

*Impact of mid-to-late Holocene
precipitation changes on vegetation
across lowland tropical South America: a
palaeo-data synthesis*

Article

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1 **Impact of mid-to-late Holocene precipitation changes on vegetation**
2 **across lowland tropical South America: a paleo-data synthesis**

3

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12 **ABSTRACT**

13 A multi-proxy paleo-data synthesis of 110 sites is presented, exploring the impact of mid-to-
14 late Holocene precipitation changes upon vegetation across Southern Hemisphere tropical
15 South America. We show that the most significant vegetation changes occurred in south-
16 west Amazonia and south-east Brazil, regions reliant on precipitation derived from the South
17 American summer monsoon (SASM). A drier mid Holocene in these regions, linked to a
18 weaker SASM, favoured more open vegetation (savannah/grasslands) than present, while
19 increased late-Holocene precipitation drove expansion of humid forests (e.g. evergreen
20 tropical forest in south-west Amazonia, *Araucaria* forests in south-east Brazil). The tropical
21 forests of central, western and eastern Amazonia remained largely intact throughout this
22 6000-year period. North-eastern Brazil's climate is 'antiphased' with the rest of tropical South
23 America, but a lack of paleo data limits our understanding of how vegetation responded to a
24 wetter(drier) mid(late) Holocene. From this paleo-data perspective, we conclude that
25 ecotonal forests already close to their climatic thresholds are most vulnerable to predicted
26 future drought, but the forest biome in the core of Amazonia is likely to be more resilient. Of
27 greater concern is widespread deforestation and uncontrolled anthropogenic burning, which
28 will decrease ecosystem resilience, making them more vulnerable than they might be
29 without current anthropogenic pressures.

30

31 **KEYWORDS**

32 Amazonia; tropical South America; Holocene; climate change; paleoecology; data synthesis

33 INTRODUCTION

34 The response of the vegetation across tropical South America to long-term climate change is
35 of great concern, given the importance of the ecosystem services this region provides. Of
36 particular concern is how vegetation will respond to a drier climate, given the future
37 projections of more intense dry seasons and increased frequency of severe drought events
38 (Joetzjer et al., 2013; Boisier et al., 2015; Duffy et al., 2015). The extensive work carried out
39 by the RAINFOR ecological monitoring project (Malhi et al., 2002) has demonstrated the
40 short-term vulnerability of Amazonian forests to severe drought events (Phillips et al., 2009;
41 Doughty et al., 2015; Feldpausch et al., 2016). However, whilst the effects of these short-
42 term severe drought events are relatively well understood (e.g. Rowland et al., 2015),
43 considerable uncertainty exists as to how long-term climate change will affect the vegetation
44 of tropical South America. Results of future model simulations using process-based dynamic
45 global vegetation models (DGVMs) range from catastrophic large-scale Amazonian forest
46 die-back as a result of positive feedbacks between the biosphere and atmosphere (Cox et
47 al., 2000; 2004), to other studies suggesting that the forests will be resilient to climate
48 change (Cowling and Shin, 2006; Huntingford et al., 2013). One problem in predicting future
49 vegetation dynamics is the lack of direct long-term observational data of vegetation
50 responses to long-term climate change in the past. However, the use of proxy-based
51 vegetation reconstructions allows us to extend our observational period back millennia
52 through times of significant, long-term climate change. The role of paleoecology in
53 increasing our understanding of long-term vegetation dynamics is well established within the
54 paleo-data community, and is playing an increasingly important role in helping to understand
55 mechanisms and uncertainties within model simulations through initiatives such as PMIP
56 (Paleoclimate Modelling Intercomparison Project) (Joussaume and Taylor, 1995; Braconnot
57 et al., 2011).

58

59 Several mid-late Holocene paleoecological syntheses have been undertaken in the past, but
60 these are now relatively outdated (e.g. Mayle and Power, 2008; Marchant et al., 2009) due

61 to the publication of both new paleoecological and paleoclimate records over the past
62 decade. Furthermore, more recent syntheses (e.g. Prado et al., 2013b; Flantua et al., 2016)
63 have used paleoecological data (predominantly pollen) to reconstruct past climate, which
64 precludes examination of vegetation-climate relationships. We therefore present an updated
65 multi-proxy synthesis of published paleoecological records from across lowland tropical
66 South America from the mid Holocene (ca. 6000 years ago, 6 ka) to the present. This time
67 period is important both paleoecologically and paleoclimatologically, as there is widespread
68 evidence that millennial-scale changes in insolation (driven by the precessional cycle of
69 Earth's orbit) caused long-term precipitation changes, and associated vegetation changes,
70 across the region (Mayle and Power, 2008; Prado et al., 2013a; Baker and Fritz, 2015).
71 Therefore, we will consider the paleoecological records alongside key paleoclimate records
72 from across the study region in order to assess any vegetation changes in the context of
73 long-term climate change.

74

75 This synthesis will provide new insights into the spatio-temporal dynamics of biome-scale
76 vegetation changes on a sub-continental scale over the past 6000 years, in the context of
77 climate change inferred from independent paleoclimate data. Although there is increasing
78 evidence that pre-Columbian (pre-AD1492) peoples managed the floristic composition of
79 their forest resources (especially by promoting palms, e.g. Watling et al., 2017), there is little
80 evidence, to date, that they practiced large-scale deforestation. We therefore expect natural
81 drivers (i.e. climate change) to be the most likely explanation for any biome-scale vegetation
82 shifts over the broad, regional scales that we consider in this synthesis – an assumption
83 borne out by a recent study of local-scale human land use nested within regional-scale,
84 climate-driven, forest-savannah biome turnover (Carson et al., 2014). However, if the
85 vegetation history of a given site(s) is inconsistent with independent paleoclimate data from
86 the area, we will consider whether human land use can reconcile this apparent vegetation-
87 climate mismatch.

88

89 **Modern environmental setting**

90 *Modern climatic setting*

91 Figure 1 shows long-term mean precipitation over South America for austral winter (June,
92 July, August, Fig. 1a) and austral summer (December, January, February, Fig. 1b), along
93 with mean wind speed and direction at 850 mb. The relatively narrow, longitudinally
94 orientated belt of precipitation over the tropical oceans marks the location of the Intertropical
95 Convergence Zone (ITCZ). The ITCZ refers to a band of low pressure and convergence of
96 the moist trade winds over the equatorial oceans and is associated with rising air and
97 intense convective precipitation. The rising air at the ITCZ diverges polewards when it nears
98 the tropopause, and descends when over the subtropics, causing semi-permanent high
99 pressure cells over the subtropical oceans such as the South Atlantic subtropical high
100 (SASH – Fig. 1); this loop of air movement is known as the Hadley cell circulation (Garreaud
101 et al., 2009). The different thermal properties of the continental land mass of South America
102 and the surrounding oceans gives rise to a distinct seasonal cycle of precipitation over most
103 of the tropical South American continent. During austral winter, when the thermal equator
104 and ITCZ are located further north, maximum precipitation over the continent is located in
105 northern South America, whereas central South America experiences its dry season (Fig.
106 1a). Southern Brazil maintains an important source of moisture from both moist winds fed
107 into the region by the circulation of the SASH and extra-tropical frontal systems (Cruz et al.,
108 2006; Garreaud et al., 2009). During austral spring/summer the thermal equator moves
109 south and heats the central South American land mass up relative to the surrounding
110 oceans. This continental heating causes areas of intense convection to form over central
111 Brazil and southern Amazonia, which are fed with moist easterly trade winds blowing in from
112 the Atlantic Ocean, helped by an intensified SASH. This marks the onset of a system
113 commonly referred to as the South American Summer Monsoon (SASM) (Fig. 1b - Zhou and
114 Lau, 1998; Raia and Cavalcanti, 2008; Silva and Kousky, 2012). As the moist easterly trade
115 winds reach the Andean mountain range, they are diverted southward and are intensified by
116 an area of deep low pressure that forms over the Gran Chaco region (the 'Chaco Low'). This

117 flow creates a feature known as the South American Low Level Jet (SALLJ), associated with
118 very strong low-level winds that are channelled southwards by the eastern Andes and the
119 Brazilian planalto highlands (Marengo et al., 2002). The SALLJ helps to transport moisture
120 from Amazonia into subtropical south-east Brazil where the South Atlantic Convergence
121 Zone (SACZ) is intensified (Carvalho et al., 2004).

122

123 In contrast to the central and southern areas of tropical South America, the north-east of
124 Brazil is conspicuously dry throughout most of the year (Garreaud et al., 2009). The intense
125 updrafts in the central part of the continent (in particular the Chaco Low) during the mature
126 phase of the SASM requires compensating subsidence in surrounding regions. This
127 subsidence manifests as an upper tropospheric low pressure feature called the 'Nordeste
128 Low', which suppresses rainfall over the region of north-east Brazil (Chen et al., 1999; Cruz
129 et al., 2009). This east-west difference in precipitation caused by zonal overturning
130 circulations has been referred to as the east-west South American precipitation dipole
131 (Cheng et al., 2013). Interannual variability in precipitation over tropical South America is
132 linked to the El Niño Southern Oscillation (ENSO); during El Niño episodes, precipitation
133 rates are below average across eastern Amazonia and north-eastern Brazil (Garreaud et al.,
134 2009).

135

136 *Modern vegetation setting*

137 The lowlands of tropical South America support a wide variety of ecoregions, ranging from
138 humid rainforests to xeric scrublands (Fig. 2a). The ecoregions described here refer to the
139 *potential* ecoregions, as the *actual* vegetation cover has been highly affected by modern
140 deforestation, agriculture and industrialisation. The Amazon humid evergreen tropical forest
141 (HETF) is the largest biome of tropical South America, covering most of northern and
142 western Brazil and extending into neighbouring countries to the west and north where
143 annual precipitation is high (>1600 mm). The southern and eastern ecotonal margins of the
144 Amazon HETF exist in a much more seasonal climate with longer dry seasons. Small

145 patches of savannah can occur within the Amazon HETF where edaphic conditions are
146 favourable (Adeney et al., 2016). Along the foothills of the Andes lies a band of Yungas
147 forest, a transitional area ranging from moist evergreen lowland forest to montane forests.
148 The Atlantic forest biome, supporting a mix of lowland and montane evergreen forests,
149 exists on the east coast of Brazil where coastal and orographic rainfall maintain a moist
150 climate (Fig. 2c). The *Araucaria* moist forest biome (characterised by the high abundance of
151 the evergreen tree *Araucaria angustifolia*) exists on the highlands of southern Brazil where
152 annual precipitation is high (~2000 mm) and there is a short dry season (< 2 months)
153 (Hueck, 1953; Behling and Pillar, 2007).

154

155 In between the Amazon and Atlantic rainforests exists the 'dry diagonal' (Prado and Gibbs,
156 1993). This is a large area, characterised by highly seasonal rainfall, that contains a mixture
157 of deciduous and semi-deciduous trees, shrubland and savannah. Most of this area is
158 covered by the Cerrado savannah biome. Due to the variety of climatic, edaphic and
159 topographic features in the region, the savannah types range from open grassland to more
160 dense shrub and savannah tree cover (Silva and Bates, 2002). Gallery forests can occur
161 along the streams that flow through the Cerrado, as well as small patches of closed canopy
162 deciduous and semi-deciduous trees where edaphic conditions are favourable (Silva and
163 Bates, 2002; Werneck, 2011). Larger areas of semi-deciduous tropical dry forests (SDF)
164 exhibit a fragmentary distribution. 'Nuclei' of SDF exist across: the Chiquitano region of
165 eastern lowland Bolivia; across southern Brazil along the Paraná and Paraguay rivers and
166 into the Misiones province of northern Argentina; and inland areas of the Atlantic forest
167 biome. SDF exist in highly seasonal climates, with annual precipitation <1600 mm and a dry
168 season length of ~5 – 6 months (Gentry, 1995; Werneck, 2011). These SDF areas exist
169 under similar climatic conditions to the Cerrado savannah, but are restricted to soils with
170 higher nutrient content and high pH (Pennington et al., 2000; Werneck, 2011). The Caatinga
171 region of north-eastern Brazil supports a complex mosaic of xerophytic vegetation types that
172 range from dense SDF cover, more open tree cover with a shrubby sub-canopy, to open

173 thorn scrubland and savannah. The semi-arid climate is the main control upon this Caatinga
174 vegetation; precipitation rates are low and erratic meaning that long periods of drought are
175 common (Sampaio, 1995). However, small 'islands' of humid evergreen rainforest and semi-
176 deciduous tropical dry forests do exist on isolated plateaus inland and near the coast where
177 orographic and coastal rainfall can maintain a humid microclimate (Sampaio, 1995; Montade
178 et al., 2014).

179 **METHODS**

180 A database of 110 paleoecological sites from 87 previously published papers was created
181 through literature searches and interrogation of repositories such as the Latin American
182 Pollen Database (LAPD - Flantua et al., 2015) and Neotoma (<http://www.neotomadb.org>)
183 (Table 1). This synthesis considers sites from the Southern Hemisphere tropical lowlands,
184 extending into the subtropics of south-east Brazil (a latitudinal range extending from the
185 equator to 30°S)(Fig. 2). We do not include coastal mangrove sites, as vegetation changes
186 at these sites are predominantly driven by sea level change (e.g. Behling et al., 2001b;
187 Guimarães et al., 2012; 2013b; Lorente et al., 2014). For each paleoecological site, we
188 assign a vegetation classification at 500-year time slices from the mid Holocene (6 ka) to the
189 present, based on a critical evaluation of the authors' interpretations of the proxy data. The
190 broad scale vegetation classifications we use are outlined in Table 2. A 'mosaic'
191 classification (a combination of any two vegetation types) was used when interpretation
192 suggests that the vegetation cover at a site was most likely a mixture of vegetation types.
193 Ideally, a site will cover the whole period from 6 ka to the present, although there are a
194 number of sites that cover a shorter period. It does not seem appropriate to ignore sites that
195 do not quite cover the whole period as they may still provide valuable information about
196 vegetation trends in a particular area. Therefore, the sites included in our synthesis must
197 have a vegetation reconstruction spanning from earlier than 4 ka, up to at least 2 ka; this
198 ensures that the sites cover a period where there is strong evidence that the region
199 underwent long-term climate change.

200

201 Imposing strict criteria on the chronological quality of each site is problematic in this
202 research area. Sedimentation rates are highly variable between samples; sites with low
203 sedimentation rates are particularly problematic as a relatively short core could encompass
204 many millennia. Sub-sampling resolution also varies between sites depending on the length
205 of the record and the specific research questions of the authors. The paucity of sites across
206 tropical South America means that rejecting sites based on low chronological resolution

207 would result in only a handful of sites being considered. Therefore, we have been relatively
208 flexible in our consideration of sites with lower chronological resolution; this means that this
209 synthesis can only provide an overview of the broad scale vegetation trends in the region
210 over the last 6000 years, rather than exact timings of any changes. Where possible,
211 calibrated radiocarbon dates and age-depth models that are presented in the original
212 paper(s) of each site are used to inform the timings of any changes at that site. If a site
213 records key vegetation changes through its record but does not present calibrated dates or
214 an age-depth model, we use the Bacon age-depth model v2.2 in R (Blaauw and Christen,
215 2011) to produce an independent age-depth model for that site using the raw chronological
216 data from the paper. This is the case with 26 of the sites, indicated in Table 1. The IntCal13
217 calibration curve (Reimer et al., 2013) was chosen over SHCal13 (Hogg et al., 2013), given
218 the hydrological links of the study area with the northern hemisphere (through the SASM and
219 ITCZ).

220

221 We acknowledge that other more quantitative methods of classifying vegetation from
222 paleoecological data are available, such as Biomisation (Prentice et al., 1996; Prentice and
223 Webb, 1998) and the REVEALS/LOVE Landscape Reconstruction Algorithm (Sugita, 2007a;
224 2007b). However, these methods are based predominantly on pollen data from lakes,
225 require access to the raw data of each site, and, in the case of REVEALS, require a high
226 density of sites of multiple sizes in a given area. Furthermore, the REVEALS model has yet
227 to be proven in a Neotropical setting where important assumptions about anemophily are
228 violated by most taxa. The paucity of pollen sites that extend back to the mid-Holocene in
229 our research area limits the usefulness of these quantitative methods (which focus solely on
230 pollen data) in producing a thorough synthesis. For example, in the most recent application
231 of the Biomisation method across Latin America (Marchant et al., 2009), there are only
232 around 24 pollen records in our research area that date back to the mid Holocene. Our
233 method allows us to consider other vegetation proxies in addition to pollen (e.g. phytoliths,
234 stable carbon isotopes) and other paleoecological archives in addition to lakes (e.g. soil

235 pits), thus increasing the number of sites we can include in our synthesis by utilising the full
236 suite of paleovegetation data available. In addition, our method allows us to take advantage
237 of the in-depth knowledge that the author(s) will have about their site (e.g. pollen
238 taphonomy, catchment), which is lost when using a standardised objective method.

239

240 **Proxy types**

241 This synthesis includes a variety of paleoecological proxy types, all of which have strengths
242 and limitations that must be considered. The two most common proxy types in this synthesis
243 are fossil pollen and stable carbon isotopes ($\delta^{13}\text{C}$). Fossil pollen analysis is the most widely
244 used paleovegetation proxy as it gives a direct indication of what vegetation was growing in
245 an area at a given time. However, care must be taken in interpreting a fossil pollen record as
246 pollen loading into a basin does not necessarily reflect the true vegetation assemblage in the
247 catchment area due to previously mentioned taxonomic-differences in pollen productivities
248 and dispersal characteristics. Additionally, the taxonomic resolution of pollen is highly
249 variable; very few are identifiable to species level, some are identifiable to genus level, and
250 many are only identifiable to family level. These issues mean that reliable interpretation of
251 fossil pollen records is dependent upon modern 'pollen rain' studies whereby pollen traps
252 are left in an area for a set time, after which the pollen assemblages are compared with
253 floristic inventories to determine pollen-vegetation relationships (e.g. Behling et al., 1997;
254 Bush and Rivera, 2001; Gosling et al., 2005; 2009; Jeske-Pieruschka et al., 2010;
255 Guimarães et al., 2014). Stable carbon isotope fractionation ($\delta^{13}\text{C}$) utilises the fact that C_3
256 vegetation (woody plants) and C_4 vegetation (savannah grasses and sedges) have distinct
257 $\delta^{13}\text{C}$ carbon isotope signatures (Boutton, 1996; Pessenda, 2004). Whilst this differentiation
258 between C_3 and C_4 vegetation is quite broad, it does reveal whether the landscape was
259 closed-canopy forest or open savannah, especially if bolstered by knowledge of the modern
260 isotopic-vegetation relationships in a given area. We also include a small number of sites
261 with phytolith (plant silica bodies)-based vegetation reconstructions (Piperno, 2006). Unlike

262 pollen, phytoliths preserve well in oxidised environments (e.g. soils) and are particularly
263 useful in increasing the taxonomic resolution of grass. Although few phytolith-based
264 paleoecological studies have yet been undertaken, recent studies have shown the
265 effectiveness of phytoliths in distinguishing between modern tropical ecosystems in the
266 Amazon (Dickau et al., 2013; Watling et al., 2016).

267

268 Several other proxies can provide important complementary information for pollen, $\delta^{13}\text{C}$,
269 and/or phytolith studies. Charcoal analysis is commonly used to reconstruct past fire activity,
270 which can be an indication of past changes in climate and vegetation characteristics (Power
271 et al., 2008). Isotopic analysis of nitrogen ($\delta^{15}\text{N}$) and chemical analyses of carbon/nitrogen
272 (C/N) ratios can indicate whether the organic matter in a sediment record originates from an
273 aquatic source (elevated levels of ^{15}N , low C/N ratios) or a terrestrial source (low levels of
274 ^{15}N , high C/N ratios) (Meyers, 1994; Horák et al., 2011). Measurements of chemical element
275 concentrations, using methods such as X-ray fluorescence (XRF), can reveal catchment
276 erosion which in turn may be linked to local/regional environmental change.

277

278 **Archive types and spatial scale of reconstructions**

279 When drawing paleoecological inferences from vegetation proxy data, it is important to
280 consider the spatial scale that the latter represents. This spatial scale is influenced by both
281 the type of proxy, as well as the size and type of deposit that the proxy came from. It is
282 widely accepted in the field of palynology that the spatial scale represented by pollen
283 assemblages in lake sediments is related to the size of that lake; small lakes (and bogs)
284 represent local-scale vegetation, whereas large lakes represent regional-scale vegetation
285 (Davis, 2000). This relationship has been shown through practical experiments that correlate
286 pollen signals from lake surface-sediment samples to vegetation inventories at increasing
287 distances from the lake, as well as being formerly quantified in a pollen deposition/dispersal
288 model (Prentice, 1985; Sugita, 1993; 1994). Whilst most of this research has been done for

289 mid to high latitudes, the pattern is expected to be valid for the tropics. Soil pits are a
290 common archive type that usually use $\delta^{13}\text{C}$ isotope as a paleoecological proxy (and in some
291 cases phytoliths). These records essentially represent a 'point' scale (i.e. a record of the
292 vegetation that grew directly in that soil) and as such transects/networks of soil pits are often
293 taken to help represent a larger spatial area. For this synthesis, we categorise each site into
294 one of 4 archive types: lakes, peat bogs, terrestrial (e.g. unspecified sediment hollows or
295 swamps) and soil pits. In an attempt to visually represent the spatial scale that each record
296 represents, we display different sized circles in Figure 4 based on the rules defined in Table
297 3. In some cases, the display of soil profiles that are very close together have been
298 combined; this has been indicated in Table 1 whenever this is the case.

299

300 **Paleoclimate records**

301 To assess the relationship between vegetation change and long-term climate change, we
302 have selected 8 key paleoclimate records from across the region (Figs. 2 and 3). Five of
303 these sites (El Condor, Tigre Perdido, Huaguapo, Botuvera Cave and Rio Grande do Norte)
304 have precipitation reconstructions based on speleothem stable oxygen isotope ($\delta^{18}\text{O}$)
305 records, while precipitation records of the other sites are based upon lake-level
306 reconstructions (Lake Titicaca and Laguna La Gaiba) or $\delta^{18}\text{O}$ analyses of lake calcite
307 deposits (Lake Junin). As with the paleoecological records, we rely upon the authors' expert
308 knowledge of these sites to inform our interpretations. This is particularly important for the
309 speleothem records, as changes in isotopic composition can be influenced by a number of
310 factors, including changes in moisture source, temperature, and/or rainfall amount (Lachniet,
311 2009).

312 **SYNTHESIS AND DISCUSSION**

313 Figure 4 shows the paleovegetation reconstruction for each site at 500-year time slices from
314 6 ka to present. Figure S1 in the supplementary information provides a summary of the
315 changes at each site for each area defined in Figure 2. Our discussion of these
316 paleovegetation records is divided into the areas defined in Figure 2, within the context of
317 precipitation changes inferred from key paleoclimate records from across the study area
318 (Figure 3). The main mechanism for these millennial scale precipitation changes has been
319 attributed to changes in austral summer insolation driven by the precessional cycle of
320 Earth's orbit. During the mid Holocene, lower austral summer insolation levels caused a
321 northward shift in the mean position of the ITCZ (Haug et al., 2001) and a decrease in
322 intensity of the SASM (Cruz et al., 2005; Wang et al., 2007; Vuille et al., 2012). In addition,
323 lower austral summer insolation during the mid-Holocene dampened ENSO activity and
324 reduced associated interannual variability of rainfall associated with El Niño/La Niña events
325 (Moy et al., 2002; Koutavas and Joanides, 2012). Individual interpretations of the
326 paleoclimate records will be drawn upon in the sections below.

327

328 **Central and western lowland Amazonia (CW)**

329 Speleothem records from the western Peruvian Amazon show slightly elevated $\delta^{18}\text{O}$ values
330 at the mid-Holocene (Fig. 3 a-b). This finding suggests that convective precipitation may
331 have been slightly reduced at this time, consistent with a weakened SASM linked to lower
332 summer insolation (Haug et al., 2001; van Breukelen et al., 2008). However, an overall
333 reduction in total rainfall amount across western lowland Amazonia was probably relatively
334 small due to mechanisms such as the important source of moisture from transpiration
335 processes across central and eastern Amazonia (Eltahir and Bras, 1994; Spracklen et al.,
336 2012; Cheng et al., 2013). The paleovegetation records support the idea that moisture levels
337 have been relatively stable in this region from 6 ka to present. The sites from across central
338 and western lowland Amazonia show that the HETF biome stayed largely intact in this
339 region throughout the mid-to-late Holocene. Evidence of this biome stability comes from

340 consistent HETF pollen signals from large lake sites (reflecting regional scale vegetation
341 signals - e.g. Behling et al., 2001c; Horbe et al., 2011) and small sites (reflecting local
342 vegetation signals - e.g. Liu and Colinvaux, 1988; Behling et al., 1999; Bush et al., 2004b).
343 Even if moisture levels were slightly lower during the mid-Holocene, it is clear this was not
344 enough to cause biome turnover. This is currently one of the wettest parts of tropical South
345 America (annual precipitation >3000 mm Fig. 2c) with little or no dry season, therefore
346 precipitation levels would have to reduce drastically to cause widespread forest die-back or
347 biome turnover.

348

349 **South-Western Amazonia (SW)**

350 The area of south-western Amazonia contains the modern ecotonal boundary between the
351 southern Amazonian HETF, the Chiquitano SDF and the Cerrado savannah (Fig. 2a).
352 Precipitation levels in this region are highly dependent on the strength of the SASM,
353 especially with regards to the development of the Chaco low and the SALLJ that help to
354 divert precipitation from central Amazonia along the Andes and southwards into eastern
355 Bolivia. As a result, this area has a modern precipitation regime that is much more seasonal
356 than that of the central Amazon basin, with longer dry seasons and lower total annual
357 precipitation of ~1500-1600 mm (Fig. 2c). Therefore, the HETF that grows here is much
358 closer to its climatic limit and is more likely to be sensitive to even small changes in
359 precipitation. During the mid Holocene, paleoclimate records from the high Andes suggest
360 this region was drier than present (Fig. 3 c-e). Although these records come from the high
361 Andes, they can be considered as representative of lowland south-west Amazonia, at least
362 in regards to the direction of precipitation changes, as they too are dependent on the
363 components of the SASM to divert moisture from central Amazonia. Lake levels at Lake
364 Titicaca on the Bolivian altiplano were ~100m lower than modern at 6 ka (Baker et al., 2001),
365 and enriched $\delta^{18}\text{O}$ values from the Huaguapo speleothem and Lake Junin suggest reduced
366 convective activity and lower moisture levels (Seltzer et al., 2000; Kanner et al., 2013).
367 These Andean records show that modern levels of precipitation were not reached until ca. 4

368 – 3 ka. A similar pattern of increasing precipitation through the mid-to-late Holocene is found
369 in the paleoclimate record from the lowland site of Laguna La Gaiba (LLG, Fig. 3f), although
370 this record suggests that modern moisture levels perhaps were not reached here until ca.
371 2.5 – 2 ka. Overall, the signals from these sites are consistent with the explanation of a
372 gradual increase in SASM strength in response to increased insolation through the mid-to-
373 late Holocene (Burbridge et al., 2004; Kanner et al., 2013; Baker and Fritz, 2015). The time
374 delay between the Andean records and LLG reaching modern levels could suggest a lag
375 between precipitation increasing in the Andean highlands and in the south-west Amazonian
376 lowlands.

377

378 Two key lake sites, Laguna Bella Vista (LBV, id = 6) and Laguna Chaplin (LCH, id = 7),
379 provide strong evidence of vegetation shifts through the mid-to-late Holocene in response to
380 the changes in precipitation (Mayle et al., 2000; Burbridge et al., 2004). These are very large
381 lakes (> 3 km diameter) and so their pollen assemblages are assumed to represent regional
382 scale vegetation signals. They currently lie in HETF, 130 km (LBV) and 30 km (LCH) north of
383 the modern HETF/SDF/savannah ecotone. However, during much of the mid-to-late
384 Holocene (ca. 6 ka to 2 ka) a mosaic of SDF/savannah vegetation dominates the catchment
385 of these lakes, providing evidence that the HETF/SDF/savannah ecotone was at least 130
386 km further north than at present. This SDF/savannah mosaic is persistent in the area until
387 ca. 2 ka, when HETF expanded southward into the catchment of LBV; it is not until ca. 1 ka
388 when HETF reached the catchment of LCH. Another large lake record (Laguna Oricore, id =
389 5), located 200 km to the west of LBV, shows a consistent pattern of a SDF/SAV dominated
390 landscape changing to HETF at ca. 2 ka (Carson et al., 2014). The two small sites near to
391 Oricore record a later expansion of HETF at ca. 0.5 ka, but this delay has been attributed to
392 pre-Columbian human land management by the authors (Carson et al., 2014; 2016). To the
393 east of these records on the eastern edge of the Chiquitano SDF, the regional pollen record
394 from Laguna La Gaiba (id = 8) suggests that there was no significant contraction of the SDF
395 biome associated with mid-Holocene drought (Whitney et al., 2011). Around 600 km north of

396 LBV lies a series of natural savannah 'islands' located within the dense Amazon rainforest.
397 Evidence that these savannah islands expanded by ~60 km at the expense of HETF during
398 the mid Holocene comes from $\delta^{13}\text{C}$ data from a 200 km transect of soil pits between Porto
399 Velho and Humaita (de Freitas et al., 2001; Pessenda et al., 2001), spanning the savannah
400 islands. A contemporaneous drying out of a nearby bog (Cohen et al., 2014), together with
401 the 100 m lowstand in Lake Titicaca in the high Andes (Baker et al., 2001) suggests that a
402 drier climate likely drove these savannah island expansions. The subsequent contraction of
403 these savannah islands began between ca. 2.5 and 2 ka, with modern $\delta^{13}\text{C}$ values reached
404 by ca. 1.5 ka, concurrent with the forest expansion seen in north-eastern Bolivia (Mayle et
405 al., 2000).

406

407 A weaker SASM in the mid Holocene is likely to have increased the length and severity of
408 the dry season, and decreased annual precipitation below the ~1500 mm climatic threshold
409 between HETF and SDF/SAV, thus driving the northward ecotonal movement. The
410 resilience of the SDF in the eastern Chiquitano region suggests that climate was not
411 sufficiently dry to cause a drastic vegetation shift to dry savannah/scrubland or Caatinga-
412 type vegetation such as that seen in the modern nordeste region of Brazil. Severe drought
413 events were likely more common, which would have favoured the opportunistic expansion of
414 the savannah vegetation into the vulnerable areas of HETF in the savannah island region,
415 perhaps aided by more frequent fire events. The ca. 1000-year time lag between HETF
416 expansion at LCH versus LBV could reflect the latitudinal time-transgressive nature of
417 precipitation increase, and/or a degree of hysteresis in vegetation response (Burbridge et al.,
418 2004). It is important to note that sites from the western Bolivian/south-eastern Peruvian
419 Amazon show stability of HETF through the last 6000 years (Bush et al., 2004b; 2007b;
420 Urrego et al., 2013). This area receives more precipitation than eastern Bolivia, partly due to
421 its location on the Andean flank and the associated orographic rainfall (Killeen et al., 2007).
422 Even if moist winds associated with the SASM and SALLJ were reduced in the mid

423 Holocene, the orographic processes are still likely to have maintained a moist windward
424 Andean flank (Killeen et al., 2007; Urrego et al., 2013).

425

426 **South-Eastern Brazil (SB)**

427 South-eastern Brazil marks the 'exit region' of the SASM; during the mature phase of the
428 SASM moisture is transported from central Amazonia to this region via the SALLJ – helped
429 by the Chaco Low and the channelling of the Andes and south Brazilian highlands (Fig. 1b).
430 The speleothem records from Botuvera Cave (Wang et al., 2007; Bernal et al., 2016) provide
431 evidence that this region was drier during the mid-Holocene as less moisture was being
432 received from the Amazon Basin (Fig. 3g), consistent with the paleoclimate records from the
433 Andes (Baker et al., 2001) and the interpretation of a weaker SASM in response to lower
434 austral summer insolation. The enhancement of moisture transport from the Amazon Basin
435 into south-east Brazil is recorded from ca. 4 ka, around the same time that precipitation
436 levels are shown to increase in the Andean speleothem records. Modern moisture levels
437 were not reached until ca. 2 to 1.5 ka. Bernal et al. (2016) note that even though the region
438 receives moisture from extratropical sources, the changes in total rainfall for south-eastern
439 Brazil during the mid-to-late Holocene were predominantly driven by insolation changes and
440 associated SASM intensity.

441

442 The paleovegetation records from south-eastern Brazil suggest that open vegetation was
443 more widespread at 6 ka, with increases in arboreal vegetation types through to the present.
444 However, given the diverse range of landscapes in this region, it is unsurprising to find that
445 the timing, magnitude and type of forest expansion is highly variable between different
446 areas. The sites located in the SDF region in the SE Brazilian state of Minas Gerais suggest
447 that this area of SDF remained largely intact through the mid-to-late Holocene. This pattern
448 is exemplified by the reconstructions from two large lakes in the core of this area of SDF,
449 Lago Silvana (id = 9, Rodrigues-Filho et al., 2002) and Dom Helvecio (id = 10, Ybert et al.,
450 2000; Turcq et al., 2002), that show consistent SDF pollen signals, depleted $\delta^{13}\text{C}$ and low

451 erosional rates throughout the last 6 ka. However, records from smaller sites do reveal more
452 localised vegetation changes from increased SAV in the mid-Holocene (6 ka) to an increase
453 in SDF cover between ca. 5 – 4 ka and again in the last ca. 1 ka. These timings are roughly
454 consistent with the precipitation pattern interpreted from the Botuvera Cave speleothem.
455 Development of dry forest occurred near the borders of the Misiones SDF region from ca. 2
456 – 1 ka (Pessenda, 2004; Zech et al., 2009). This SDF expansion suggests that whilst the
457 mid-Holocene climate was not dry enough to cause biome turnover from SDF to savannah,
458 there was sufficient drying, due to an increase in dry season length, to cause an opening of
459 more marginal areas of SDF. The limited records from within the central Brazilian Cerrado
460 show the expansion of gallery forests from ca. 3.5 – 3 ka (Silva et al., 2008), and in the
461 southernmost Brazilian Cerrado at ca. 1.5 ka (Behling et al., 2005). However, the paucity of
462 these sites means that it is uncertain whether this gallery forest expansion happened across
463 the Cerrado biome.

464

465 Across the southern Brazilian highlands, there is clear evidence of extensive areas of SAV
466 type vegetation (most likely campos grassland) from ca. 6 – 4 ka. An expansion of montane
467 forests along the coastal mountains of São Paulo and Rio de Janeiro states occurred from
468 ca. 5 – 4 ka, and expansion of *Araucaria* forest on the southern Brazilian highlands occurred
469 from ca. 4 – 3.5 ka. Further expansion of *Araucaria* forests occurred within the last ca. 1.5 –
470 1 ka. The *Araucaria* forests were likely to have been particularly sensitive to even small
471 changes in the precipitation regime, as they currently grow where there is high annual
472 precipitation and a short, or ill-defined, dry season. The drier mid-Holocene climate and
473 associated expansion of campos grassland was probably linked with an increased dry
474 season length of around 3 months (Behling, 1997a; 1998; Behling and Pillar, 2007). The
475 initial phase of *Araucaria* expansion from ca. 4 – 3.5 ka was likely in the form of gallery
476 forests where moisture levels could be maintained more easily (Behling, 1997a; Behling et
477 al., 2004). The second phase of expansion from ca. 1.5 ka marks a more regional expanse
478 of *Araucaria* forest, suggesting that the precipitation regime was back to near-modern levels,

479 with high annual precipitation and a short, or ill-defined, dry season (Behling and Pillar,
480 2007). Again, these timings seem to match well with the Botuvera Cave paleoclimate
481 records, which record increased tropical moisture source from ca. 4 ka, and a return to
482 modern moisture levels from ca. 2 – 1.5 ka. The timings of *Araucaria* expansion also
483 coincide with increasing human activity in the region, raising the possibility that humans
484 could have taken advantage of a wetter climate and influenced the expansion of this
485 economically useful taxon (Bitencourt and Krauspenhar, 2006; Iriarte and Behling, 2007;
486 Iriarte et al., 2016).

487

488 **Eastern Amazonia (EA)**

489 A recently published speleothem record from Paraíso cave in eastern Amazonia suggests
490 that this region may have been wetter than present at the mid Holocene (Wang et al., 2017),
491 in contrast to other areas of the Amazon basin that record a drier mid-Holocene. The
492 explanation for this pattern is still unclear; early-mid Holocene warming could have
493 increased moisture supply, while weaker ENSO activity during the mid-Holocene may have
494 reduced drought events in the eastern Amazon (Koutavas and Joanides, 2012; Wang et al.,
495 2017), but these explanations do not necessarily account for the apparent wetter-than-
496 present mid Holocene. Clearly, the robustness of, and potential mechanisms for, such a
497 pattern requires more investigation. Vegetation reconstructions from most sites near to this
498 speleothem record (e.g. site id's 1, 21-25) show stable HETF cover at the mid-Holocene
499 (Behling and da Costa, 2001; Irion et al., 2006; Bush et al., 2007a), which is unsurprising if
500 climate was wetter at this time.

501

502 This story is clearly a more complicated one if we consider the evidence of mid-to-late
503 Holocene vegetation changes near to the south-eastern Amazonian ecotone, which appear
504 to contradict Paraíso cave's mid-to-late Holocene precipitation history. A number of sites
505 located on the Serra Sul dos Carajás plateau (ids = 30 – 32) indicate dominance of
506 savannah and dry-adapted SDF arboreal taxa during the mid-Holocene (6 – 5 ka),

507 suggesting drier conditions, after which humid evergreen forest elements gradually increase
508 up to ca. 4 – 3 ka, suggesting increasing moisture (Absy et al., 1991; Sifeddine et al., 2001;
509 Hermanowski et al., 2014). Even though human occupation has been recorded in this region
510 for at least the last 10 ka (Kipnis et al., 2005), the decrease in fire occurrences on the
511 Carajás plateau that are recorded during the mid-Holocene at Lagoa de Cachoeira (id = 31)
512 would suggest that the more open vegetation at this time was not initiated by human land
513 management. In fact, a more likely scenario is the abandonment of the plateau by humans
514 at this time (so fewer anthropogenic fires) due to a reduction in both water sources and
515 forest resources (Hermanowski et al., 2014). Therefore, the apparent mismatch between
516 these vegetation changes and the climate change at Paraíso Cave is unlikely to be due to
517 human impacts. Around 175 km north-east of the Carajás plateau, the Lake Marabá record
518 (id = 29) indicates a switch to a HETF dominated signal at ca. 5 ka (Guimarães et al.,
519 2013a).

520

521 Some important considerations must be noted with regards to these records that seem to
522 contradict the regional paleoclimate history. There is clearly a paucity of paleoecological
523 sites across this south-eastern Amazonian ecotonal area, so it is difficult to infer any regional
524 scale vegetation changes. Furthermore, the sites we do have are predominantly located on
525 the Serra Sul dos Carajás plateau. It has long been debated as to how well the HETF
526 surrounding the plateau is represented in the plateau based pollen records (Absy et al.,
527 1991; 2014; Guimarães et al., 2014). The consensus at this time is that the plateau
528 vegetation, along with some input from the forests growing on the slopes, dominates the
529 pollen assemblages of the lake and bog records from the plateau, suggesting that the mid-
530 to-late Holocene Carajás records only reflect local changes on the plateau itself
531 (Hermanowski et al., 2012a; 2012b; 2014). At the nearby Lake Marabá record, the
532 vegetation changes could be due to successional vegetation changes after the formation of
533 the lake (Guimarães et al., 2013a). Even given these caveats, there is still a mismatch
534 between vegetation reconstructions apparently indicating a drier mid-Holocene (at a local

535 scale) and the Paraíso cave record indicating a wetter regional climate. Clearly more work
536 needs to be done to reconcile these differences.

537

538 **North-Eastern Brazil (NE)**

539 As the modern east-west precipitation dipole between north-eastern Brazil (dry climate) and
540 the central South American tropics (wet climate) is largely controlled by the strength of the
541 SASM and associated features, it is not unexpected to find that the paleoprecipitation history
542 of the Rio Grande do Norte speleothem shows a distinct 'anti-phased' relationship to the rest
543 of tropical South America (Cruz et al., 2009; Cheng et al., 2013). During the mid-Holocene,
544 when insolation levels were low and the south and west SASM region was drier, the
545 nordeste was wetter than at present (Fig 3h). Mechanistically, this is most likely due to a
546 weaker SASH and weaker convective activity in the core of the SASM region reducing the
547 strength of the nordeste low and subsidence over the region (Cruz et al., 2009; Cheng et al.,
548 2013). Weaker ENSO activity during the mid-Holocene may also have reduced severe
549 drought events in this region (Koutavas and Joanides, 2012; Wang et al., 2017). As
550 insolation levels increase through the Holocene, the region becomes gradually drier,
551 reaching approximately modern levels at ca. 4 ka. Reconstructing the paleovegetation
552 history of this region in response to this sort of long-term precipitation change is of great
553 interest, for example in terms of revealing important information about the potential
554 connectivity between the Amazon and Atlantic rainforests (De Oliveira et al., 1999; Behling
555 et al., 2000; Costa, 2003; Batalha-Filho et al., 2013). However, a fundamental issue in this
556 semi-arid region is the difficulty in finding permanent lake basins, bogs, or undisturbed
557 locations for taking soil profiles, that would provide suitable records for paleoecological study
558 (De Oliveira et al., 1999; Pessenda et al., 2010).

559

560 The pollen record from the site Saquinho (id = 34), taken in the Caatinga region in the Rio
561 Icatu river valley, suggests that a more humid mid-Holocene may have promoted the
562 expansion of palms and gallery forests at the expense of Caatinga/savannah vegetation.

563 Between ca. 5 and 4.5 ka, the trend of increasing aridity in the region is marked by an
564 increase in Caatinga and Cerrado taxa as well as a reactivation of dune activity shown by
565 thermoluminescence data (De Oliveira et al., 1999). The Maranguape bog core taken from
566 the Serra de Maranguape mountains on the north coast (id = 28) records continuous forest
567 cover through the mid-to-late Holocene, though compositional changes in the pollen record
568 suggest increased disturbance at ca. 4.5 ka, contemporaneous with the start of drier
569 conditions in the nordeste (Montade et al., 2014). However, other records in this region do
570 not seem to reflect the more humid mid-Holocene in their paleovegetation reconstructions,
571 though this is most likely due to the unique characteristics of their site locations. A transect
572 of soil profiles on the Araripe Plateau in the central Caatinga region (ids = 78 – 80) records
573 gradual depletion of $\delta^{13}\text{C}$ from the mid-Holocene to present, suggesting greater savannah
574 extent before ca. 3.5 – 3 ka, after which forested areas increase. A transect of soil profiles
575 on the east coast of Paraíba state (ids = 76 – 77) also show some indications of more open
576 vegetation in the mid-Holocene, with an increase in forest cover after ca. 3 ka. The modern
577 rainforest enclaves on plateaus such as Araripe and on higher elevations near the coast are
578 maintained by significant orographic rainfall derived from easterly winds that help to mitigate
579 against the arid conditions caused by the persistent subsidence (Andrade-Lima, 1982;
580 Sampaio, 1995). Even though this subsidence was likely reduced during the mid-Holocene
581 causing the region in general to become less arid, changes to low-level divergent circulation
582 patterns and Walker cell dynamics may also have reduced the moist easterlies (Cruz et al.,
583 2009) that helps maintain these plateau-based forests. Whilst these small plateaus and
584 coastal areas can yield suitable sites, clearly they may not be representative of vegetation
585 changes across the Caatinga on a regional scale. The site of Lagoa do Caçó (id = 11) is
586 located on the northernmost reach of the Cerrado savannah biome and records no major
587 changes in the Cerrado vegetation through the mid-to-late Holocene (Ledru et al., 2006).
588 The increase in gallery forests around the lake shown in the nearby soil pits may indicate
589 increased moisture after ca. 4 ka, though it is difficult to say whether this is due to climate,
590 natural vegetation succession or sea level dynamics. The authors suggest that the location

591 of this lake lies in a transitional area between the east-west climate zones and as such,
592 precipitation changes may be fairly stable in contrast to the surrounding areas (Pessenda et
593 al., 2005; Ledru et al., 2006).

594 **CONCLUSIONS**

595 Our multi-proxy paleoecological data synthesis shows how the vegetation from different
596 regions of tropical South America responded to orbitally forced long-term precipitation
597 changes through the mid-to-late Holocene (Cheng et al., 2013; Baker and Fritz, 2015). The
598 HETF biome of central and western Amazonia remained intact, even though paleoclimate
599 records suggest that this region may have been slightly drier than present during the mid-
600 Holocene. In eastern Amazonia, similar HETF stability is recorded, however the apparent
601 mid-Holocene savannah expansion at the eastern Amazonian ecotone (from the Serra Sul
602 dos Carajás plateau) is difficult to reconcile with new paleoclimate data from Paraíso cave
603 that suggests this region was wetter than present at this time (Wang et al., 2017). The
604 Paraíso cave record perhaps only reflects precipitation conditions from far north-east
605 Amazonia, and is not representative of Carajás' location in south-east Amazonia. Nearer to
606 the south-eastern Amazonian ecotone and the Carajás plateau, local lake level records
607 appear to indicate lower lake productivity and water levels during the mid-Holocene,
608 indicative of a drier climate (Cordeiro et al., 2008). Clearly more investigation is needed in
609 this area to reconcile local and regional paleoclimate and paleoecological records. The
610 north-east of Brazil was wetter than present during the mid Holocene, due to a suppression
611 of the subsidence across the region resulting from a weaker SASM and SASH (Cruz et al.,
612 2009). However, the lack of paleovegetation records means a regional interpretation of
613 vegetation response is problematic.

614

615 Significant vegetation changes are recorded in south-west Amazonia and south-east Brazil.
616 These regions are more reliant on SASM-derived precipitation and so vegetation here is
617 likely to be especially susceptible to long-term changes in SASM strength. The vegetation
618 reconstructions during a drier mid-Holocene show: a more northerly location of the
619 HETF/SDF/SAV ecotone in north-eastern Bolivia; greater expanse of campos grassland
620 across the south Brazilian highlands; and decreased expanse of montane forests and HETF
621 across the southern Atlantic forest region. As precipitation levels gradually rose through the

622 mid-to-late Holocene, vegetation responded as follows: progressive southward expansion of
623 the HETF in north-east Bolivia from ca. 2 ka; expansion of Araucaria on the south Brazilian
624 highlands from ca. 4 ka, with enhanced expansion from ca. 1.5 – 1 ka; expansion, or greater
625 canopy density, of SDF in the Misiones and interior Atlantic forest regions; increase of
626 gallery forests in the south-east Brazilian Cerrado. The difference in the timing of forest
627 expansion between these two regions is probably due to the important extra-tropical source
628 of precipitation that mitigates somewhat against a weaker SASM in south-east Brazil.

629

630 Whilst this synthesis includes more sites than previous studies, in part due to inclusion of
631 non-pollen proxy reconstructions, it is clear that more sites are needed to help increase our
632 understanding of long-term vegetation dynamics across the region. In south-west Amazonia,
633 more sites could help to quantify the maximum extent of the HETF/SDF/savannah mid-to-
634 late Holocene ecotonal shift. We particularly highlight eastern Amazonia, north-east Brazil
635 and the cerrado region of central Brazil as key areas that need more paleoecological data.
636 We recognise that the paucity of suitable lake sites in these areas is a big hindrance to
637 improving the regional coverage of pollen-based vegetation reconstructions. However, in
638 such regions, where suitable lakes/bogs are scarce, soil-based proxies – such as $\delta^{13}\text{C}$
639 isotopes and, in particular, phytoliths – which have hitherto been underutilised by the
640 paleoecological community, show considerable potential for paleovegetation reconstruction
641 (Dickau et al., 2013; Watling et al., 2016; 2017).

642

643 With regards to possible implications for future climate change, this study highlights that the
644 ecosystems most vulnerable to long-term climate change are those that are already close to
645 their climatic limits. However, given the resilience of the central Amazonian HETF biome to
646 past climate change, future projections of widespread forest dieback across Amazonia (Cox
647 et al., 2000; 2004) seem unlikely. It is important to point out that we have used the mid-to-
648 late Holocene as a period in which we can assess regional vulnerability to long-term climate
649 changes, not as a direct analogue for a future drier climate. Factors such as temperature

650 and CO₂ levels will be significantly different between the future and the mid-Holocene, which
651 will undoubtedly have an impact on vegetation responses (Rammig et al., 2010; Huntingford
652 et al., 2013). In addition, huge anthropogenic pressures, such as widespread deforestation
653 and uncontrolled burning, will only act to reduce the ability of vegetation to maintain local
654 feedbacks and thus reduce overall ecosystem resilience (Laurance et al., 2000; Malhi et al.,
655 2008; Levine et al., 2016).

656

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662 (TRMM) data (<https://trmm.gsfc.nasa.gov>) were processed by the TRMM Science Data and
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667 manuscript.

668 **LIST OF TABLES**

669 **Table 1.** List of paleoecological sites. 'ID' number refers to location number in Fig. 2a. Size
670 categories refer to those outlined in Table 3. Subscript numbers next to site names refer to
671 the proxy types used in that study: 1 = pollen analysis; 2 = charcoal analysis; 3 = isotopic
672 analysis; 4 = physio-chemical analysis. Asterisk next to site ID indicates a site where an
673 independent age-depth model was created (see methods).

674

675 **Table 2.** Description of the broad vegetation classifications used in this study

676

677 **Table 3.** Size categories representing the different catchment areas of the paleoecological
678 sites

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680 **Figure 1.** Observed long-term mean precipitation (mm/day), 850 mb wind speed and wind
681 direction for (a) June, July and August (JJA), and (b) December, January, February (DJF).
682 Labels indicate key climate features: Intertropical Convergence Zone (ITCZ), South
683 American Low Level Jet (SALLJ), Chaco Low (CL), South Atlantic Convergence Zone
684 (SACZ), South Atlantic Subtropical High (SASH), and Nordeste Low (NL) - see text for
685 details. Precipitation data taken from Tropical Rainfall Measuring Mission v7 (TRMM) 3B43
686 dataset (1998-2014) (Huffman et al., 2007). Wind data taken from NCEP Climate Forecast
687 System Reanalysis (CFSR) dataset (1979-2010) (Saha et al., 2010a; 2010b).

688

689 **Figure 2.** Overview maps of study area, (a) location and numeric ID of each site
690 corresponding to Table 1, (b) broad modern vegetation biomes, modified from Olson et al.
691 (2001), (c) long term average annual precipitation based on Tropical Rainfall Measuring
692 Mission v7 (TRMM) 3B43 dataset (1998-2014) (Huffman et al., 2007). The polygons shown
693 in (b) and (c) represent the regions discussed in text: CW = Central and western lowland
694 Amazonia, EA = Eastern Amazonia, SW = South-Western Amazonia, SB = South-eastern
695 Brazil, NE = North-eastern Brazil. The blue squares in (b) and (c) show locations of the
696 paleoclimate sites discussed in text: 1 = El Condor, 2 = Cueva del Tigre Perdido, 3 = Lake
697 Junin, 4 = Huaguapo, 5 = Lake Titicaca, 6 = Laguna La Gaiba, 7 = Botuvera Cave, 8 = Rio
698 Grande do Norte, 9 = Paraíso Cave

699

700 **Figure 3.** Selected paleoclimate records representing proxy records for precipitation
701 changes through the last 6 ka, shown alongside calculated January insolation at 15°S
702 (Berger and Loutre, 1991; Berger, 1992) (a) $\delta^{18}\text{O}$ of stalagmite Core A and Core B from El
703 Condor Cave (Cheng et al., 2013), (b) $\delta^{18}\text{O}$ of stalagmite records NC-A and NC-B from
704 Cueva del Tigre Perdido (van Breukelen et al., 2008), (c) $\delta^{18}\text{O}$ of calcite from Lake Junin
705 (Seltzer et al., 2000), (d) $\delta^{18}\text{O}$ of speleothem record Huaguapo (Kanner et al., 2013), (e)

706 lake-level changes as measured by $\delta^{13}\text{C}$ at Lake Titicaca (Rowe et al., 2002), (f)
707 *Pediastrum*-inferred lake-level change at Laguna La Gaiba (Whitney and Mayle, 2012), (g)
708 $\delta^{18}\text{O}$ of speleothem record BTV3a, Sr/Ca of speleothem BTV21a from Botuvera Cave (BTV)
709 site (Wang et al., 2007; Bernal et al., 2016), (h) $\delta^{18}\text{O}$ of speleothem records FN1, RN1 and
710 RN4 from the Rio Grande do Norte (RGDN) record (Cruz et al., 2009).

711

712 **Figure 4.** Paleoecological reconstructions at 0.5 ka time slices from 6 ka to present.

713 Background of modern vegetation biomes, modified from Olson et al. (2001). Vegetation
714 classifications outlined in Table 2. Size of circles represents catchment area of that site,
715 outlined in Table 3.

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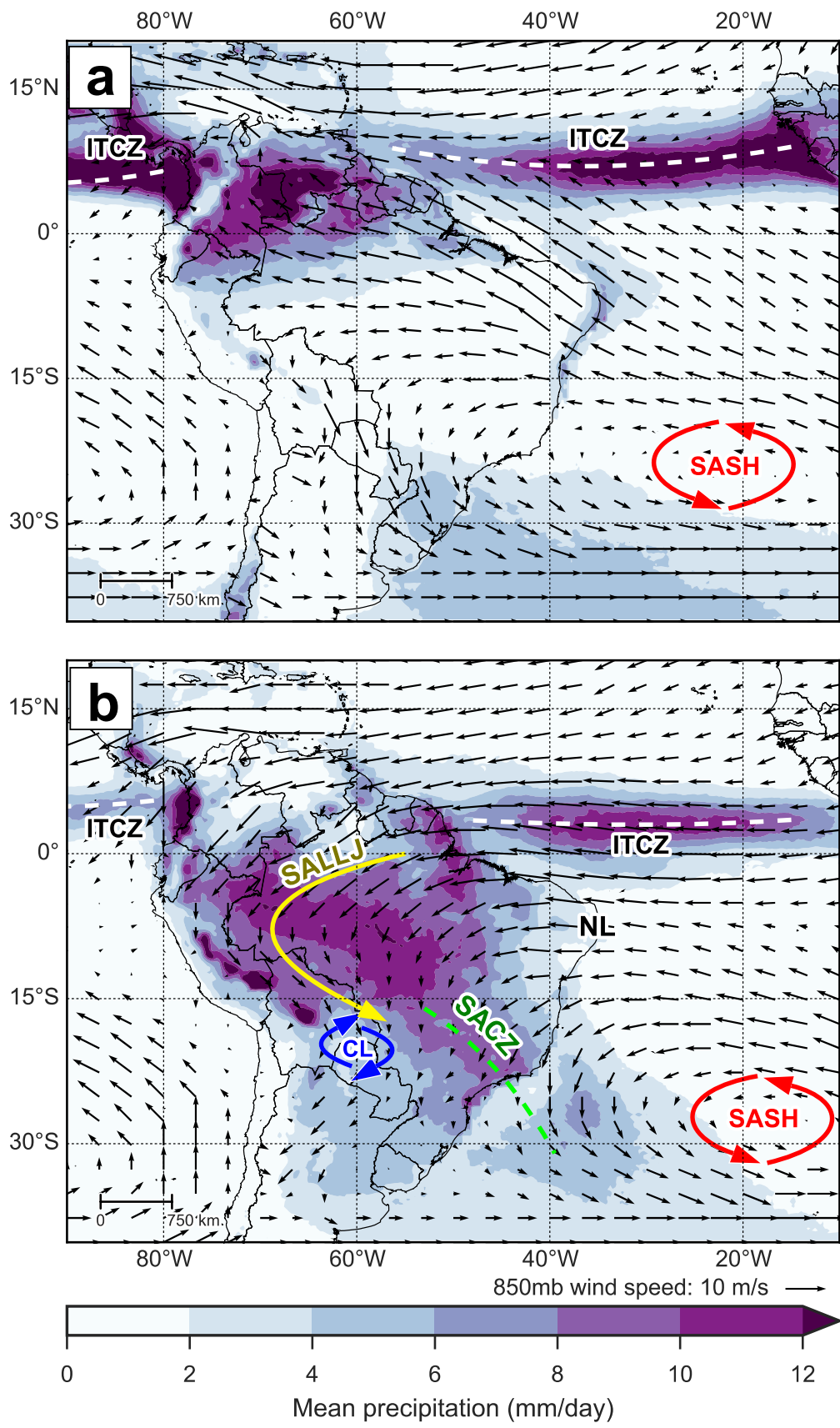


Figure 1.

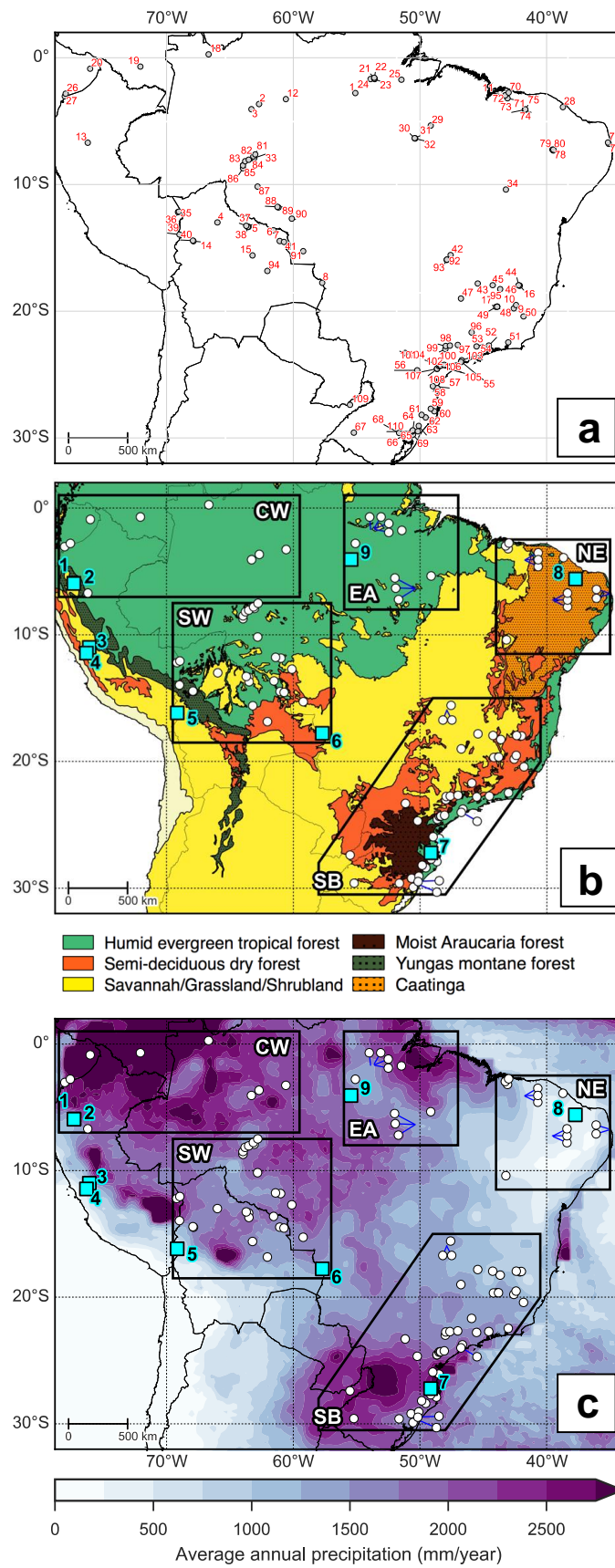


Figure 2.

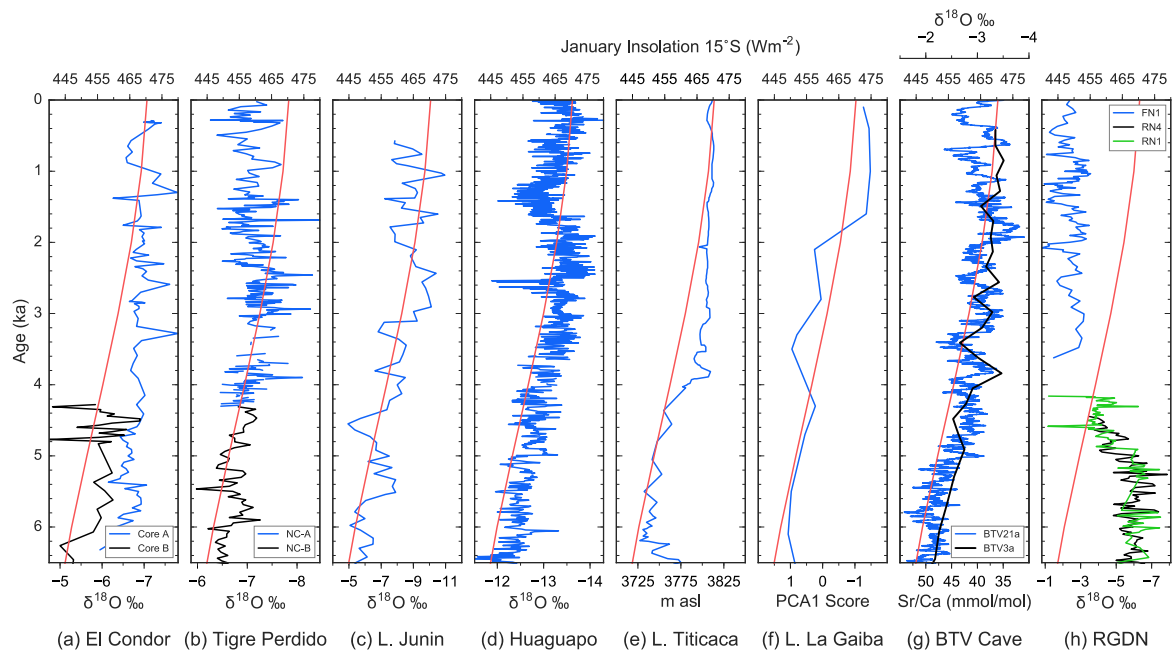


Figure 3.

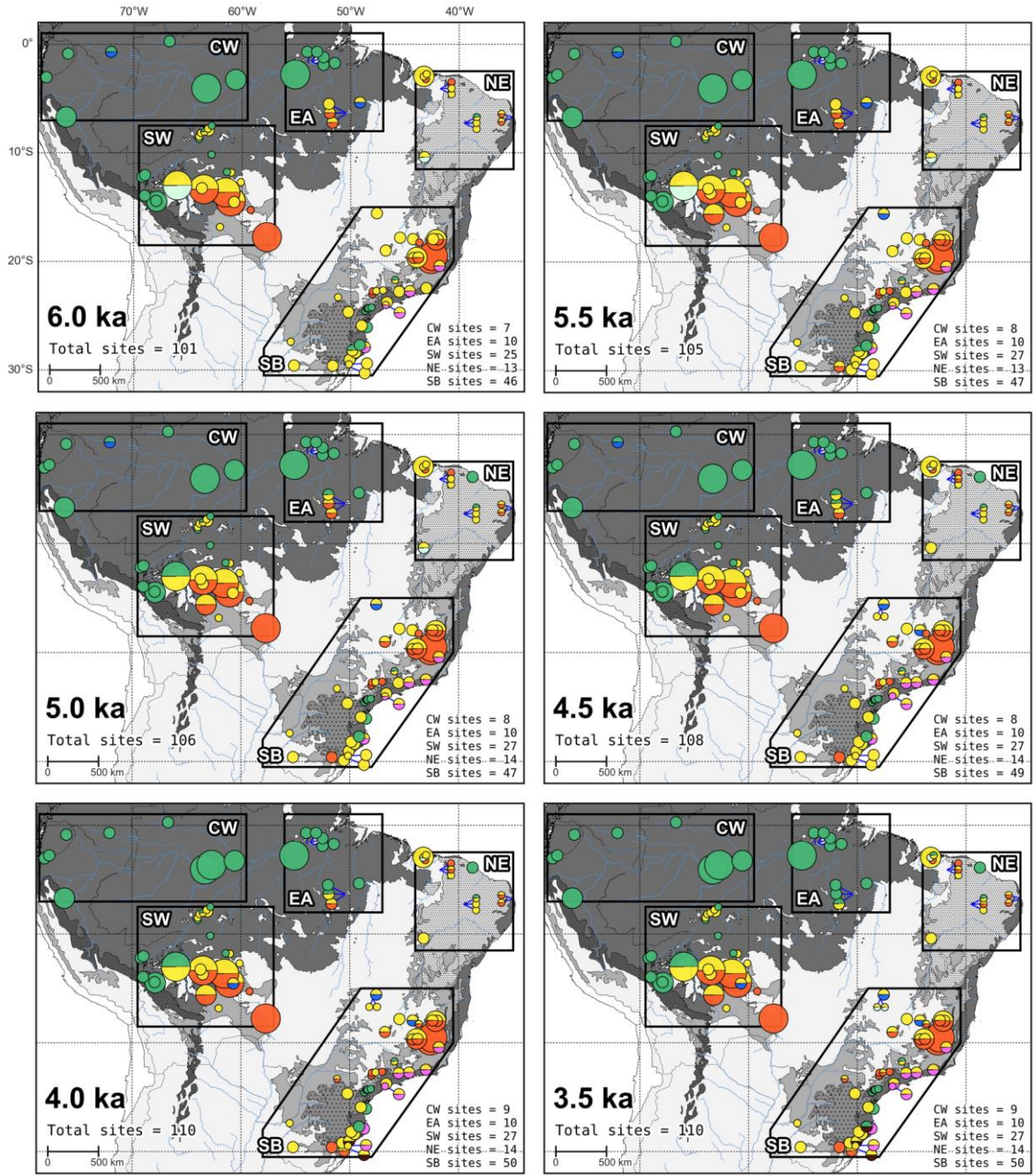


Figure 4.

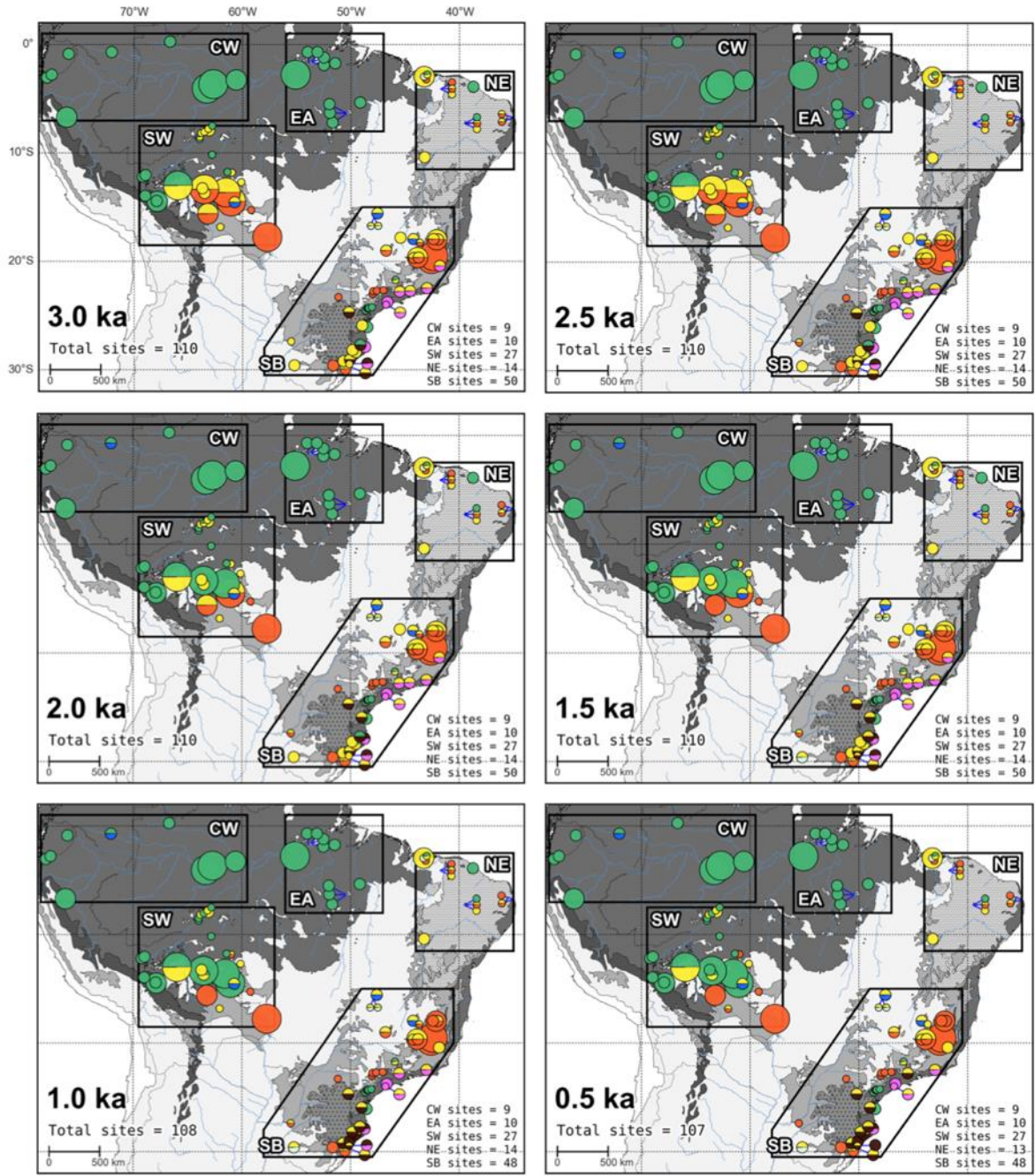


Figure 4. (continued)

Table 1.

ID	Site Name	Latitude	Longitude	Reference(s)
Size category: Large (L)				
1	Lago Tapajós TAP02 _{1,2,3,4}	2°47.14'S	55°6.13'W	(Irion et al., 2006)
2*	Acará lake _{1,3,4}	3°39.32'S	62°42.07'W	(Horbe et al., 2011)
3*	Coari Lake _{1,3,4}	4°3.85'S	63°18.11'W	(Horbe et al., 2011)
4	Lago Rogaguado _{1,2}	12°59.84'S	65°59.16'W	(Brugger et al., 2016)
5	Laguna Orícore _{1,2}	13°20.74'S	63°31.53'W	(Carson et al., 2014)
6	Laguna Bella Vista _{1,2}	13°37.00'S	61°33.00'W	(Mayle et al., 2000; Burbridge et al., 2004)
7	Laguna Chaplin _{1,2}	14°28.00'S	61°4.00'W	(Mayle et al., 2000; Burbridge et al., 2004)
8	Laguna La Gaiba _{1,3,4}	17°45.69'S	57°42.95'W	(Whitney et al., 2011; Metcalfe et al., 2014)
9*	Lagoa Silvana _{1,4}	19°31.00'S	42°25.00'W	(Rodrigues-Filho et al., 2002)
10*	Lake Dom Helvécio _{1,2,3,4}	19°46.94'S	42°35.48'W	(Ybert et al., 2000; Turcq et al., 2002; Sifeddine et al., 2004)
Size category: Medium (M)				
11	Lagoa do Caçó _{1,2,3}	2°57.64'S	43°15.20'W	(Sifeddine et al., 2003; Pessenda et al., 2005; Ledru et al., 2006)
12*	Lago Calado _{1,4}	3°16.00'S	60°35.00'W	(Behling et al., 2001b)
13	Lake Sauce _{1,2}	6°42.28'S	76°13.07'W	(Bush et al., 2016)
14	Lake Santa Rosa _{1,2}	14°28.61'S	67°52.48'W	(Urrego et al., 2013)
15	Laguna Yaguarú _{1,2,3}	15°36.00'S	63°13.00'W	(Taylor et al., 2010)
16	Lago Aleixo _{1,3,4}	17°59.27'S	42°7.13'W	(Enters et al., 2010)

1 = pollen analysis; **2** = charcoal analysis; **3** = isotopic analysis; **4** = physio-chemical analysis.

ID	Site Name	Latitude	Longitude	Reference(s)
17*	Lagoa Santa ₁	19°38.00'S	43°54.00'W	(Parizzi et al., 1998)
Size category: Small (S)				
18	Lake Pata ₁	0°16.00'S	66°41.00'W	(Colinvaux et al., 1996; Bush et al., 2004a)
19*	Pantano de Monica ₁	0°42.00'S	72°4.00'W	(Behling et al., 1999)
20	Maxus 4 _{1,2}	0°52.00'S	76°2.00'W	(Weng et al., 2002)
21	Lake Santa Maria _{1,2}	1°34.76'S	53°36.41'W	(Bush et al., 2007a)
22	Lake Geral _{1,2,4}	1°38.75'S	53°35.95'W	(Bush et al., 2000; 2007a)
23	Lake Saracuri _{1,2}	1°40.82'S	53°34.21'W	(Bush et al., 2007a)
24*	Lake Comprida _{1,2,4}	1°40.93'S	53°53.83'W	(Bush et al., 2000)
25*	Rio Curuá _{1,2,4}	1°44.12'S	51°27.79'W	(Behling and da Costa, 2000)
26*	Lake Kumpaka ₁	2°50.20'S	77°57.68'W	(Liu and Colinvaux, 1988)
27	Lake Ayauchi _{1,2}	3°2.72'S	78°2.07'W	(Bush and Colinvaux, 1988; McMichael et al., 2012)
28	Maranguape ₁	3°53.67'S	38°43.22'W	(Montade et al., 2014)
29*	Lake Marabá _{1,2,3,4}	5°21.00'S	49°9.00'W	(Guimarães et al., 2013)
30*	Carajás CSS2 _{1,3,4}	6°20.51'S	50°25.16'W	(Absy et al., 1991; Sifeddine et al., 1994; 2001)
31	Lagoa da Cachoeira _{1,2}	6°21.30'S	50°23.59'W	(Hermanowski et al., 2014)
32	Pântano da Maurítia _{1,2,4}	6°22.55'S	50°23.16'W	(Hermanowski et al., 2012a; 2012b)
33	Humaitá HU01 _{1,3,4}	7°55.43'S	63°4.99'W	(Cohen et al., 2014)
34*	Saquinho _{1,2}	10°24.00'S	43°13.00'W	(De Oliveira et al., 1999)
35	Lake Parker _{1,2}	12°8.47'S	69°1.30'W	(Bush et al., 2007a; 2007b)
36	Lake Gentry _{1,2}	12°10.64'S	69°5.86'W	(Bush et al., 2007a; 2007b)
37	Laguna Granja _{1,2,5}	13°15.73'S	63°42.62'W	(Carson et al., 2014; 2015)

1 = pollen analysis; **2** = charcoal analysis; **3** = isotopic analysis; **4** = physio-chemical analysis.

ID	Site Name	Latitude	Longitude	Reference(s)
38	La Luna _{1,2}	13°21.33'S	63°35.03'W	(Carson et al., 2016)
39	Lago Consuelo ₁	13°57.00'S	68°59.00'W	(Bush et al., 2004b)
40	Lake Chalalán _{1,2}	14°25.67'S	67°55.25'W	(Urrego et al., 2013)
41	Huanchaca _{2,3,5}	14°32.18'S	60°43.93'W	(Maezumi et al., 2015)
42*	Vereda de Águas Emendadas VAE _{2,1,2}	15°34.00'S	47°35.00'W	(Barberi et al., 2000)
43	Vereda Laçador ₁	17°49.06'S	45°26.47'W	(Cassino and Meyer, 2013)
44*	Lago do Pires ₁	17°56.85'S	42°12.62'W	(Behling, 1995a; 1998)
45	Vereda Juquinha ₁	17°56.96'S	44°15.51'W	(Pires et al., 2016)
46*	Lagoa Nova _{1,2}	17°58.00'S	42°12.00'W	(Behling, 2003)
47*	Salitre de Minas _{1,2,3,5}	19°0.00'S	46°46.00'W	(Ledru, 1993; Alexandre et al., 1999; Pessenda, 2004)
48	Lagoa Olhos D'Água ₁	19°38.92'S	43°54.59'W	(Raczka et al., 2013)
49	Lagoa dos Mares ₁	19°39.79'S	43°59.26'W	(Raczka et al., 2013)
50	Primeiro Rancho _{1,2}	20°24.83'S	41°49.57'W	(Nuno Veríssimo et al., 2012)
51	Serra dos Órgãos _{1,2}	22°27.50'S	43°1.69'W	(Behling and Safford, 2010)
52	Serra da Bocaina _{2,1}	22°42.83'S	44°34.00'W	(Behling et al., 2007)
53*	Morro de Itapeva _{1,2}	22°47.00'S	45°32.00'W	(Behling, 1997; 1998)
54	Colônia Crater ₁	23°52.00'S	46°42.34'W	(Ledru et al., 2005; 2009)
55*	TU Peat Bog ₁	23°59.00'S	46°44.75'W	(Pessenda et al., 2009)
56*	Serra Campos Gerais _{1,2}	24°40.00'S	50°13.00'W	(Behling, 1997; 1998)
57*	Serra do Araçatuba _{1,2}	25°55.00'S	48°59.00'W	(Behling, 2007)
58	Volta Velha ₁	26°4.00'S	48°37.98'W	(Behling and Negrelle, 2001)
59*	Serra da Boa Vista ₁	27°42.00'S	49°9.00'W	(Behling, 1995b; 1998)
60	Serra do Tabuleiro _{1,2}	27°53.81'S	48°52.09'W	(Jeske-Pieruschka et al., 2012)

1 = pollen analysis; **2** = charcoal analysis; **3** = isotopic analysis; **4** = physio-chemical analysis.

ID	Site Name	Latitude	Longitude	Reference(s)
61*	Morro da Igreja ₁	28°11.00'S	49°52.00'W	(Behling, 1995b; 1998)
62*	Serra do Rio Rostro ₁	28°23.00'S	49°33.00'W	(Behling, 1995b; 1998)
63	Cambará do Sul _{1,2}	29°3.15'S	50°6.07'W	(Behling et al., 2004; Behling and Pillar, 2007)
64*	Fazenda do Pinto ₁	29°24.00'S	50°34.00'W	(Behling et al., 2001a)
65	Rincão das Cabritas _{1,2}	29°28.58'S	50°34.37'W	(Jeske-Pieruschka and Behling, 2011)
66	Alpes de São Francisco ₁	29°29.59'S	50°37.30'W	(Leonhardt and Lorscheitter, 2010)
67	Itajuru Farm _{1,2}	29°35.20'S	55°13.03'W	(Behling et al., 2005)
68*	Serra Velha ₁	29°36.37'S	51°38.92'W	(Leal and Lorscheitter, 2007)
69	Santo Antônio da Patrulha _{1,2}	29°44.75'S	50°32.93'W	(Macedo et al., 2010)
Size category: Extra small (XS)				
70	Combination of soil profiles: C17, C20, C25, C54, F15 _{2,3}	2°45.00'S	43°0.00'W	(Pessenda et al., 2004; 2005)
71	Combination of soil profiles: F46, C78 _{2,3}	3°12.00'S	43°5.33'W	(Pessenda et al., 2004)
72	Combination of soil profiles: LCF50, LCF150, LCF200 ₃	2°57.98'S	43°16.03'W	(Pessenda et al., 2004; 2005)
73	Combination of soil profiles: Parna I, Parna IV _{2,3}	4°5.69'S	41°43.71'W	(Pessenda et al., 2010)
74	Combination of soil profiles: Parna II, Parna VII _{2,3}	4°7.81'S	41°42.65'W	(Pessenda et al., 2010)
75	Combination of soil profiles: Parna III, Parna V, Parna VI, Parna VIII _{2,3}	4°4.45'S	41°41.17'W	(Pessenda et al., 2010)
76	Combination of soil profiles: Rebio I, Rebio II, Rebio III,	6°47.79'S	35°5.98'W	(Pessenda et al., 2010)

1 = pollen analysis; **2** = charcoal analysis; **3** = isotopic analysis; **4** = physio-chemical analysis.

ID	Site Name	Latitude	Longitude	Reference(s)
	Rebio IV _{2,3}			
77	Combination of soil profiles: Rebio V, Rebio VI, Rebio VII, Rebio VIII _{2,3}	6°41.42'S	35°9.67'W	(Pessenda et al., 2010)
78	Combination of soil profiles: Flona km4, Flona km8 _{2,3}	7°19.20'S	39°28.20'W	(Pessenda et al., 2010)
79	Combination of soil profiles: Flona km6', Flona km12' _{2,3}	7°15.00'S	39°33.00'W	(Pessenda et al., 2010)
80	Combination of soil profiles: Flona km0, Flona km0' _{2,3}	7°15.00'S	39°28.20'W	(Pessenda et al., 2010)
81	Combination of soil profiles: BR319 km178.5, BR319 km179 ₃	7°37.80'S	63°0.00'W	(de Freitas et al., 2001)
82	Combination of soil profiles: BR319 km154, BR319 km188 ₃	7°47.00'S	63°9.00'W	(de Freitas et al., 2001)
83	Combination of soil profiles: BR319 km80, BR319 km82, Humaitá C, Humaitá D ₃	8°10.00'S	63°48.00'W	(de Freitas et al., 2001)
84	Combination of soil profiles: BR319 km100, BR319 km111, BR319 km142, BR319 km161 ₃	8°3.00'S	63°31.00'W	(de Freitas et al., 2001)
85	Combination of soil profiles: BR319 km46, BR319 km68, Humaitá A, Humaitá B, Humaitá E ₃	8°30.00'S	63°58.00'W	(de Freitas et al., 2001)
86	BR319 km5 ₃	8°43.00'S	63°58.00'W	(de Freitas et al., 2001)
87	Ariquemes ₃	10°10.00'S	62°49.00'W	(Pessenda et al., 1998)
88	Pimenta Bueno - forest ₃	11°46.00'S	61°15.00'W	(Pessenda et al., 1998)

1 = pollen analysis; **2** = charcoal analysis; **3** = isotopic analysis; **4** = physio-chemical analysis.

ID	Site Name	Latitude	Longitude	Reference(s)
89	Pimenta Bueno - cerradão ₃	11°49.00'S	61°10.00'W	(Pessenda et al., 1998)
90	Vilhena ₃	12°42.00'S	60°7.00'W	(Pessenda et al., 1998)
91	Pontes e Lacerda _{2,3}	15°16.00'S	59°13.00'W	(Gouveia et al., 2002)
92	Pitoco ₃	15°55.87'S	47°52.61'W	(Silva et al., 2008)
93	Taquara ₃	15°57.22'S	47°53.32'W	(Silva et al., 2008)
94	Laguna Sucuara _{3,4}	16°49.60'S	62°2.60'W	(Zech et al., 2009)
95	Pau-de-Fruta _{3,4}	18°15.45'S	43°40.06'W	(Horák et al., 2011)
96	Machado soil core _{3,5}	21°40.70'S	45°55.45'W	(Calegari et al., 2013)
97	Jaguariúna _{2,3}	22°40.00'S	47°1.00'W	(Gouveia et al., 2002; Pessenda, 2004)
98	Piracicaba _{2,3}	22°43.00'S	47°38.00'W	(Pessenda, 2004)
99	Anhembi _{2,3}	22°45.00'S	47°58.00'W	(Gouveia et al., 2002; Pessenda, 2004)
100	Botucatu _{2,3}	23°0.00'S	48°0.00'W	(Gouveia et al., 2002; Pessenda, 2004)
101	Londrina _{2,3}	23°18.00'S	51°10.00'W	(Pessenda, 2004)
102	Combination of soil profiles: CER1, CER2, PCN, LN, AC, AF, FSM, EG, EG ₃	24°0.15'S	46°45.97'W	(Pessenda et al., 2009)
103	Saibadela ₃	24°14.42'S	48°4.87'W	(Saia et al., 2008)
104	Bairro Lajeado ₃	24°18.31'S	48°21.91'W	(Saia et al., 2008)
105	Base do Carmo ₃	24°18.41'S	48°24.86'W	(Saia et al., 2008)
106	Bulha D'Água ₃	24°20.25'S	48°30.15'W	(Saia et al., 2008)
107	Bairro Camargo Baixo ₃	24°32.53'S	48°39.19'W	(Saia et al., 2008)
108	Iporanga ₃	24°33.32'S	48°39.45'W	(Saia et al., 2008)
109	Misiones _{3,4}	27°23.40'S	55°31.50'W	(Morrás et al., 2009; Zech et al., 2009)

1 = pollen analysis; **2** = charcoal analysis; **3** = isotopic analysis; **4** = physio-chemical analysis.

ID	Site Name	Latitude	Longitude	Reference(s)
110	Centro de Pesquisas e Conservação da Natureza ₃	29°28.48'S	50°9.79'W	(Dümig et al., 2008)

1 = pollen analysis; **2** = charcoal analysis; **3** = isotopic analysis; **4** = physio-chemical analysis.

Table 2.

Code	Vegetation classification	Description
HETF	Humid evergreen tropical forest	Tall, closed canopy evergreen forest occurring in climates of > ~1600 mm annual precipitation. Can occur in seasonal conditions with dry season length < ~ 4 months.
SDF	Semi-deciduous tropical forest	Shorter trees, varying canopy cover, deciduous/semi-deciduous drought adapted taxa common, < ~1600 mm annual precipitation, marked dry season of 5 – 6 months
GAL	Gallery forest	Occur along streams and rivers where moisture levels can be maintained
ARF	Araucaria forest	Exist on high elevations (500 – 1800 m) under moist conditions, annual precipitation ~2000 mm and a short or no marked dry season
CLF	Cloud/montane forest	Mostly evergreen, closed forests with medium sized trees and shrubs, existing at high elevations (> ~ 1000 m), where orographic rain and persistent low-level clouds can maintain moisture levels
SAV	Savannah/ Grassland/ Scrubland	Generally, refers to open savannahs with few arboreal elements indicative of low annual precipitation (< ~1500 mm) and a long dry season (> 5 – 6 months). We also include sub-tropical campos grassland in this classification to represent open vegetation on the south Brazilian highlands that can exist in climates with dry season lengths ~ 3 months.

Code	Vegetation classification	Description
PSW	Palm swamp	Flooded, wetland areas (often due to poor soil drainage), often dominated by the palm <i>Mauritia flexuosa</i>

Table 3.

Category	Definition
Large (L)	Lakes larger than ~5 km ² , vegetation reconstructions representative of regional scale
Medium (M)	Lakes between ~800 m ² and 5 km ² , vegetation reconstructions representative of local to regional scale
Small (S)	Peat bogs, terrestrial swamps, lakes less than 800 m ² , vegetation reconstructions representative of local scale
Extra-small (XS)	Soil pits, representative of point-scale (i.e. wherever the pit was taken)

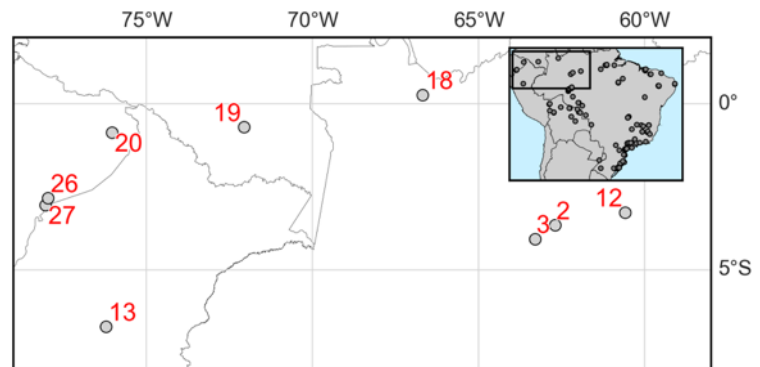
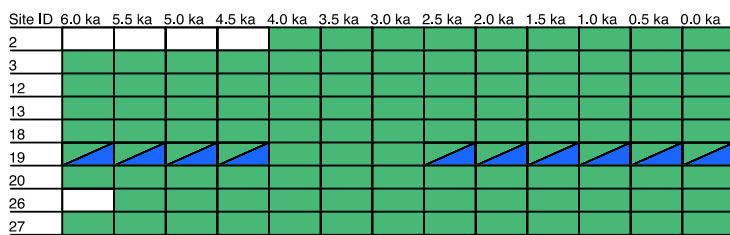
Impact of mid-to-late Holocene precipitation changes on vegetation across lowland tropical South America: a palaeo-data synthesis:

Authors: Richard J. Smith and Francis E. Mayle

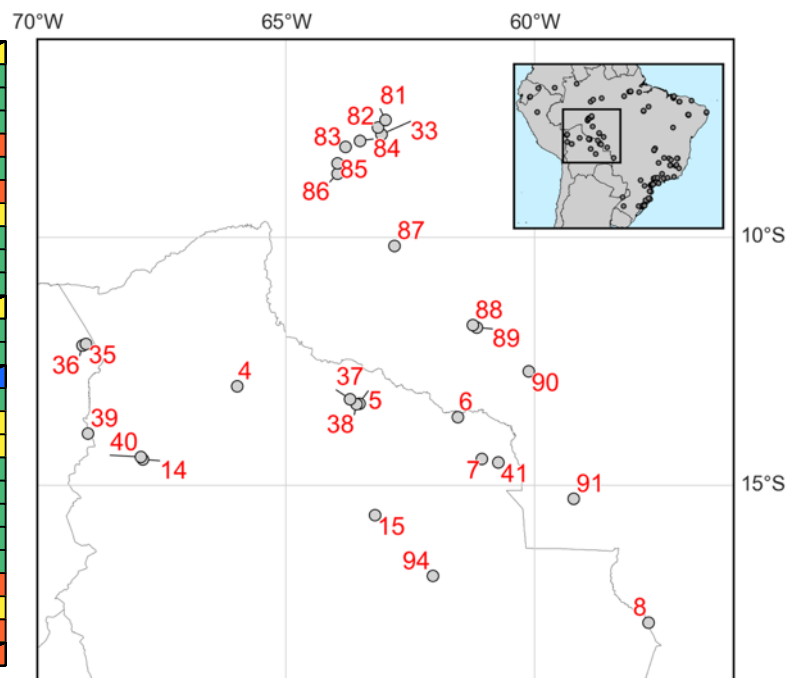
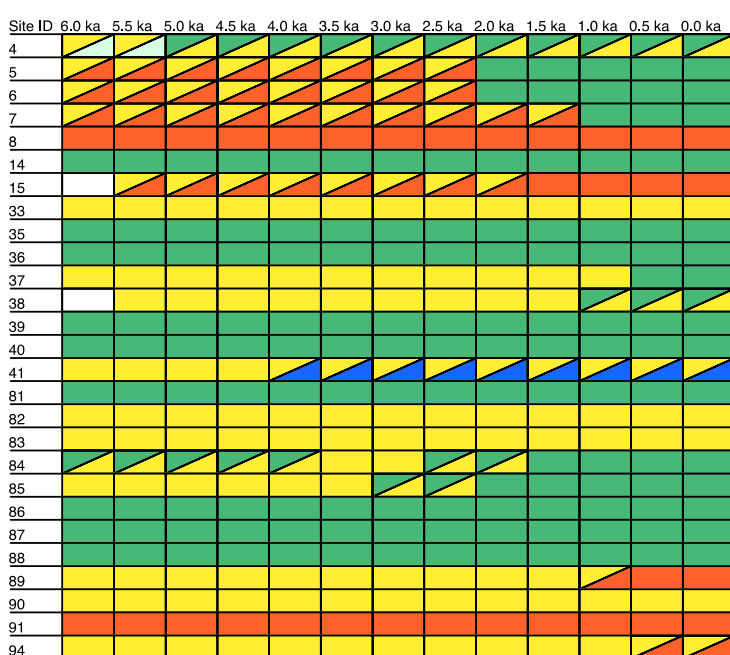
Supplementary Information

Figure S1. Summary tables of vegetation changes at each palaeoecological site, alongside regional maps of the location of each site. Site IDs correspond to those in Table 1.

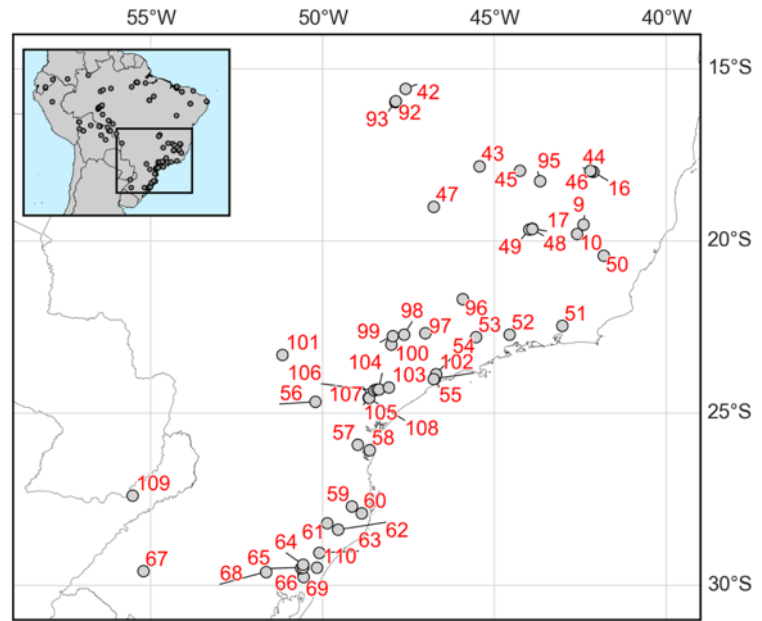
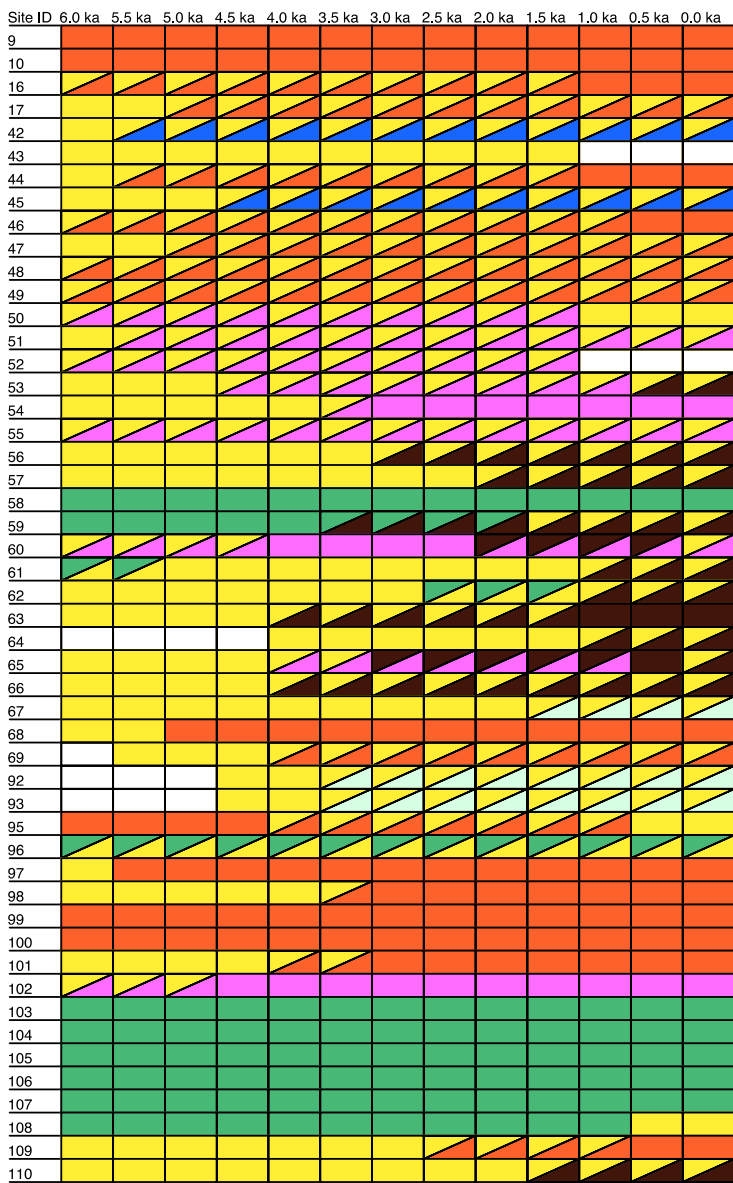
(a) Central and western lowland Amazonia



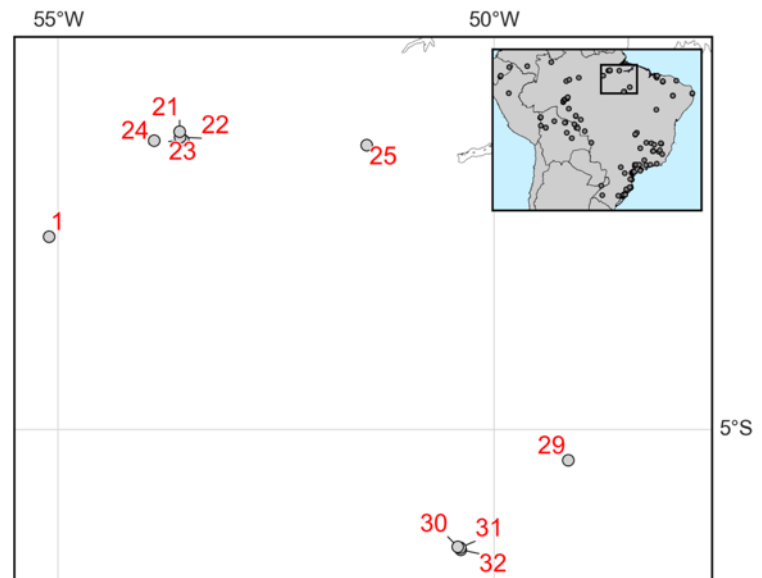
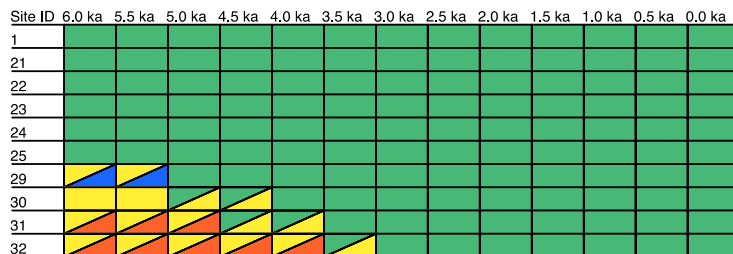
(b) South-Western Amazonia



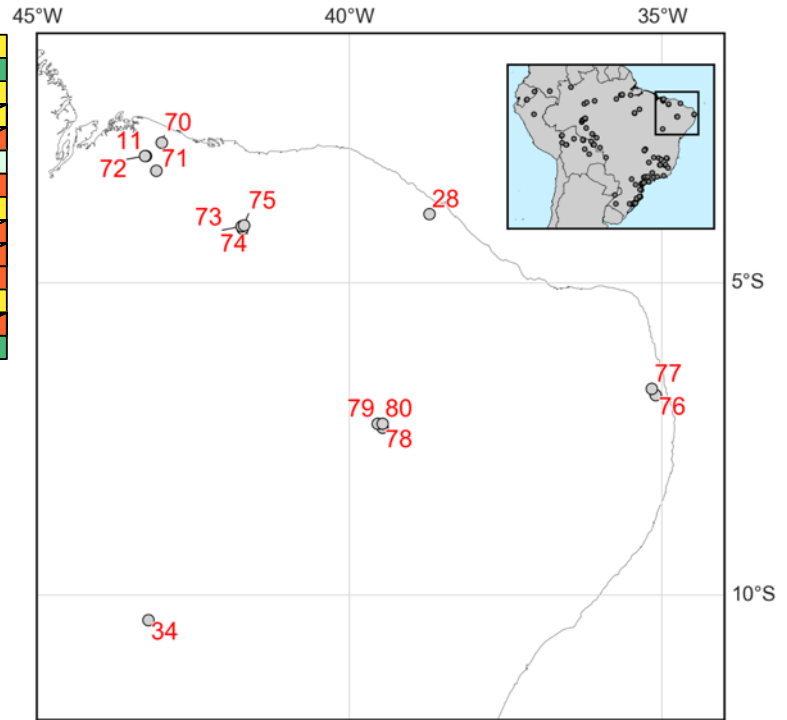
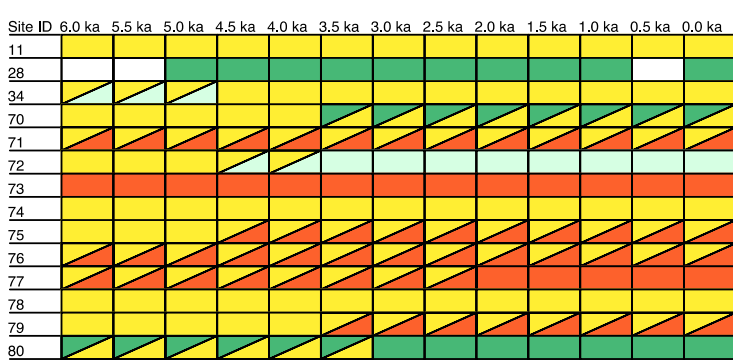
(c) South-eastern Brazil



(d) Eastern Amazonia



(e) North-eastern Brazil



Palaeoecological classifications

