landscape located in the south of Minas Gerais State, SE Brazil. The climate of the region is primarily controlled by the southern subtropical jet stream and polar air masses (Nimer, 1989). During winter, the dominance of the South Atlantic Anticyclone and the absence of the Atlantic Polar frontal system result in reduced regional cloud cover and monthly average temperatures ranging from 13 to 15 ^{o}C. In summer, regional temperatures rise and cloud cover increases due to the more southerly position of the ITCZ (Intertropical Convergence Zone) and deep convection over Amazonia (Marengo, 1995). Summer average temperatures reach 27-28 ^{o}C. Precipitation is strongly seasonal with ca. 88 % of the 1500 mm annual precipitation falling between November and March (Lucas and Abreu, 2004).

Prior to European colonization in the 16th century, the vegetation was dominated by a mosaic of semi-deciduous forest and cerrado (Warming and Ferri, 1973). The most abundant woody species were *Acacia polyphylla* (Fabaceae), *Astronium fraxinifolium* (Anacardiaceae), *Cassia ferruginea* (Fabaceae), *Cedrela fissilis* (Meliaceae), *Chorisia speciosa* (Malvaceae), *Hymenaea stilbocarpa* (Fabaceae), *Protium heptaphyllum* (Burseraceae), *Tapirira guianensis* (Anacardiaceae), *Vochysia tucanorum* (Vochysiaceae), and more locally *Caryocar brasiliensis* (Caryocaraceae), *Qualea grandiflora* (Vochysiaceae), and *Kielmeyera coriacea* (Clusiaceae).

The karst landscape of the Lagoa Santa region has been a target of paleontological and archaeological studies for more than 150 years, starting with the Danish naturalist Peter W. Lund (Cartelle, 1994; Lund, 1844). This region is rich in caves and sink holes, where bones have been collected and it continues to be one of the most important locations for paleontological and archaeological studies in South America (Berbert-Born, 2002). The oldest records of human occupation in Brazil (c. 16,000 - 12,700 years ago) come from caves within the region (Feathers et al., 2010; Neves et al., 1999; Neves and Hubbe, 2005). The Lagoa Santa region is also distinguished by the vast diversity of paleontological sites with co-occurring megafaunal and human remains (Hubbe et al., 2013). Despite an immense diversity of megafaunal fossils in such a small area, the majority of data are descriptive (Cartelle et al., 2008; Cartelle and Hartwig, 1996; Dantas et al., 2005; Lessa et al., 1998; Marinho et al., 2010). Few quantitative studies assess the landscape (Ghilardi et al., 2011; Pires et al., 2014) or climatic conditions within which these animals lived. Some examples of megafauna recovered from the caves of Lagoa Santa include: Glyptodontidae, Megalonichidae, Mylodontidae, Tapiridae, Tayassuidae, Equidae, Gomphortheriidae, Ursidae, Camelidae, Megatheridae (Fig. 1) (Dutra et al., 1998). A causal linkage of human and megafaunal co-occurrence beyond taphonomic coincidence or that caves were favored by both entities, has yet to be made.

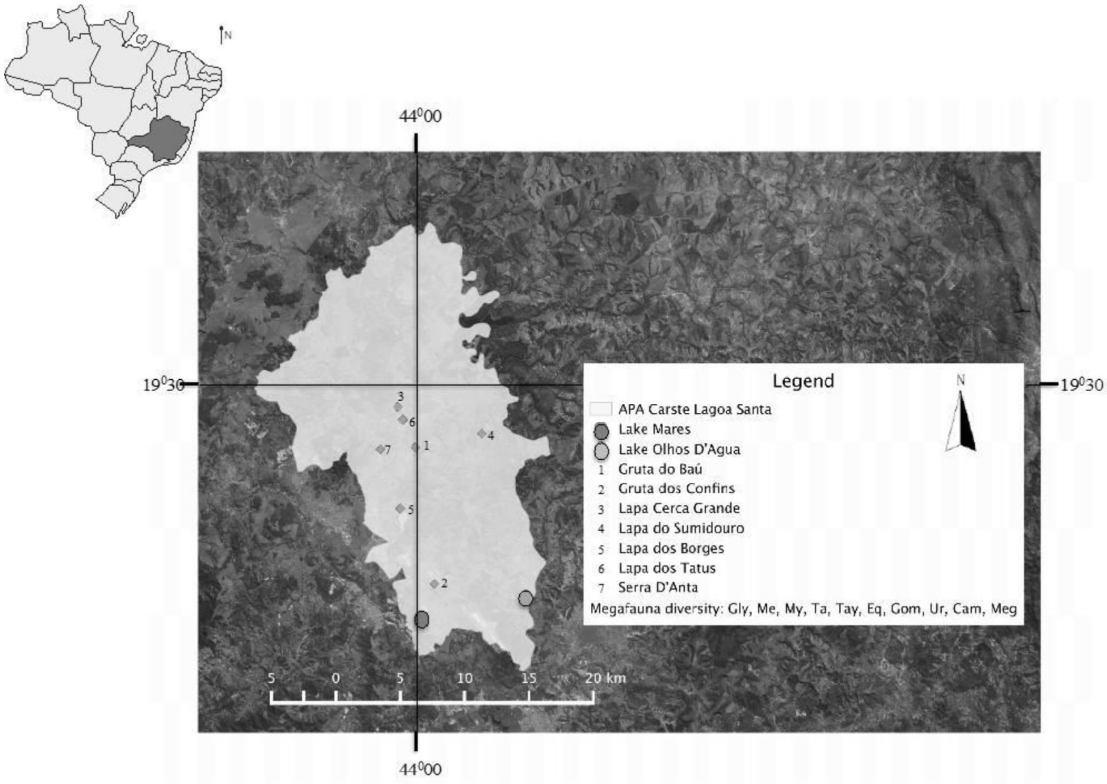

Figure 1: Map of the study area in Minas Gerais state showing the locations of Lake Mares and Lake Olhos d'Agua, and the major paleontological site inside the Lagoa Santa protected area. The diversity of the megafauna found at the sites consist of Glyptodontidae (Gly), Megalonichidae (Me), Mylodontidae (My), Tapiridae (Ta), Tayassuidae (Tay), Equidae (Eq), Gomphortheriidae (Gom), Ursidae (Ur), Camelidae (Cam), Megatheridae (Meg) (Dutra et al., 1998).

The lakes upon which this study is based, Lake Mares (19°39'46.54"S/ 43°59'17.67"W) and Lake Olhos d’Agua (19°38'53.24"S/ 43°54'35.24"W), are both shallow, ca. 2.6 m and 3.5 m at the deepest point, respectively. The modern lakes are similar in size, both occupying ca. 2 km^2, and are thought to be oligotrophic (De Oliveira, 1992).

HeinricMaterial and Methods

Sediment cores were recovered using a Colinvaux–Vohnout coring rig operated from a floating platform (Colinvaux et al., 1999). The Lake Olhos d’Agua core was collected in 2005 and the one from Lake Mares in 2008. The lithologies of the cores were described, and sediments sub-sampled for palynological analysis.

Fossil pollen was prepared following standard procedures as described by Faegri & Iversen (1989). An exotic marker, *Lycopodium clavatum*, was added to calculate pollen concentration (Stockmarr, 1971). A total of 300 pollen grains were counted per sample. Microscopic particles of charcoal and *Sporormiella* were counted alongside pollen. Every microscopic particles of charcoal > 25 µm was tallied. Smaller pieces were not included to minimize the impact of particles that might have broken during chemical preparation. The age of each core was established with ^{14}C (AMS) dating performed by Beta Analytic, Inc., and the chronology was established using the package Bchron (Parnell, 2016) with statistical program R (R Core Team, 2015). Pollen diagrams were made using Tilia/TiliaGraph version 2.0.41. The detrended correspondence analysis (DCA) was calculated using every taxon found with an abundance greater than 1% of the total pollen sum. The DCA was performed with the R-package vegan (Oksanen et al., 2007) and the species evenness calculation was completed using every taxon found, including rare taxa, with the software PAST version 3.11 (Hammer et al., 2001).

Results

Chronologies and lithology

The radiocarbon chronology of Lake Mares and Lake Olhos d’Agua provide inferred rates of accumulation. We found no evidence to suggest a sedimentary hiatus at Lake Mares (Fig. 2), however, a possible hiatus was observed at Lake Olhos d’Agua centered on ca. 14,500 cal. BP (between 1.61 and 1.59 m core depth).

At Lake Mares, the sediment was characterized by the presence of sandy gray clay (Munsell Color 12.5/N) in the basal portion of the core, below 2.22 m. Overlaying these sediments was a black organic clay (5Y2.5/1) between 2.22 m and 1.4 m. From 1.40 m to 1.0 m depth, the sediments were a sandy gray clay (12.5/N) overlain by a layer of black organic clay from 1.0 cm to 0.4 m (5Y2.5/1). etween 0.4 m to about 0.28 m core depth, a layer of sandy gray clay (12.5/N) was evident. The uppermost 0.28 m of sediment was a brown organic clay (10YR 4/2), which probably reflected the unconsolidated sediment of the modern lake bottom.

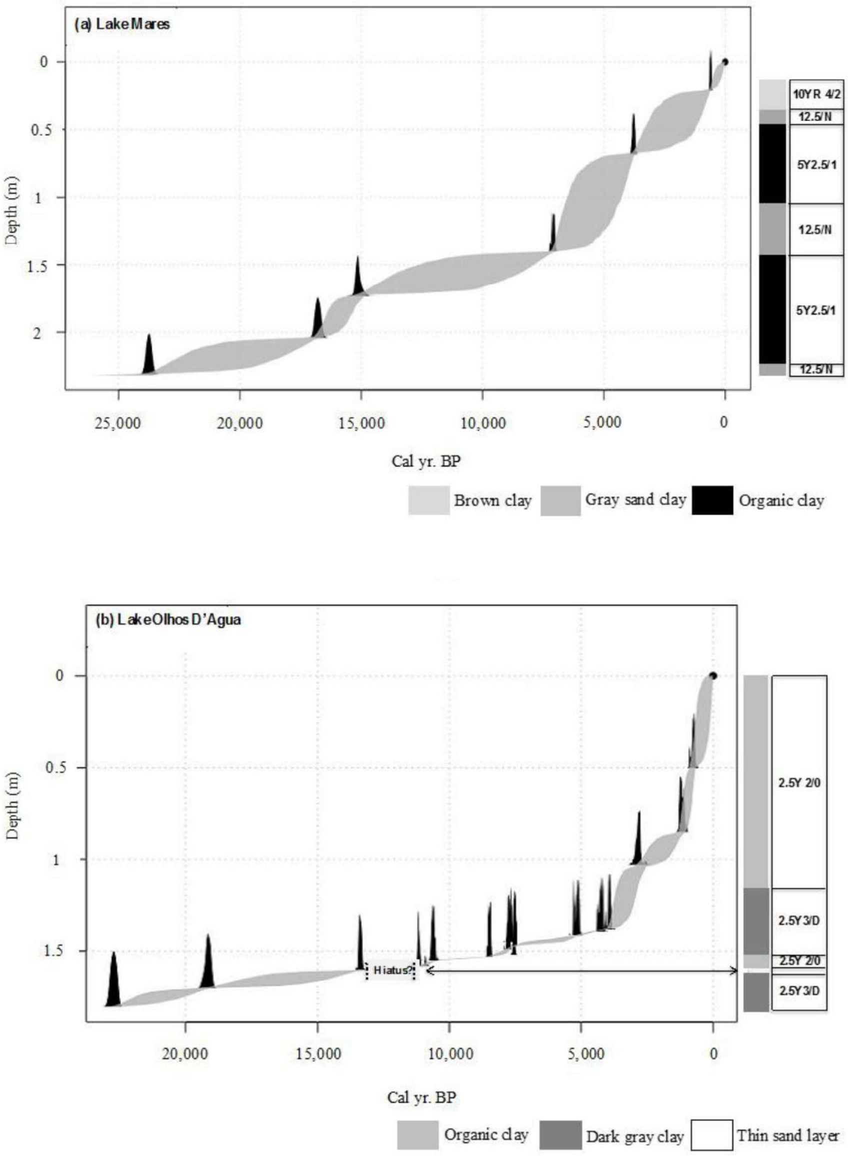

Figure 2: Age model from Lake Mares (a) and Lake Olhos d'Agua (b). The chronology was generated using Bchron (Parnell, 2016), and it was based on the probability density function for all calibrated radiocarbon ages. The stratigraphic descriptions of the sediments include Munsell color values.

The oldest sediment of Lake Olhos d'Agua was a dark grey clay containing some quartz particles from 1.8 to 1.61 m. Overlying this deposit was a thin layer of fine sand between 1.61 and 1.59 m depth. A layer of black organic clay (2.5Y2/0) was present between 1.59 and 1.5 m. Overlying this layer was a dark gray clay (2.5Y3/D) from 1.5 to 1.16 m. A black organic clay (2.5Y 2/0) formed the remainder of the core.

Pollen records

Lake Mares 2.22 m to 1.4 m (ca. 23,500 – 7,200 cal. BP)

A diversity of arboreal pollen types was found, including the cold tolerant taxa *Araucaria* and *Podocarpus* (2% - 5%). Cerrado forest taxa were represented in this interval by Myrsinaceae, Ericaceae, *Protium*, *Alchornea*, Anacardiaceae, Apocynaceae, Arecaceae, Bignoniaceae, *Caryocar*, *Schefflera* (*ex Didymopanax*), *Hedyosmum*, *Ilex*, Melastomataceae, Fabaceae (M), Myrtaceae, *Psychotria*, Rubiaceae, Sapindaceae, *Sebastiania*, *Symplocos*, and *Vernonia.* The majority of the arboreal pollen types were individually ca. 1% - 4% of the pollen sum between 23,500 and 8,000 cal. BP. Among the herbs, Asteraceae (8% - 20%), *Eryngium* (6% - 13%), Cyperaceae (ca. 16%), and Poaceae (27% - 42%) were the most abundant pollen types in most samples. Some terrestrial herbs were represented in low percentages (ca. 1%), e.g. *Gomphrena*. Aquatic taxa, e.g. Alismataceae, *Eichornia*, *Hyptis*, and *Ludwigia* were present, generally with percentages below 3%. *Sporormiella* values in this interval were between ca. 6% and 19%, while microscopic particles of charcoal were rare (Fig.3).

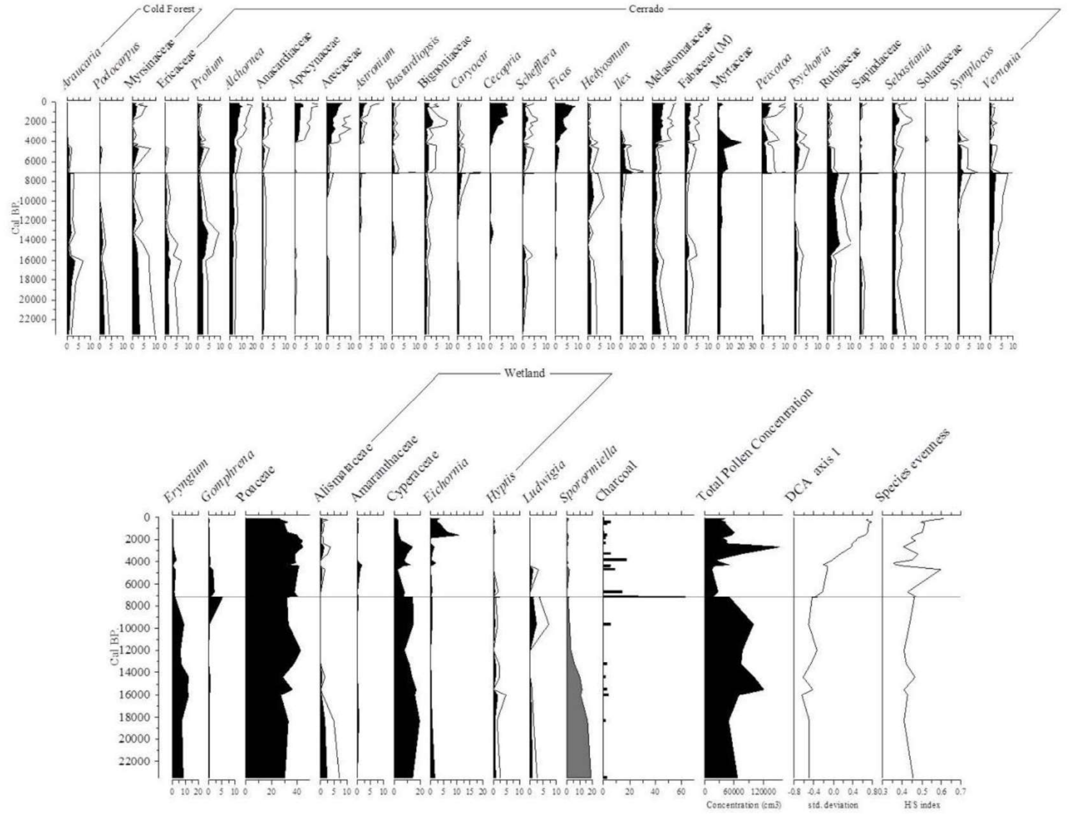

Figure 3: Pollen diagram of the percentage data for the most abundant pollen taxa recovered from the sediments of Lake Mares. 5x exaggeration is shown for values <5%. Gray silhouettes indicate the cold tolerant taxa. Total pollen concentration is expressed in grains per cm^3. DCA Axis 1 sample scores plotted against time in units of standard deviation of species turnover. Microscopic particles of charcoal are expressed as percentages of the total pollen sum.

Lake Mares 1.4 m to 0.05 m (ca. 7,200 cal. BP to modern)

During this interval, cold tolerant taxa, which were previously present in the fossil record, disappear. The most representative taxa from cerrado forest group were *Alchornea* (5% - 11%), Apocynaceae and Arecaceae (5% - 7%), *Cecropia* and *Ficus* (2% - 13%), and Melastomataceae (~5%). Other aroboreal taxa were represented in lesser abundance by Myrsinaceae, *Protium*, Anacardiaceae, *Astronium*, *Bastardiopsis*, Bignoniaceae, *Caryocar*, *Schefflera, Hedyosmum*, *Ilex*, Fabaceae (M), Myrtaceae, *Peixotoa*, *Psychotria*, Rubiaceae, Sapindaceae, *Sebastiania*, *Symplocos*, and *Vernonia*. Poaceae was the most abundant pollen type with values between 30% and 40%. Asteraceae, which started this zone with percentages of ca. 19%, progressively dropped to 14%. Cyperaceae, taken to represent wetland species, fluctuated between 6% and 17%. No other aquatic type exceeded 2%. *Sporormiella* values were between 0 and 3% from the beginning of this interval onwards. microscopic particles of charcoal peaked at ca. 7,500 cal. BP (Fig. 3).

Lake Olhos d'Agua 1.8 m to 1.5 m (ca. 23,000 – 8,000 cal. BP)

The basal sediments of Lake Olhos d'Agua were relatively rich in cold-tolerant arboreal taxa, such as *Podocarpus* (2% - 5%) and *Araucaria* (0 - 5%). The most representative cerrado forest taxa were *Myrsine*, *Caryocar*, Myrtaceae with values greater than 4%. Other arboreal elements with low abundance or that appear later in this interval were *Lithraea*, Fabaceae (M), *Alchornea*, Melastomataceae, Apiaceae and Arecaceae. Poaceae (as high as 57%) and Asteraceae dominated the herb pollen spectra in this interval. A sample at ca. 17,800 cal. BP had a spike of Cyperaceae (58%). *Sporormiella* spores were abundant, with values around 15.6 % and concentrations up to 4200 spores per cm^3 dropping to 0 at ca. 11,500 cal. BP. Microscopic particles of charcoal, ranging from 25-50 μm in size, reached a maximum of ca. 2000 particles per cm^3 ca. 10,500 cal. BP (Fig. 4).

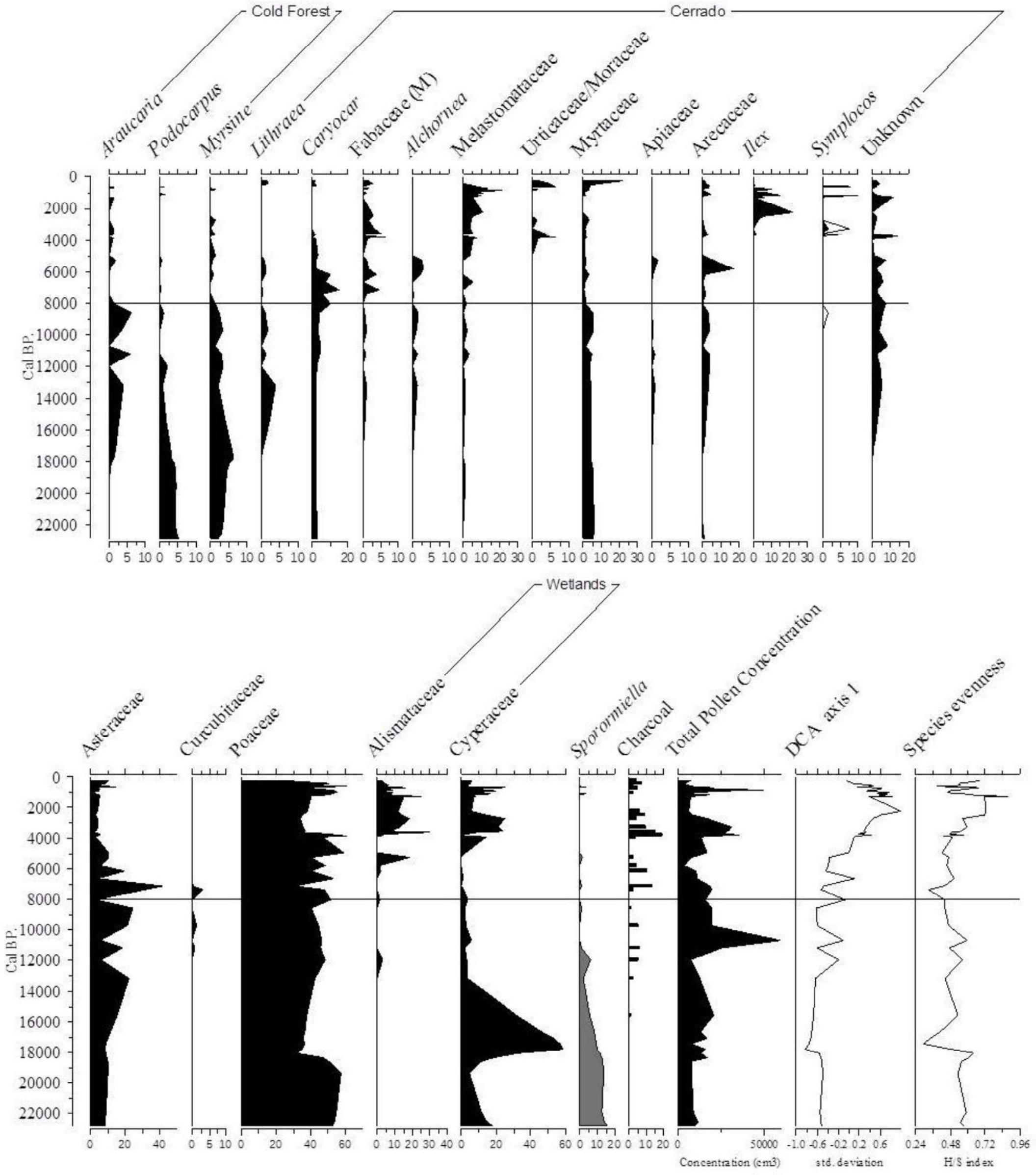

Figure 4: Pollen diagram of the percentage data for the most abundant pollen taxa recovered from the sediments of Lake Olhos d'Agua. 5x exaggeration is shown for values <5%. Gray silhouettes indicate the cold tolerant taxa. Total pollen concentration is expressed in grains per cm^3. DCA Axis 1 sample scores plotted against time in units of standard deviations of species turnover. Microscopic particles of charcoal are expressed as percentages of the total pollen sum. The gray band represents the possible hiatus in this sediment record.

Lake Olhos d'Agua 1.5 m to 0 (ca. 8,000 cal. BP to modern)

Cold tolerant taxa dropped to values below 2% during this interval. The most abundant cerrado forest taxa were *Caryocar*, Fabaceae (M), Melastomataceae, Urticaceae/Moraceae, Myrtaceae, and Ilex. Poaceae maintained high abundance, with a slight oscillation between 44% and 51% of the pollen sum. Asteraceae, on the other hand, fluctuated throughout this interval from 5% to 24%. Aquatic taxa were represented only by Alismataceae, which started this interval with values ca. 3%, dropped to zero, and then increased to ca. 20% towards modern. *Sporormiella* was recorded in a few samples, but always with values below 2%. Microscopic particles of charcoal became more frequent after 8,000 cal. BP (Fig. 4).

DCA Axis 1 vs Axis 2

DCA was performed on the percentile fossil pollen data from both lakes. At Lake Mares, DCA Axis 1 (eigenvalue 0.215, axis length 1.43) separated the samples from the bottom of the record (Pleistocene), characterized mainly by *Podocarpus*, *Araucaria*, and Ericaceae on the negative extreme of the axis from samples from the top of the sediment column (Holocene), characterized by *Acalypha, Apocynaceae, Celtis, and Cecropia* on the positive extreme of the first axis. Axis 2, (eigenvalue 0.09, axis length 1.05) separated the samples in the middle of the sediment record (early Holocene – mid-Holocene) represented by Asteraceae*, Sebastiania,* Poaceae*,* and Myrtaceae from those of the Pleistocene.

At Lake Olhos d'Agua, the DCA analysis showed a very similar pattern to that of Lake Mares. Samples scores on Axis 1 (eigenvalue 0.238, axis length 1.81), placed the samples from the bottom of the sediment record (Pleistocene) on the negative side of Axis 1, with the Late Holocene samples at the positive extreme. Just as with Lake Mares, Axis 2 (eigenvalue 0.13, axis length 1.56) separated early Holocene and mid-Holocene samples from Pleistocene-aged ones (Figs. 5 and 6).

Discussion

Fossil pollen and *Sporormiella* were well preserved in both of the Lagoa Santa records. The multivariate analysis of the pollen records provided similar results in both lakes (Figs. 3 and 4). The Late Holocene samples were seen to differ most strongly from those of the Pleistocene and early Holocene-aged samples. A clear separation of samples was evident based on age and, to a lesser extent, whether samples contained *Sporormiella* spores. DCA Axis 1, for both lakes appeared to reflect a gradient of decreasing temperature, separating taxa related to cold climates (Pleistocene) from those of warmer settings (Holocene), while Axis 2 represented decreasing precipitation (Figs. 5 and 6).

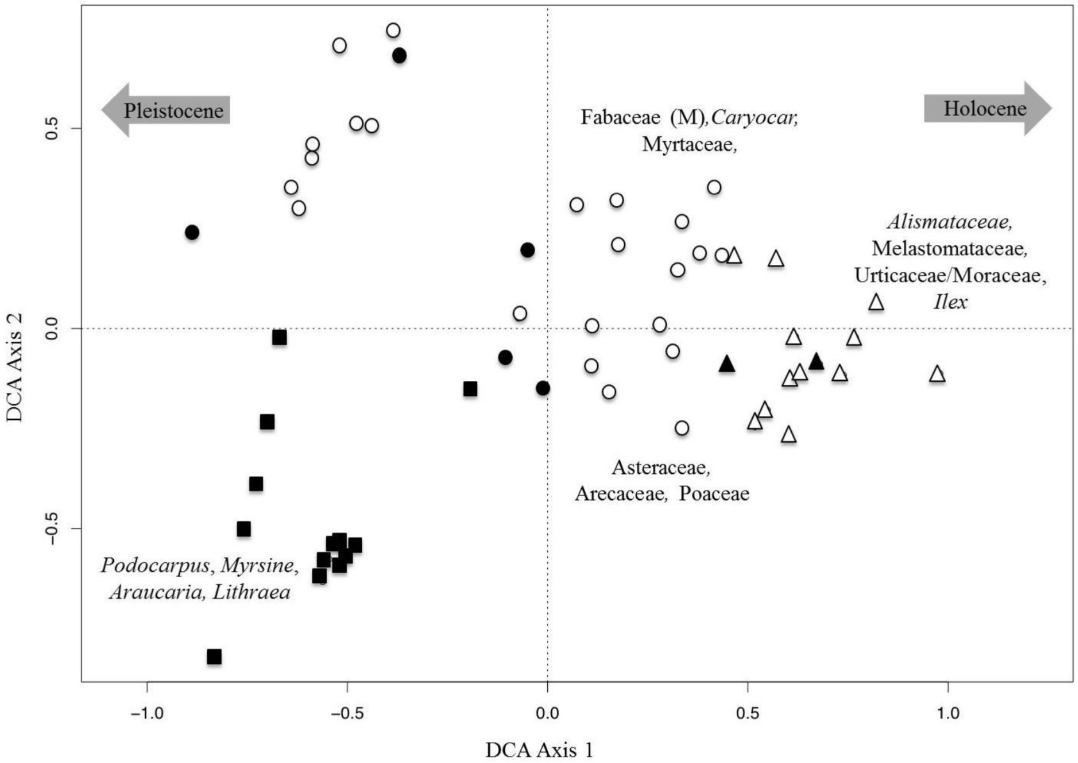

Figure 5: DCA results of the fossil pollen data of Lake Mares. Closed symbols represent samples with *Sporormiella* presence, and open symbols represent samples in which *Sporormiella* was not recorded. Squares = samples with Pleistocene ages; Circles = samples with Early to mid-Holocene ages; Triangles = samples with Late Holocene ages. Species characterizing the extremes of axes are shown.

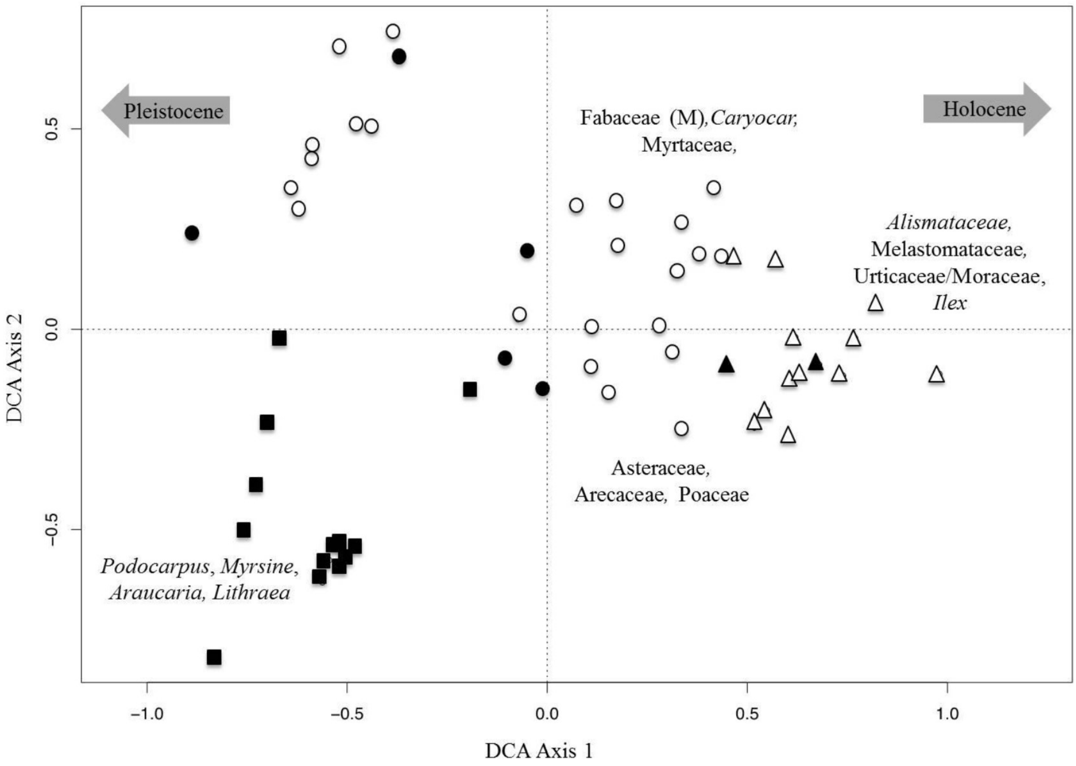

Figure 6: DCA results of the fossil pollen data of Lake Olhos d'Agua. Closed symbols represent samples with *Sporormiella* presence, and open symbols represent samples in which *Sporormiella* was not recorded. Squares = samples with Pleistocene ages; Circles = samples with Early to mid-Holocene ages; Triangles = samples with Late Holocene ages. Species characterizing the extremes of axes are shown.

Vegetation change from the Last Glacial Maximum to modern

Both lakes revealed a similar presence of cold-tolerant taxa in the deglacial period. *Araucaria* and *Podocarpus*, are regular components of the late-glacial pollen records at both Lakes Mares and Olhos d'Agua. Pollen grains of these genera are not found in the modern Lagoa Santa region and are restricted to high elevations or higher latitudes in Brazil (Fig. 7) (Behling, 1997a, 1997b, 1995). These taxa are cold-tolerant and their presence suggests a cooling relative to modern of about 5 °C. These findings are consistent with data for the downslope or northward expansion of these cold-tolerant taxa in other cerrado settings (Barberi et al., 2000; Ledru, 1993; Salgado-Labouriau et al., 1997). High

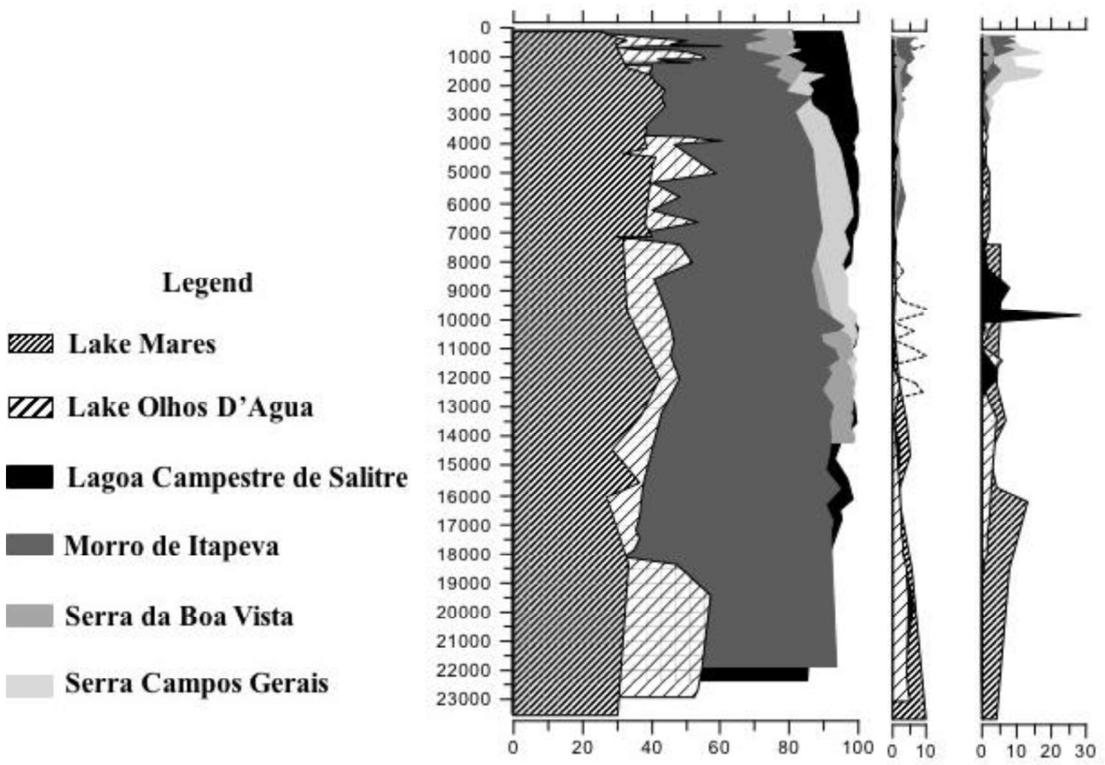

Figure 7: Trends in vegetation cover for sites where pollen records indicate the modern occurrence of *Podocarpus* and *Araucaria*. Note the modern occurrence at higher elevation or higher latitude than the Lagoa Santa sites. The pollen datasets from Lagoa Campestre de Salitre (Elev: 1050 m; mean annual temp: ~25^{0}C; 19°S - 46°46'W), Morro de Itapeva (Elev: 1850 m; mean annual temp: 13.6^{0}C; 22°47'S - 45°32'W), Serra da Boa Vista (Elev: 1160m; mean annual temp: ~15^{0}C; 27°42'S – 49°09'W), and Serra Campos Gerais (Elev: 1200m; mean annual temp: ~16.7^{0}C; 24°40'S - 50°13'W) were downloaded from the Neotoma (http://www.neotomadb.org/).

percentage values of pollen of grasses and herbaceous taxa also suggested the presence of a mosaic of forest and savanna under a relatively cool climate.

Forest elements such as *Araucaria*, *Myrsine*, and *Podocarpus*, and an abundance of Cyperaceae between ca. 23,000 and 12,000 cal. BP indicated a moister and cooler climate than present. A rapid increase in sedges (Cyperaceae) ca. 17,800 cal. BP at Lake Olhos d'Agua, could represent a falling lake level and a marsh closer to the coring site between ca. 17,800 and 15,600 cal. BP (Whitney et al., 2011), or it could represent a larger backswamp in response to higher lake level. Given that this period coincides with increased precipitation in the Botuverá Cave record, it is likely that the Cyperaceae reflect a marsh expansion because of wetter conditions. It is notable that this event was not represented in the Lake Mares record.

Poaceae and Asteraceae were the most abundant pollen types between ~23,000 and 14,000 cal. BP in both sediment records. While these elements could have represented savanna grasslands, they were also abundant components of lake, river and swamp vegetation (Ledru et al., 2015), and semi-open forests where grasses dominated (Behling, 2002; Wanderley et al., 2001). The persistence of trees coupled with elements indicative of moisture in the Lagoa Santa region indicated conditions moist enough to support woodland, but a declining representation of aquatic indicators suggested a gradual drying of the climate between 19,000 and 11,000 cal. BP. Floristically, the early Holocene, from c. 11,700 until 9000 cal. BP, was very similar to the Pleistocene, with evidence of a mixture of modern cerrado elements, e.g. *Alchornea, Caryocar*, Ericaceae, and various Anacardiaceae, growing alongside species characteristic of cool mesic forests, e.g. *Araucaria*, *Podocarpus,* and *Myrsine*. *Araucaria* was almost lost from the Lake Mares record between ca. 16,000 and 14,000 cal. BP, coincident with a dry oscillation evident in the isotopic record from Botuverá Cave. *Araucaria* returned to the record as conditions became wetter after ca. 14,000 cal. BP, and persisted well into the Holocene, only disappearing ca. 8,000 cal. BP. At Lake Olhos D'Agua, Poaceae started to decline at c. 19,000 cal. BP and *Araucaria* was first documented at 18,000 cal. BP (Fig. 5).

The Holocene portion of both records includes a period of intermittent drought between c. 8000 and 5000 cal. BP (Raczka et al., 2013). Cerrado vegetation dominated throughout this period, and was maintained as conditions became more consistent and approximated those of modern times post-4000 cal. BP.

Did Climate change cause the megafaunal extinction?

The precipitation and temperature change of the Lagoa Santa region was forced by different external factors. Regional precipitation was driven by changes in North and subtropical Atlantic Ocean circulation (McManus et al., 2004), while the cold events structuring vegetation were strongly influenced by incursions of Antarctic air (Garreaud, 2000).

At Lake Olhos d'Agua, *Sporormiella* appears to have begun its decline in abundance by ca.18,000 cal. BP. *Sporormiella* fell below the 2% threshold, used by some authors to suggest the extinction of the megafauna (Davis and Shafer, 2006) at ca. 11,160 cal. BP. At Lake Mares, the initial decline of *Sporormiella* also started ca. 18,000 cal. BP, however, *Sporormiella* fell below 2% of the pollen sum at ca. 12,000 cal. BP.

The 2% threshold identifying functional megafaunal extinction was derived for ecosystems of the western U.S., and applied to paleoecological settings as they transitioned from cold grassland to cool temperate/boreal forest (Robinson *et al.*, 2005, Gill *et al.*, 2009). The Lagoa Santa lakes were unusual, among those studied so far to investigate megafaunal population collapse, in that there was not a biome change within the record. Most other records feature a transition from grassland to forest at the time of the megafaunal loss, but at Lagoa Santa it was a remarkably constant occurrence of cool cerrado woodland throughout the deglacial and early Holocene. Thus, the probability that a major change in pollen production associated with habitat change could complicate the interpretation of the *Sporormiella* record seems more likely in the temperate rather than tropical settings.

If concentration is used to identify the functional extinction rather than percentage, the *Sporormiella* levels of the mid-Holocene provide a period when the megafauna are known to be absent, and pastoralism has yet to boost herds. Thus, *Sporormiella* values seen between c. 9000 and 7000 cal. BP, probably represent a good baseline (Figs. 3 and 4). If those criteria are applied the extinction would have taken place at 11.6 cal. BP at Lake Olhos D'Agua, and at 12 cal. BP at Lake Mares.

As can be seen, it made little difference whether the 2% threshold of Davis and Shafer (2006) or concentration (spores per cm^3) (Fig. 8) was used to estimate the timing of population collapse. Based on these data, the most constrained dates for the decline in megafaunal population showed that it was initiated by ca. 18,000 cal. BP and the functional extinction, or background level associated with the mid-Holocene, was reached between ca. 12,000 and 11,100 cal. BP (Fig 8).

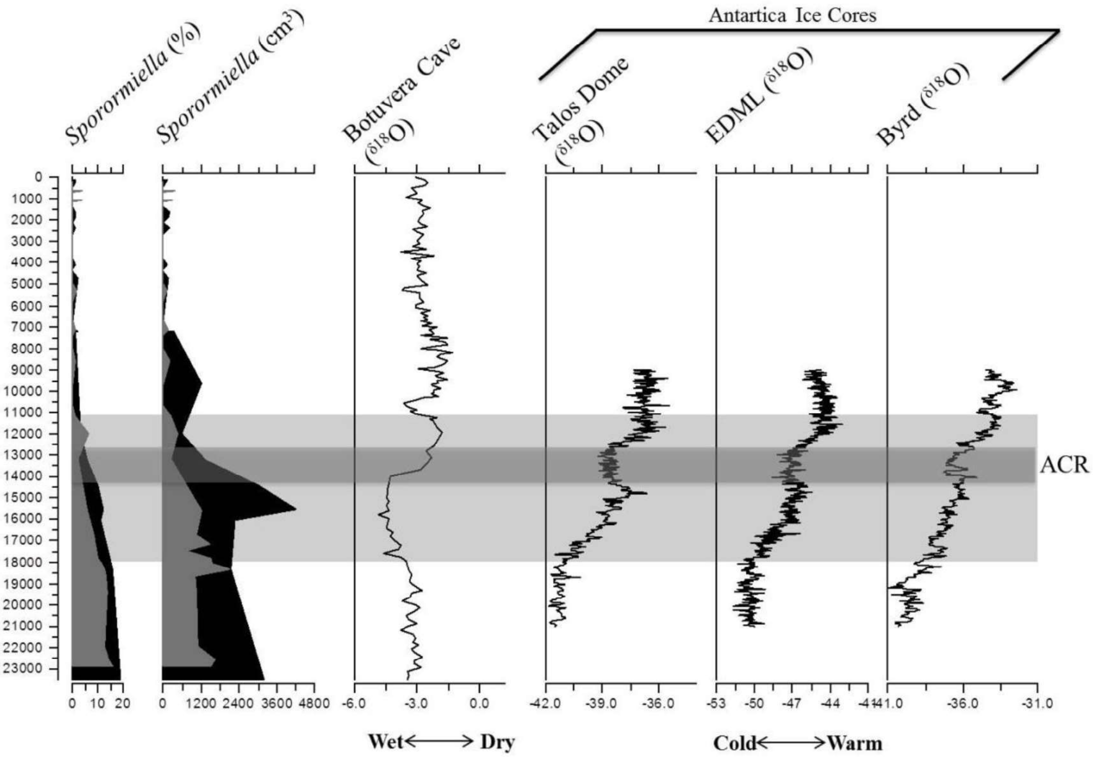

Figure 8: Comparison between *Sporormiella* data (percentage and concentration) from Lake Mares (black silhouette) and Lake Olhos d'Agua (gray silhouette), with Botuvera cave stalagmite ratios of oxygen isotopes and with ice cores from Antarctica (Pedro et al., 2011). Light gray vertical bar indicates the interval of *Sporormiella* decline. Dark gray vertical bar indicates the Atlantic Cold Reversal (ACR) episode.

These dates were later than the *Sporormiella* decline recorded at Lake Pacucha, Peru, where the herbivore population decline started at ca. 21,000 cal. BP and the functional extinction was reached at 15,800 cal. BP (Rozas-Dávila et al., 2016). The Lagoa Santa data were also later than those of Appleman Lake, Indiana, where the decline started as early as 16,000 cal. BP, with extinction inferred at ca. 13,700 cal. BP (Gill et al., 2009).

The terminal Pleistocene at Lagoa Santa was cooler than modern, and the precipitation probably varied quite markedly. The decline in megafaunal populations coincided with the onset of wetter conditions between 18,000 and 14,000 cal. BP (Fig. 8). Cooler and moister conditions associated with the Atlantic cold reversal between 14,000 and 12,300 cal. BP (Cruz et al., 2006; Pedro et al., 2015) (Fig. 8) did not reverse this trend. If populations had survived prior interglacials, there must have been equivalent downturns followed by recoveries. In this instance, although the climate should have favored a recovery, i.e. it was moving back toward more glacial conditions, there is no evidence of any increase. Given that this period falls within the window of potential human occupation, we tentatively infer that humans were applying sufficient population presuure by 14,000 years ago to prevent megafaunal recovery. The warming trend that followed the Atlantic Cold reversal is the effective start of the Holocene in many South American climate records (Haberzettl et al., 2007; Moreno et al., 2001; Urrego et al., 2010; Valencia et al., 2010). As observed in Patagonia (Metcalf et al., 2016), the functional extinction of megafauna in the Lagoa Santa region coincided with this warm event.

Was the decline of *Sporormiella* spores coincident with the formation of no-modern analog assemblages in the pollen spectra?

These data suggested that, at least in this setting, the no-modern analog assemblages were strongest during cool wet climates when megafauna were present, but persisted in warmer, drier climates after the loss of megafauna. In North America and the Andes, the functional extinction of the megafauna coincided with the establishment of no-analog floras. These communities were formed by the coexistence of cold-tolerant and cold-sensitive arboreal species, which are not currently sympatric. At Lake Mares and Lake Olhos d'Agua, *Podocarpus* and *Araucaria* were cold-tolerant taxa whose ranges were extended during the last glacial. The association of *Caryocar*, a bat-pollinated tree (Gribel and Hay, 1993) typically found in cerrado ecosystems, with the cold-tolerant taxa suggested that a landscape configuration with no-modern analog existed near Lake Mares and Lake Olhos d'Agua. Unlike the no-analog floras seen in the Andes and North America, where ice-age grasslands gave way to deglacial woodlands, Lakes Olhos d'Agua and Lake Mares supported woodland vegetation throughout the terminal ice age. In the Lagoa Santa settings, the Lake Mares record showed *Araucaria* and *Podocarpus* to be part of the system at ca. 23,000 cal. BP and there were trace amounts of *Caryocar* (Fig. 4).

Large herbivores were probably important ecosystem engineers in such parkland settings, impeding woody regeneration and maintaining open areas (Augustine and

McNaughton, 1998; Bakker et al., 2016; Ripple and Van Valkenburgh, 2010). The consequences of the extinction of large herbivores from the landscape and the role that large herbivores might have played on the vegetation remains a puzzle (Doughty et al., 2016). The extinction that took place at the end of the Pleistocene (Young et al., 2016) affected species composition and probably vegetation structure, but the effects of the megafauna extinction may have been more heterogeneous than the previously thought. While some plant species probably benefited from reduced grazing and trampling (Rozas-Davila et al. 2016), others might have suffered negative effects from increased competition or reduced seed dispersal. With the loss of dispersers, more clumped distributions of large-seeded species might be expected (Janzen and Martin, 1982). Alternatively dispersal may have been maintained by humans and small rodents (Guimarães et al., 2008; Iob and Vieira, 2008).

Large mammals are not only seed dispersers, but are voracious predators of seedlings and can profoundly influence recruitment (Wyatt and Silman, 2004). In both our study lakes, the increase of some taxa such as Arecaceae, *Lithraea*, Melastomataceae, *Ficus*, and *Caryocar* were coincident with the final decline of *Sporormiella*, which could reflect the lack of herbivory in the system.

Notably the cold-tolerant taxa, such as *Araucaria* and *Podocarpus* survived later into the Holocene than there is evidence of megafauna. The late survival of these cool-mesic forest taxa is not unique to these sites, and has been observed at other southeastern -Brazilian locations (De Oliveira, 1992). Lake shorelines may have served as microrefugia for these populations that lingered for a few thousand years before the warmer and drier conditions of the mid-Holocene extinguished them from this region.

Did the decline in *Sporormiella* abundance occur before the arrival of humans to the Lagoa Santa region?

The earliest known occupation of South America by humans is documented at Monte Verde, southern Chile, with a suggested age of 18,500 - 14,500 cal. BP (Dillehay et al., 2015, 2008). If these were foundational human populations, the process of colonization might have continued through coastal exploration (Dillehay, 1999) with an unknown rate of spread into the interior. In the Lagoa Santa region, the arrival of humans is contentious as the material that is dated via optically-stimulated luminescence provides a range of credible ages ranging from 16,000 to 12,700 cal. BP (Feathers et al., 2010; Neves et al., 2003, 1999), while the oldest ^{14}C age is ca. 11,500 cal. BP.

In other ecological records, fire is an abrupt and obvious signature of human presence, especially in systems that do not burn naturally. It has also been suggested that the loss of megafauna resulted in decreased grazing, which led to increased fuel loads and elevated fire frequency (e.g. Gill et al. 2009). No such abrupt change in fire frequency is evident in the Lagoa Santa records. Microscopic particles of charcoal are present as a rare component in almost all samples from Lake Mares with the most notable increase in charcoal frequency occurring at ca. 7200 cal. BP (Fig. 4). At Lake Olhos d'Agua, charcoal was absent from the oldest samples, but occurred in all samples after ca. 15,600 cal. BP (Fig. 5) with a mid-Holocene peak in representation. In the Pleistocene portion of both records, the fire-signal was present, but relatively weak, and did not coincide with a major change in vegetation type. The cerrado ecosystem is a naturally dry setting and fire is a long-term (pre-human arrival) component of the landscape. As species were somewhat fire-adapted, the arrival of humans, even if it did increase fire frequency somewhat would have had less of an ecological effect than in a system that did not burn naturally (Cochrane, 2009). We found no compelling evidence in this system that the loss of megafauna increased fire-frequency. Similarly, the growing human presence from ca. 12,000 years onward may have had ecological impacts that fell within the range of natural disturbance regimes and did not produce a strong signal in the pollen records.

Although a few megafaunal kill-sites have been recognized in South America (Bryan et al., 1978; Politis et al., 1995), data are still too scarce to indicate robustly that humans were a significant factor in megafaunal population declines (Prado et al., 2015). While it is abundantly clear that humans and megafauna co-existed in South America for thousands of years (Fariña and Castilla, 2007; Hubbe et al., 2009, 2007; Neves and Pilo, 2003), we conclude that the initial decline in megafaunal populations was not related to human activity. The final decline at the end of the Pleistocene, however, overlapped with human occupation in the Lagoa Santa region. Our data from the Lagoa Santa region are consistent with the emerging view that megafauna were susceptible to wet intervals, and that population recovery took place from natural lows, but when humans arrived, the synergy of hunting, climate change, and human-altered ecology, induced extinction (Cooper et al., 2015; Metcalf et al., 2016; Rozas-Dávila et al., 2016).

Conclusion

The paleoecological data gathered from Lake Mares and Lake Olhos d'Agua used fossil *Sporormiella* abundance to infer changes in megafaunal presence and abundance. Megafaunal populations began to decline ca. 18,000 cal. BP, with a functional extinction occurring between ca. 12,000 and 11,100 cal yr. BP. The age interval of our suggested functional extinction, overlapped with the oldest human evidence for the Lagoa Santa region, ca. 16,000 – 12,700 cal. BP (Feathers et al., 2010). The initial population collapse took place amid a warm wet interval, and the functional extinction took place in a warming during a relatively dry episode. The unusually stable ecosystems of the Lagoa Santa region held no-analog floras throughout the decline of the megafaunal populations and even for several millennia after their extinction. The data from Lagoa Santa region were not consistent with parallel studies from North America and the Andes that found the functional extinction of the megafauna to be simultaneous with a marked increase in the abundance of microscopic particles of charcoal and the establishment of novel floras. We suggest a synergistic effect between climate change and humans as the most parsimonious explanation of the failure of megafaunal populations to recover after a climate-induced collapse prior to the Antarctic Cold Reversal, which was expressed locally as a dry interval. Perhaps the most valuable lessons learned from this study are that the collapse of megafaunal populations did not induce the same results across different ecosystems.

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CHAPTER 8

Manuscript 7 (accepted by AABC – 2018)

New Holocene pollen records from the Brazilian Caatinga

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ABSTRACT

We present two pollen diagrams from the semi-arid Caatinga of the Catimbau National Park, in Pernambuco and from a *Mauritia* palm forest in the Caatinga/Cerrado ecotone of southern Piauí, NE Brazil, spanning the last 10,000 cal. yrs BP and the last 1750 cal yrs BP, respectively. These two records contain a signature of the local vegetation and permit the correlation of the pollen signal with regional climatic changes. The Catimbau record shows *Zizyphus* sp., a typical Caatinga taxon, in all three pollen zones indicating regional Caatinga vegetation and the predominance of local arboreal taxa adapted to high humidity from 10,000 to *ca.* 6,000 cal. yrs BP with a gradual tendency towards drier conditions revealed by a deposition hiatus between 6000 to *ca.* 2000 cal. yrs BP. This abrupt loss of sediments in both localities is interpreted as a consequence of the establishment of modern semi-arid climates. The subsequent return of humidity is signaled by increased sedimentation rates and ^{14}C date inversions in agreement with high precipitation, revealed by σ^{18}O ratios in speleothems from NE Brazil. Modern sediments deposited in the last 500 years reflect local conditions with the maintenance of humidity by geological faulting and surfacing water tables.

Key words: Paleoclimatology; Palynology; Pernambuco; Piauí; Caatinga Vegetation

INTRODUCTION

The Brazilian Caatinga appeared for the first time in the international scientific literature with the seminal study Flora Brasiliensis by Karl Friedrich von Martius in 1817, followed by various contributions on the physical and floristic characteristics of this semi-arid tropical ecosystem (Andrade-Lima 1953; Rizzini 1963; Andrade-Lima 1977; Rizzini and Mattos Filho 1992; Barbosa et al, 2006). Until recently, the Late Quaternary history of this vegetation had not been available due to a lack of palynological studies, which require organic-rich and unoxidized sediments. These were later found in the Icatu River Valley, in the mid-São Francisco River, state of Bahia, by De Oliveira et al. (1999) and revealing continuous sedimentation in the last 11,000 years. The authors observed the predominance of rainforest taxa during the Pleistocene/Holocene transition, indicating a humid phase in the Early Holocene, with a gradual loss of humidity. According to the Icatu pollen record, it became clear that rainforest as well as palm forest (buritizal) decreased gradually in abundance in that valley until the mid-Holocene and was followed by the establishment of semi-arid climate at *ca.* 4200 yrs BP.

Among other studies that contribute to the understanding of Holocene climates within the Caatinga is that of Behling et al. (2000), who analyzed the pollen signal in marine sediments deposited at the Jaguaribe River delta, in the continental platform, 90 km off the coast of Ceará. These authors show that the terrestrial signal started to decrease after 8,500 yrs BP, thus suggesting the establishment of semi-arid conditions. However, it is noteworthy the return of humid climates after *ca*. 3,200 yrs BP in high elevation regions of the semi-arid Caatinga domain of Ceará, Piauí and Paraíba (Pessenda et al. 2010) and in Serra do Maranguape, Ceará (Montade et al. 2014). In fact, the modern vegetation pattern within the Caatinga is predominantly xerophytic in the lowlands in contrast to the conspicuous presence of tropical forests containing Amazonian and Atlantic taxa in elevations higher than 1,000 meters, known as “Brejos de altitude”, maintained by orographic rains which create unusual high rainfall patterns under lower temperatures within the semi-arid domain (Sales et al. 1998).

Other paleoclimatic analyses within the Caatinga region, derived from geochemical and geological data, support unstable climates during the Holocene, with a wetter early phase, followed by dryer conditions at *ca.* 4,000 yrs BP, intercalated with a strongly rainy period *ca*. 2,000 yrs BP (Cruz et al. 2009; Novello et al. 2012; Nace et al. 2014; Mendes 2016).

Despite the recent advances in our knowledge of the vegetation and climatic dynamics, the Caatinga ecosystem remains the least known in the literature in terms of its vegetational and climate evolution. In this present contribution, we provide two new Holocene pollen records from the semi-arid region of central Pernambuco and southern Piauí, both located in an area with the lowest precipitation levels in this ecosystem, known in Brazil as Sertão or Polígono da Seca (Drought Polygon), in order to contribute to the understanding of the vegetational, climate and ecological processes during the Holocene.

STUDY SITES

Pollen analyses were conducted in two localities in the Caatinga domain: Vale do Catimbau, Pernambuco and Bom Jesus, Piaui, shown on Figure 1.

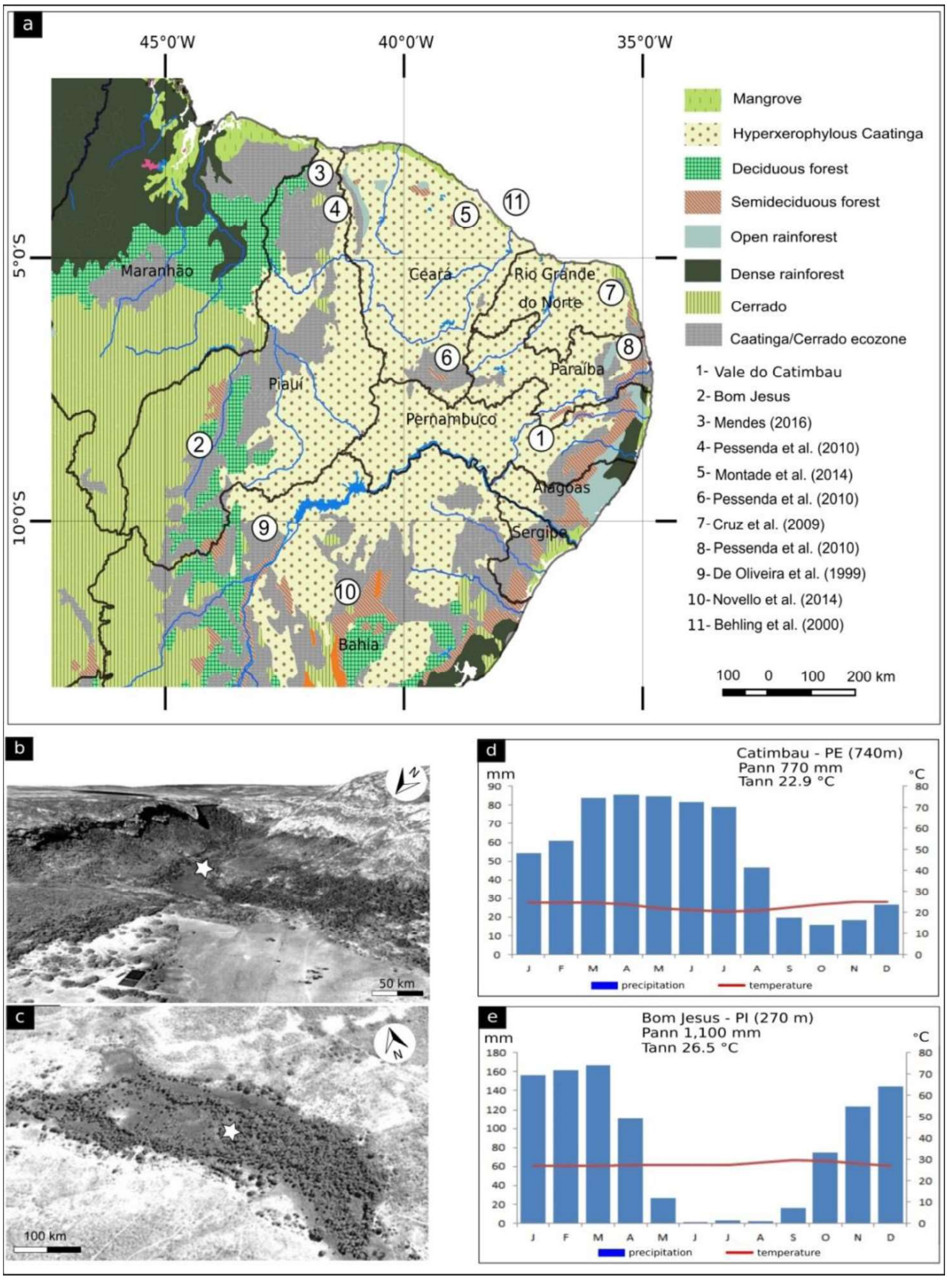

Figure 1. (a) Location map of Catimbau (1) and Bom Jesus (2) sites in relation to important paleoclimatic studies, showing the vegetational distribution of NE Brazil, drawn by Q GIS 2.18 Las Palmas software. Satellite images for both sites are in (b) and (c), respectively and reveal the position of the sampled sites in the environment. Ombrothermic diagrams show mean monthly values of temperature and precipitation and annual precipitation (Pann) and temperature (Tann), for both sites (d) and (e) respectively, calculated for the last 45 years (data from the National Institute of Meteorology, available at: www.inmet.gov.br/portal). Paleocological studies discussed in the present work are: 3 – Parnaíba River (Mendes 2016); 4 – PARNA (Pessenda et al. 2010); 5 – Serra do Maranguape (Montade et al. 2014); 6 –

FLONA (Pessenda et al. 2010); 7 – Rio Grande do Norte (Cruz et al. 2009); 8 – REBIO (Pessenda et al. 2010); 9 – Icatu River (De Oliveira et al. 1999); 10 – Diva de Maura and Torrinha Caves (Novello et al. 2012); 11 – GeoB 3104-1 (Behling et al. 2000).

In the first, sediments were collected from a peatbog 0.5 km long x 0.12 km wide in the Vale do Catimbau National Park, Arcoverde municipality, Pernambuco (8º29'26"S; 37º11'20"W), at 740 m elevation. The climate is semi-arid, with a well-defined wet season between February and August, mean annual precipitation of 700 mm, and mean annual temperature of 22.9 ºC. The geological setting of the Vale do Catimbau region is controlled by the Jatobá Basin, of Silurian-Devonian age (CPRM 1964), containing the Tacaratu Formation, composed of sandstones and conglomerates. The sedimentary rocks establish an important deep aquifer in a large section of northeastern Brazil. Geological faults in the Catimbau region (Gomes 1995), especially the São José Mountain range are responsible for surfacing waters conducive to peatbog formation (Nascimento 2008). The modern vegetation cover in Vale do Catimbau includes typical Caatinga genera such as the arboreal and herbaceous *Astronium*, *Cassia*, *Ceiba*, *Cereus*, *Croton*, *Jatropha*, *Manihot* and *Tabebuia*. Nearby islands of Cerrado contain the *Krameria*, *Hymenaea*, *Senna*, *Guapira* and *Tocoyena* and in some humid areas, rainforest elements such as *Mauritia*, *Sauvagesia* and *Justicia* are common. In some areas *Orbignya* (*Attalea*) palms (babaçu) is predominant (Sales et al. 1998), especially around the peatbog sampled for the present pollen study.

The second site, at Bom Jesus, Piaui, is located at a Caatinga/Cerrado ecotone, thus reflecting a floristic mosaic composed of species belonging to those ecosystems. Organic-rich sediments, forming a superficial peatbog underlain by mineral sediments, were collected in a location named Veredas, (9°13'40.59"S and 44°28'0.92"W), part of an extensive *Mauritia flexuosa* palm forest. The sampling location is located within an ephemeral drainage system under a semi-arid climate with a wet season from October to April, mean annual precipitation of 1,100 mm and mean annual temperature of 26.5ºC, at 270 m elevation (EMBRAPA 2016). The Bom Jesus *Mauritia flexuosa* palm forests (buritizais) are located in humid areas where the surfacing water table creates waterlogged soils colonized by Amazonian and/or Atlantic arboreal taxa such as *Mauritiella aculeata*, *Acacia*, *Anadenanthera*, *Commiphora*, *Dalbergia*, *Piptadenia*, *Poeppigia*, *Copernicia*, *Geoffroea*, *Licania* as well as *Costus* herbs (Andrade-Lima 1981).

MATERIALS AND METHODS

At the Vale do Catimbau peatbog, a peat sediment column of 161,5 cm was retrieved with a Russian sampler (Belokopytov and Beresnevich 1955) in the northern portion of that basin in order to avoid sampling of disturbed sediments previously collected at the center of the bog by Nascimento (2008). At the Bom Jesus site, a 155 cm sediment sequence was obtained with a vibrocore sampler (Martin et al. 1995) in a palm swamp characterized by clayey/organic sediments.

After the opening of the tubes under laboratory conditions, sediments were described and subsampled. A total of 32 samples of one cm^3 were collected along the Catimbau core in various depth intervals (10 cm, 5 cm and 2.5 cm), while in the Bom Jesus sequence, were collected a total of 12 samples, within 10 cm depth intervals. All of them were chemically processed according to the Quaternary Palynology protocol described in Colinvaux et al. (1999): addition of *Lycopodium clavatum* (exotic marker) spores, followed by HF (hydrofluoric acid) treatment for silicates removal and acetolysis reaction for the destruction of organic matter in the samples as well as within the pollen. Residues were mounted on glycerine and pollen/spores and other palynomorphs were counted under light microscopy. Counts proceeded until a minimum of about 300 pollen grains or 100 to 200 grains for samples with low palynomorph preservation. Pollen sums were calculated based on all pollen taxa present and belonging to the different categories such as arboreal, shrub, terrestrial and aquatic herbaceous pollen grains. Percentage and concentration values of all taxa were calculated by TILIA, TILIAGRAPH software (Grimm and Troostheide 1994), and pollen zones were established by means of a similarity dendrogram by CONISS (Grimm 1987). Accelerated Mass Spectrometry (AMS) radiocarbon dating of selected samples was carried out by Beta Analytics Laboratory, Miami, Florida. All the calibrations were done with the software CALIB 7.1 (Stuiver et al. 2017), using the calibration curve ShCal13 (Hogg et al. 2013) and the age-depth models curves were done by Oxcal 4.3 (Ramsey 2008).

RESULTS

Lithology, radiocarbon dating and sedimentation rates are presented for both sites, followed by separate palynological results.

Peatbog sediments from Catimbau are composed of very dark sandy organic sediments with fine sand laminations at 122.5 cm and from 135 and 140 cm, while the Bom Jesus sequence showed the intercalation of clays and sands (Table 1). Radiocarbon ages for the Catimbau sequence vary from 10,322 cal yrs BP to 152 cal yrs BP with dating inversion at around 1,800 cal yrs BP. The Bom Jesus sequence reached 1,749 cal yrs BP at the bottom depth of 100 cm depth, with inversions at *ca.* 1,700 cal yrs BP, at 154 cm depth (Table 2).

Table 1. Lithology of the Vale do Catimbau peat and Bom Jesus sequence

Sites	Depth(cm)	Sediments description
Vale do Catimbau	0 – 135	Sandy peat, with sand lamination at 122,5 cm
	135 – 140	Sand lamination
	140 – 161,5	Sandy peat
Bom Jesus	0 – 16,5	Brown organic matter with plant remains
	16,5 – 42	Dense clay with roots
	42 – 47	Light brown sand
	47 – 101	Yellow sandy clay
	101 – 155	Banded gray clayey sands

Table 2. Radiocarbon ages for the Catimbau and Bom Jesus samples. Calibrations were calculated by software CALIB 7.1 (Stuiver et al. 2017), ranges of 95,4% (2^{δ}). Final calibrated ages were obtained from the median probability provided of the end calibration.

Site	Sample	Nr. Beta	Conventional Ages (BP)	Calibrated ages (yr cal. BP)	Calibrated ages range	
					from	to
Catimbau	30	390149	180 +/- 30	152	284	3
Catimbau	60	431967	1100 +/- 30	956	1055	920
Catimbau	80	390150	1880 +/- 30	1778	1796	1619
Catimbau	110	390151	1830 +/- 30	1714	1830	1709
Catimbau	120	431968	5700 +/- 30	6440	6531	6320
Catimbau	130	390152	6540 +/- 30	7416	7466	7327
Catimbau	137	431969	6570 +/- 30	7446	7509	7339
Catimbau	169	370007	9200 +/- 40	10322	10486	10229
Bom Jesus	38-40	360002	460 +/- 30	516	530	500
Bom Jesus	100	390147	1810 +/- 30	1750	1822	1628
Bom Jesus	120	390148	1560 +/- 30	1462	1475	1320
Bom Jesus	152-154	360003	1320 +/- 30	1247	1300	1180

The litology and radiocarbon dating results indicate very slow sedimentation rates varying from 0.009 to 0.233 cm year^{-1}, at Catimbau, as shown on Figure 2, although a significant deposition of 30 cm occurred between the inverted dates of 1,880 and 1,830 cal. yrs BP. The rapid deposition at *ca.* 1,800 cal. yrs BP at the Catimbau site is probably associated with a humid episode, with torrential rains that could have altered the horizontally layering of the sediments. A hiatus in sedimentation is clear between 6,440 and 1,778 cal. yrs BP in the Catimbau peat core, which appears to bear a correlation to the Mid-Holocene drying climates observed for the Caatinga ecosystem at *ca.* 4,500 cal. yrs BP. An age model based on previous analyses at the Catimbau site by Nascimento (2008) shows similar results, *i.e.* low sedimentation rates at *ca.* 2,000 yrs BP followed by oscillating values. It is very likely that due to poor radiocarbon control the author was not able to detect the hiatus. On the other hand, deposition at the Bom Jesus site, also presented on Figure 2, reveals age inversions thus not allowing a thorough interpretation of its pollen data.

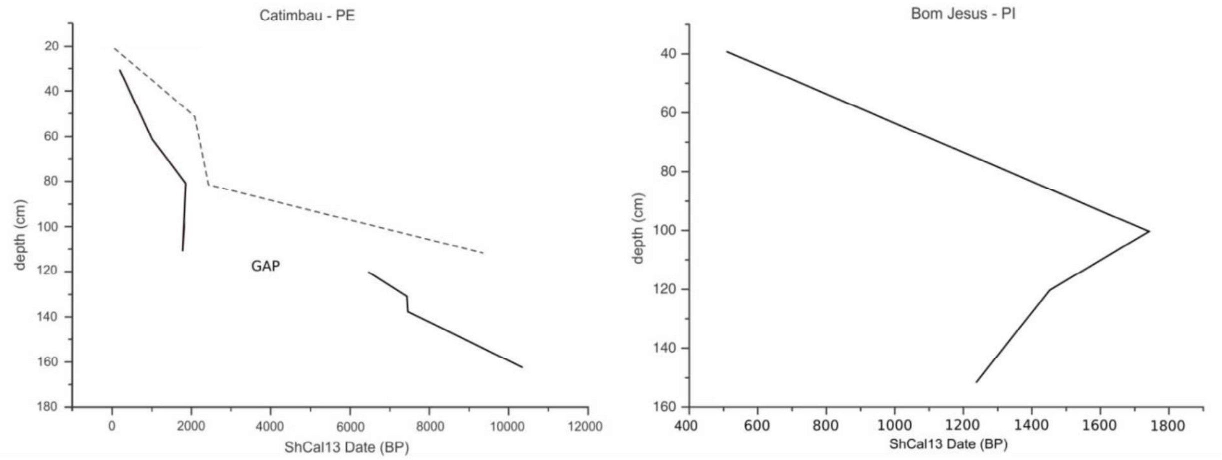

Figure. 2. Oxcal 4.3 (Ramsey 2008) calibrated age-depth models for the Vale do Catimbau and Bom Jesus peat sequences. The Catimbau data (this study) is given as a continuous line whereas the dotted line represents the age-depth models applied to Nascimento's data (2008).

Palynological analyses- Vale do Catimbau

Figure 3 and 4 show percentage and concentration pollen diagrams for different palynomorph categories, respectively. Percentage and concentration values for each taxon, given between parentheses, refer to the evolution of its representation from bottom to top of each pollen zone. In the palynomorph diagrams, aquatic herbs, pteridophytic and algal spores provide a clear signature of waterlogged conditions for the entire Catimbau deposition. These, in turn, are determined by geological fault lines allowing the surfacing of the underground water table.

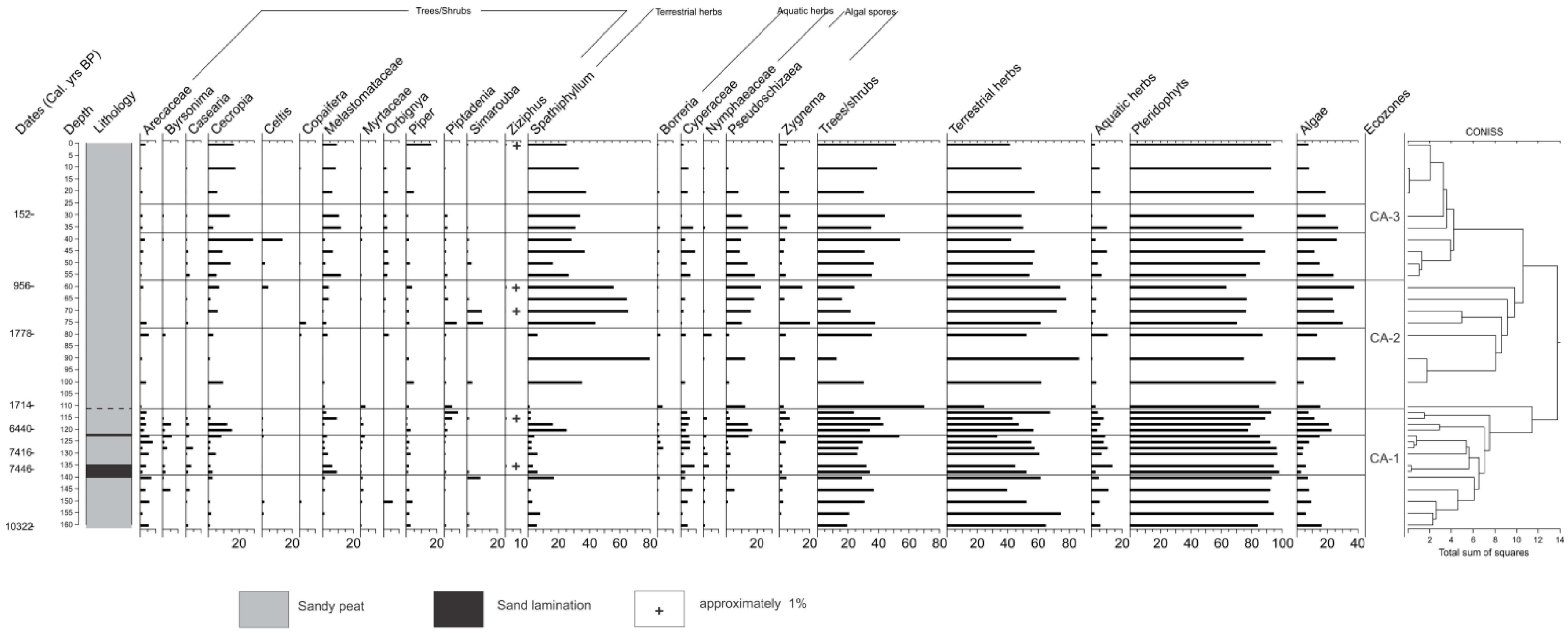

Figure 3. Percentage pollen diagram of the Vale do Catimbau peat sequence, of selected taxa and sum of categories. Dotted line in the lithology column marks a sedimentary hiatus.

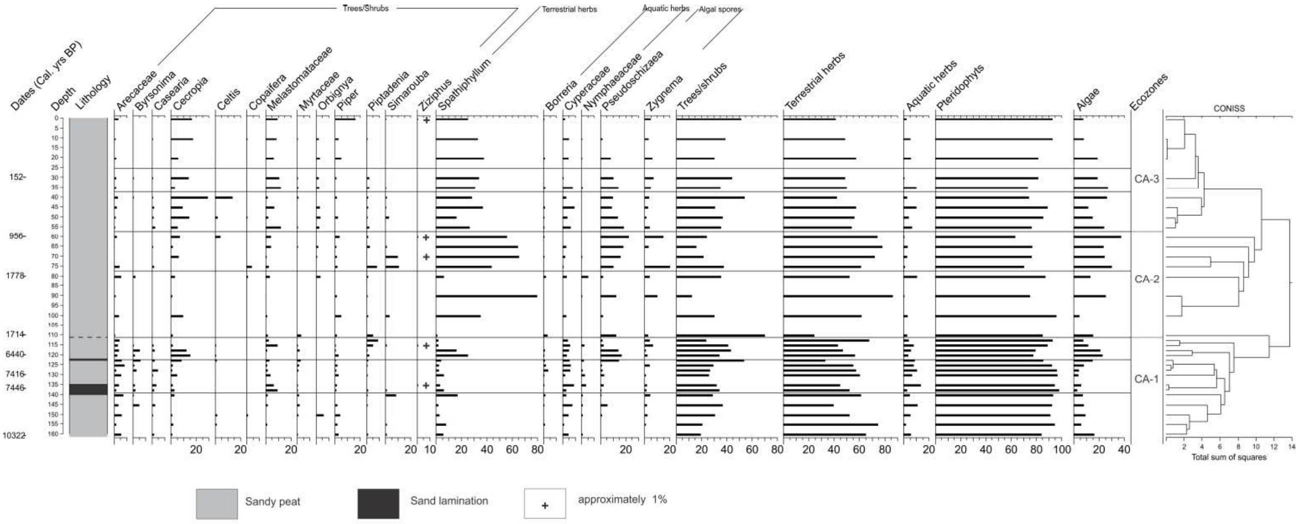

Figure 4. Concentration pollen diagram of the Vale do Catimbau peat sequence of plant categories (x 1000). Dotted line at the lithology column marks a sedimentary hiatus.

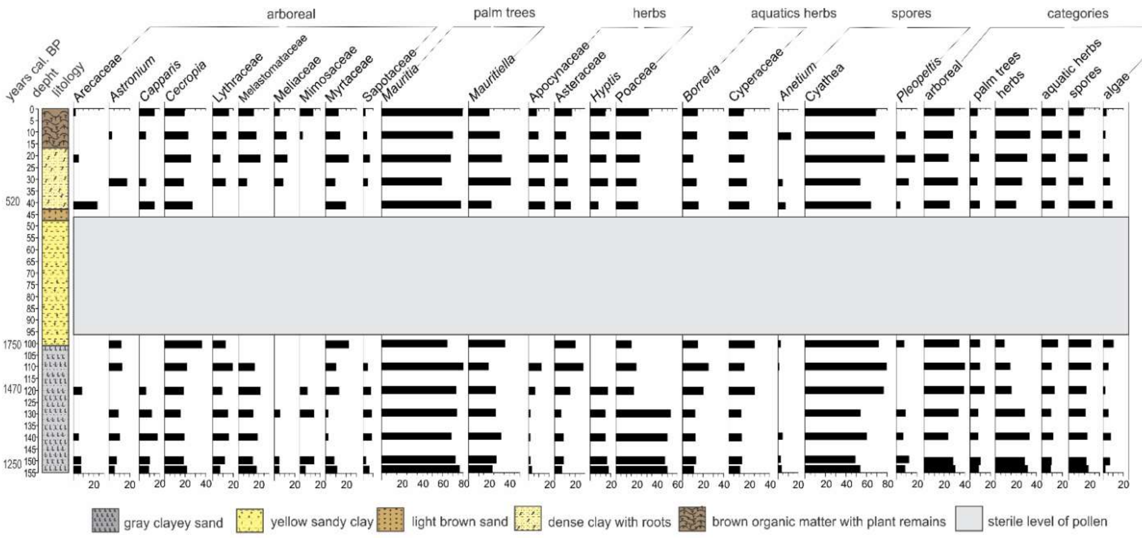

Figure 5: Percentage pollen diagram of the Bom Jesus sediment sequence.

CA-1 (160 – 111 cm; 10,330 cal. yrs BP – *ca.* 6,000 cal. yrs BP (extrapolated age) is characterized by fluctuating arboreal elements, both in percentage and concentration values, at the end of this zone. Maximum value of these components occurs at *ca.* 6,600 cal yrs BP. The most significant taxa, followed by their percent representation from bottom, middle to top of this zone, are represented by Arecaceae (5% - 4%), *Byrsonima* (4.6%- 5.4% to 0%), *Casearia* (1.5% - 4.5% to 1.2%), *Cecropia* (1% - 6% to 1.2%), Melastomataceae (1.5% - 15% to 1.2%), Myrtaceae (0.7%- 2.5% to 2%), *Piptadenia* (0.5% - 1.7% to 0%) and others. *Orbignya* (*Attalea*) palm pollen appeared in the record at an extrapolated age of *ca.* 9,000 cal. yrs BP represented by less than 6% of the total pollen sum, whereas *Ziziphus*, a xerophytic Caatinga indicator, fluctuated in this zone with values under 2%. Concentration values, *i.e.* number of grains per cubic centimeter of sediment (g/cc), of each taxa, follows the same trend observed in the percentage profile. These values shows a clear preponderance of humid adapted taxa in the Early Holocene, gradually decreasing in representation towards the Mid Holocene: Arecaceae (15724 -1010 gr/cc), Myrtaceae (1,429 – 2,511 to 167), *Cecropia* (2,859 – 5,718 to 502), Melastomataceae (2,654 – 10,191 to 606), Moraceae (2,534 – 326 to 502), *Ziziphus* (619 to 167). Pollen grains belonging to *Orbignya* (*Attalea*) are represented by 9,911 g/cc and are possibly a consequence of human influence on the local landscape.

CA-2 (110 – 57 cm; 1,714 – 956 cal. yrs BP). The position of sample 110 cm within the contact between reworked and non-reworked layers, as suggested by radiocarbon age inversion, did not allow it to be included in the Ecozone CA-1. It is noteworthy that the CONISS dendrogram separates this sample depth from all previous samples due to reduced similarity between them. CA-2 is subdivided into two sections: a reworked zone from 110 cm to 80 cm interval with date inversion, and a non-disturbed sequence from 79 to 57 cm (1,778 cal. yrs BP to 956 cal. yrs BP). The latter is characterized by the presence of *Copaifera* (0.75% - 4%), together with Arecaceae (5% to 2%), *Simarouba* (10% to 9%), *Celtis* (4%) in synchrony with a steady increase in *Cecropia* (3% to 7%), Melastomataceae (3% to 4%) and *Piptadenia* (<1% to 7%) while *Ziziphus* continued its local representation until present conditions fluctuating within 1% of the pollen sum. Another change in this zone is marked by high *Spathiphyllum* concentration values, a terrestrial herb found presently at the site in very moist rocky habitats next to the peatbog. In contrast to *Spathiphyllum*, other herbaceous groups such as Poaceae (Gramineae) and Asteraceae (Compositae) are found in smaller percentage and concentration values. *Orbignya* (*Attalea*) palm returns to the Catimbau record at 1,778 cal. yrs BP (80 cm).

Concentration values within this zone, from its beginning to its end, of arboreal taxa is mostly represented by non-*Orbignya* Arecaceae pollen (1,300 – 6,094), Melastomataceae (741 – 13,421), *Cecropia* (743 – 22,713), *Ziziphus* (663 – 1032), *Orbignya* (743 – 1327). Myrtaceae, which was already in decline in the previous zone, was found in only one sample with 261 g/cc. The herbaceous component is well-represented by Asteraceae (2,590 – 11,356) and Poaceae (7433 – 29,940) whereas aquatic associations are defined mainly by *Borreria* (371 – 1,032), Cyperaceae (743 – 2,617) and ferns by *Cyathea* (1,486 – 3,097) and trilete spores (1,672 – 6,694).

CA-3 (56 – 0 cm; 956 cal. yrs BP – Present). The pollen content of zone CA-3 is represented by Arecaceae, fluctuating between 0.7% to 3%, *Casearia* (2.4% to 0.7% and 0.5%), *Celtis* (2% - 13.4% to 0.3%), Melastomataceae (12% to 9%), *Orbignya* (*Attalea*) in steady levels around 2.5 % and *Piptadenia* (2% - 0.2%). Successional elements are represented by *Cecropia* (5% to 29% and 16%) and *Piper* (2% - 4.4% to 16%). The presence of nearby Caatinga vegetation is given by *Ziziphus*, which continued to appear in steady low percentages (around 0.3%) as it did in the previous zone. Concentration values for selected arboreal taxa are given as follows: Arecaceae (1,250 – 10,221), *Cecropia* (4,385 – 51,106), Myrtaceae (1,000 – 350), Melastomataceae (10,215 – 28,805), *Orbignya* (2.088 – 9,911). Herbs are represented by Asteraceae (4,176 – 10,619 to 5,575), Poaceae (13,990 – 9,724 to 31,592) and aquatic plants by Cyperaceae (5,220 – 16,106 to 6,504) and ferns by *Cyathea* (30,486 – 1,351).

Palynological analyses - Bom Jesus

The percentage diagram of the botanical elements of the Bom Jesus (PI) *Mauritia* palm swamp is presented in two intervals, containing age inversions in its lower section (155-100 cm) and modern, undisturbed deposition ranging from 40 cm to 0 cm (Figure 5). Due to the low resolution of this record, coupled with the fact that it represents a reworked sedimentary record, CONISS zonation was not determined. Pollen percentage and concentration values given below for each taxon represent their overall distribution range within each sedimentary interval as follows:

Interval 155 -100 cm (1,250 – 1,750 yrs cal BP) is represented by the predominance of *Mauritia* (70% - 80%) and its associated taxon *Mauritiella* (24% - 36%), followed by other arboreal elements typically found in humid soils such as *Crecropia* (15% - 22%) and Melastomataceae (14 % - 20%). Herbaceous layer indicators are Poaceae (17% - 50%), Asteraceae (6% - 15%), *Hyptis* (14% -18%). Aquatic herbs belong to *Borreria* (10% - 25%) and Cyperaceae (11% - 32%), whereas fern representatives are *Cyathea* (50% -80%), *Pleopeltis* (7% - 12%) and *Anetium* (3% - 4%).

The undisturbed interval containing the upper 40 cm of deposition (520 yrs cal. BP) is characterized by *Mauritia* (60% - 80%), *Mauritiella* (20% - 40%), other Arecaceae (2% - 24%), *Astronium* (3% - 18%), *Cecropia* (20% - 27%), Lythraceae (7% -15%), Melastomataceae (8% - 21%), Meliaceae (6% - 12%), Mimosaceae (2% - 12%), Myrtaceae (9% - 20%) and Sapotaceae (3% - 8%). Among the herbs, the pollen spectra contain Asteraceae (11% -17%), *Hyptis* (8% - 18%) and Poaceae (20% - 30%). The aquatic herb component is given primarily by *Borreria* (10% - 15%) and Cyperaceae (15% - 20%) and ferns by *Cyathea* (65% - 77%), *Pleopeltis* (4% - 18%) and *Anetium* (4% - 12%).

The Catimbau vegetation during the Holocene can be thought of as a local oasis-like ecosystem within a semi-arid domain maintained by tectonics. Underlain Silurian-Devonian sedimentary rocks function as a source of ground water in a deep aquifer (CPRM 1964) which surfaced possibly due to Mesozoic/Cenozoic geological faulting (Gomes 1995; Nascimento 2008). This geological feature might explain the overall abundance and a prolific representation of *Spathiphyllum* along the Catimbau record. This herbaceous taxon, restricted to humid rocks and soils (Croat 1988) within semi-arid regions, remained stable in the Catimbau site despite regional climatic fluctuations during the Holocene.

The occurrence of *Cecropia* in this period is significant. This arboreal taxon, known for its invasive habits and predominance in secondary vegetation, cannot survive in semi-arid climates and can therefore be used as an indicator of successional events under humid climates or in moist soils maintained by edaphic factors (Lorenzi 1998). Humid signals in both sites are given also by the presence of *Borreria* and Cyperaceae, in association with pteridophytic and algal spores. *Borreria*, although commonly found in terrestrial settings, has macrophytic species adapted to soils under prolonged flooding such as *B. eryngioides*, *B. quadrifaria* (Pott and Pott 1994), *B. saponariifolia* and *B. capitata* (Lorenzi 2000). Likewise, Cyperaceae is a large family comprising *ca* 4,500 species found mainly in waterlogged conditions (Souza and Lorenzi 2005).

Unlike the Late Pleistocene/Holocene and Early Holocene humid phase displayed by the Icatu record in the Bahian semi-arid Caatinga (De Oliveira et al 1999), the pollen signal at Catimbau is of very local and not of regional amplitude. This restricted signal is controlled by a peatbog surrounded by a rocky amphitheater, where its abundant pollen signature, maintained by local trees and herbs, masks regional anemophilous sources. However, it is noteworthy the presence of *Ziziphus*, very likely to be *Z. joazeiro*, a well-known evergreen tree species of the xerophyhtic Caatinga of the Sertão region in NE Brazil, thus suggesting nearby semi-arid vegetation around this humid site, throughout the Holocene.

The tendency towards drying of the landscape after the Mid-Holocene shown regionally by the Icatu pollen record (De Oliveira et al. 1999) and by $\delta^{18}O$ ratios in cave speleothems for NE Brazil (Wang et al. 2004, Cruz et al. 2009, Nace et al. 2014, Mendes 2016), is possibly represented in the Catimbau record by the lack of sediment deposition after *ca.* 6,400 and prior to *ca.* 1,800 cal yrs BP. This was likely to be a consequence of lowering water tables under a regional and strong semi-arid climatic phase. However, it is possible that humid conditions, concomitantly with sediment deposition, persisted during the Mid-Holocene in the climatically closed system of Catimbau, shown by the presence of various moist-adapted taxa either side of the hiatus (*ca*. 6,400 yrs to 1714 cal. yrs BP). This sedimentation hiatus is possibly correlated to a phase of generalized drying of that portion of NE Brazil as suggested by the Syntrace Climatic Model (Nace et al. 2014) and by the isotopic data from cave speleothems in State of Rio Grande do Norte (Cruz et al. 2009). In both studies, there is a clear tendency toward arid phases, reaching a peak at *ca.* 4,000 cal. yrs BP. Under this context the surfacing water table (Costa Filho et al. 2005) at the Catimbau site had been lowered.

This Mid-Holocene climatic phase is possibly correlated with the return of a moist phase in the Early Holocene as detected by Novello et al. (2012); Nace et al. (2014); Mendes (2016). It is possible that the same climatic episode had occurred at Bom Jesus, which could explain the inverted ages as well as the high mineral content (sandy sediments) of its sequence, as well as loss of older deposits.

The increase of *Spathiphyllum* sp. and sedimentation rates between 2,000 and 1,500 cal yrs BP at Catimbau and Bom Jesus and the date inversions in both sites are suggestive of sediment transport and reworking under intense high energy precipitation. Such storm conditions have been reported for the same time period by Mendes (2016) and Viana et al. (2014).

After *ca.* 500 cal yrs BP towards modern times the pollen signal at the Catimbau site is characterized by a gradual decrease in taxa adapted to high levels of humidity such as aquatic herbs and algae. A semi-arid climatic pattern is also present in the Icatu record where a decline in the arboreal component is in synchrony with an increase of charred particles indicating higher natural or anthropogenic fire frequencies. Both dry scenarios are in agreement with the climatic phases given by Novello (2012), derived from isotopic data in cave speleothems in southern Bahia. These climatic scenarios are well supported by concentration values in the Catimbau pollen signal. One example of this trend is given by Myrtaceae which declined from 1,000 to 350 g/cc, however other elements expected to behave the same way such as *Cecropia*, Melastomataceae, Arecaceae and *Orbignya* (*Attalea*), followed a contrary pathway, and instead increased in the local landscape. The first two taxa are well known elements found in disturbed vegetation (Prather 2014, Shiels and González 2014, Rodríguez-Zorro et al. 2015), whereas the palm family, and particularly *Orbignya* (*Attalea*), are important taxa in cultural forests (Balée 2013).

The presence of *Orbignya* (*Attalea*) pollen in the Catimbau sediments was already attributed by Nascimento (2009) to human manipulation of the vegetation at around 5,000 yrs BP. Our study shows the occurrence of the *Orbignya* (*Attalea*) pollen type as early as 9,000 cal. yrs BP, decreasing during the Mid-Holocene drying event and returning afterwards. Such distribution therefore might suggest Early Holocene human manipulation at the Catimbau site.

CONCLUSIONS

The pollen analysis carried out at the Catimbau site is indicative of an anomalous island of humidity amidst a semi-arid environment created and maintained by geological features such as the Mesozoic/Cenozoic fault systems that permitted the surfacing of ground water. This in turn has allowed this area to function as a refuge for arboreal and herb elements typically found in moist forest ecosystems such as *Cecropia*, *Cedrela*, *Simarouba*, *Piptadenia*, Melastomataceae, Myrtaceae, *Copaifera* as well as the conspicuous modern *Orbignya* (*Attalea*) palm.

The low geographical amplitude of the pollen signal obtained in this site, contrary to the Icatu sequence which appears to be in synchrony with regional climatic scenarios of NE Brazil, is still useful in determining the presence of nearby Caatinga by the fluctuating presence of *Ziziphus* pollen in all three zones of the Catimbau record.

The Mid-Holocene drying climatic signal, widely recognized by the Icatu pollen record and by $\delta^{18}O$ ratios in cave speleothems in NE Brazil, is likely to be represented by a long term sedimentation hiatus, lasting from 6,000 to 2,000 cal. yrs BP in the Catimbau.

The return of humid conditions both in the Catimbau and in the Bom Jesus site has left a signature in the sedimentation pattern of both locations, marked by higher sedimentation rates and radiocarbon ages inversions.

After *ca.* 500 cal yrs BP towards modern times the pollen signal at the Catimbau site demonstrates a gradual decrease in concentration values of taxa adapted to high levels of humidity such as aquatic herbs and algae. *Spatiphyllum*, for example, decreases from *ca.* 184,000 g/cc at 950 cal. yrs BP to *ca.* 78,000 g/cc in the modern surface of the deposit.

By and large, the Holocene records provided by these two new pollen diagrams, although representative of the local vegetation, do show the presence of *Ziziphus*, an important Caatinga indicator, that appeared to have tolerated a great deal of climatic change since the humid phases of the Early Holocene to the intensification of semi-arid climates since the Mid Holocene. However, such a pattern is very likely to be explained by its tolerance to wide precipitation ranges, varying from 315 mm to 1700 mm/year^{-1} (Gomes and Fernandes 1985), which is not expected to be found in most elements of the Caatinga flora.

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CHAPTER 9

Final Considerations and conclusions

This document, presented to the Institute of Geosciences of the University of São Paulo (IGc/USP) as partial fulfillment for the Livre Docência Degree in Quaternary Palynology and Paleobotany, contains the most important research results developed by the candidate after 2013, year of admittance in the teaching and research staff of the Department of Sedimentary and Environmental Geology.

In synthesis, the most significant contributions of these analyses to the understanding of environmental changes within important Brazilian Ecosystems can be summarized in three lines of knowledge: a). generalized plant migration under intensified phases of cooling and high humidity levels within different periods of the last glacial cycles; b). appearance of novel plant communities with no modern analogs, as a consequence of generalized plant migrations, which are likely to have brought significant changes in Late Pleistocene megafaunal populations and c). undisputable evidence for maintenance of forested e/or humid environments throughout the last glacial cycle to western Amazonia, central and southeastern Brazil.

During times of climatic change, notably those related to oscilations in summer insolation and Heinrich events, conducive to more intensified incursion of polar air masses, many tropical plant taxa were able to expand their realized niche. *Podocarpus* and *Drimys*, for instance, were able to migrate from south/southeastern Brazil to Amazonia and northeastern Brazil (Chapters 2, 3 and 4). The revision of pollen records from sediments dated to the LGM and Heinrich events (Chapter 2), available for Brazil, allows the inference of two major plant migration routes, which in turn provide strong evidence that some of the modern disjunct plant distributions found in Southeastern Brazil had been established or maybe reestablished to a certain degree in the Late Pleistocene.

The migrational movement of plant species here reported is the origin of a widespread phenomenon in the neotropics: the arisal of novel plant communities (Chapter 2 and 7). These new associations of plant species now called non-analog communities was one of the most significant discoveries of Tropical Quaternary Palynology. For one side, it revealed the genetic plasticity of many taxa, able to tolerate unfavourable climatic conditions and on the other side it is driving primarily by temperature as demonstrated in the late 1970´s and 1980´s for North America. The entire palynological data set from many investigators, concerning the climatic and vegetational changes during the Late Pleistocene/Holocene of Brazil, also support the Individualistic Concept of Gleason, in detriment of the Closed Community hypothesis of Clements. This is knowledge is presently considered one of the most important ecological discoveries within the field of Theoretical Ecology. The available data demonstrate that in the neotropics plant taxa were also able to migrate to very distant areas, during times of environmental change, as plant species of North America. With this process in motion, very substantial modifications took place on local landscapes and in some cases rainforest substituted caatinga and cerrado, shifing the boundaries of these ecosystems. As a result many modern Brazilian plant biogeographic patterns have now a considerable imprint of these changes, some of which can be recognized as relictual populations or even isolated species living in microrefuges, sometimes under unfavourable environmental conditions, a possible evidence for their wide genetic plasticity. Some of these isolated microrefugia appear fragile and might eventually become extinct due to global climatic change and/or due to increased habitat loss carried out by human acitivities.

Knowldege on novel plant communities has been shown to impact other important topics related do the Late Quaternary of South America. This is demonstrated on Chapter 7, which provides an important line of evidence correlating no-analog plant communities to direct impact on animal populations, notably the extinction of the Pleistocene megafauna in Brazil, during the Pleistocene/Holocene transition. It´s important to remember that, in this case, the trend towards extinction started in the last three milenia of the Pleistocene and it gained momentum with the increase of predation pressure by the early humans in Southeastern Brazil. Therefore, it is advocated here that the Pleistocene megafauna extinction in this particular section of South America was a climatically driven phenomenon that gained speed by human predation pressure.

The last line of evidence emanating from the present contributionsis concerns the refutal of the Pleistocene Refuge Hypothesis, although it´s important to state clearly that this speciation model is likely to be the source of some animal biogeographical patterns prior to the Late Pleistocene, as shown by molecular data in some animal groups. The 81 pollen studies available for Brazil do not show one single grain of Cactaceae, *Zizyphus* and other bona-fide indicator taxa in the LGM of any Brazilian ecosystem. Therefore, it is highly recommended that the Ab´Saber´s interpretation of the Brazilian landscape of the Late Pleistocene of Brazil can no longer be used. On the contrary, the paradigm presently available is that of a humid and very cold landscapes in the southern hemisphere during times of ice expansion in the final phases of the last glaciation. It is hypothesized here that in Southeastern Brazil, with grasslands shifted to lower elevations of the last glacial cycle due to temperature decline, in consortium with high humidity levels, and not to aridity. The decrease in grassland cover during the Holocene of Curucutu (Chapter 4) is here interpreted as consequence of upward plant migration as consequence of Holocene warming, thus providing support for the hypothesis that the present tree line at ca. 2000 m elevation in the Brazilian Highlands had been established sometime during the Pleistocene/Holocene transition. One issue that has not been addressed by Quaternary palynologists is the role of reducing CO_2 concentrations in the global atmosphere during ice ages. How much of the change we see in vegetation patterns during, especially in Southeastern Brazil, is actually played by this parameter, remais unanswered.