

# *Cold and humid Atlantic forest during the late glacial, northern Espírito Santo state, southeastern Brazil*

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1 **Cold and humid Atlantic forest during the late glacial, northern Espírito Santo state,**  
2 **southeastern Brazil**

3

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25

26 **Abstract**

27 The Atlantic Rainforest, covering the area from the northern Espirito Santo to Southern  
28 Bahia states, has been considered as a stable forest during Pleistocene Glacial times.  
29 Despite the modelling and phylogenetic studies, this hypothesis has never been tested  
30 with empirical paleo-data and vegetation reconstruction. By using palynology,  
31 radiocarbon dating, carbon and nitrogen elemental and isotope of organic matter, we  
32 reconstructed the vegetation dynamics and inferred climatic changes since Late  
33 Pleistocene in the centre of this global biodiversity hotspot. Our results show that the  
34 forest biome was resilient to Last Glacial Maximum - LGM conditions, but floristics has  
35 changed when compared to nowadays. Since late glacial, the dense forest changed from  
36 cold to warm specimens. Major vegetation changes also occurred during early and mid-  
37 Holocene less humid conditions, with an opening of the forest, suggesting that future  
38 drought may have negative impacts and highlighting the importance of forest  
39 conservation to keep the Atlantic Rainforest biodiversity.

40 **Keywords:** Palynology, Carbon Isotope, Radiocarbon dating, LGM, Tropical forest

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42

43

## 1. Introduction

44           Some theories have been proposed to explain the high percentage of endemism  
45 (Prance, 1982, 1987; Mori et al. 1981), the greatest diversity of species (Smith, 1962),  
46 and botanical uniqueness (Mori et al. 1981) of tropical forests. From Northern Espírito  
47 Santo to Southern Bahia, the Atlantic Rainforest was considered stable during  
48 Pleistocene, referred to as Bahia forest refuge (Prance, 1982) or as the most "historically  
49 stable regions of Atlantic forest" (Carnaval and Moritz, 2008), considered a global  
50 biodiversity hotspot (Carnaval et al. 2009).

51           In this context, paleoenvironmental studies have contributed to understanding  
52 the Atlantic Rainforest vegetation dynamics, its distinct local response to Quaternary  
53 climate and instigated the debate about forests refuge hypothesis, especially in ecotone of  
54 forests versus savanna.

55           A wide range of climatic conditions can be noted in the Atlantic forest along  
56 Brazil, and three main areas based on fossil pollen records can be defined as follows:  
57 North Atlantic Forest (NAF; 5°-15°S), Central Atlantic Forest (CAF; 15°-23°S), and  
58 South Atlantic Forest (SAF; 23°-30°S; Ledru et al. 2017). The southern area host mainly  
59 species adapted to cool wet climate as *Araucaria angustifolia*, the central area, where the  
60 study area is located, is composed of coastal forest and inland areas dominated by semi-  
61 deciduous forests, whereas north represents a moist cool semi-deciduous forests restricted  
62 to the coastal zones, lowland and mountaintops (Ledru et al. 2016, 2017).

63           In central and western regions of Atlantic Forest, the Last Glacial Maximum  
64 (LGM) was characterized by the expansion of grasslands and savannas elements and  
65 decrease of arboreal pollen (Behling and Lichte, 1997; Stevaux, 2000; Ledru et al. 2005;  
66 Ledru et al. 2009) or isotopic variations from C<sub>3</sub> to C<sub>4</sub> plants recorded in soil organic  
67 matter (Gouveia et al. 2002; Pessenda et al. 2004; Saia et al. 2008) in the Late

68 Pleistocene/Mid-Holocene interval. Other studies have shown no evidence of forest's  
69 reduction, but the maintenance of the local humidity or the mosaics (forest and  
70 grasslands), even during LGM (De Oliveira, 1992; Cruz Junior et al. 2006, 2007;  
71 Pessenda et al. 2009), corroborating to the hypothesis of the existence of stable tropical  
72 forested areas during glacial times.

73 Studies of ecological niche models under paleoclimate compared to small  
74 animal's indicators and DNA proposes that the areas referred as forest refuge were  
75 maintained as stable forests, whose high contemporary diversity allowed the development  
76 of high local biodiversity (Carnaval and Moritz, 2008; Carnaval et al. 2009; Leite et al.  
77 2016).

78 The key aim of this study was to provide empirical paleovegetation data obtained  
79 from the middle of the area considered historically stable Rainforest, which has the  
80 highest biodiversity compared to the entire Atlantic forest biome and test if the rainforest  
81 was stable through the Late Quaternary as previously indicated by DNA and Modelling-  
82 based hypothesis. Our question in this paper is to check how this area responded to LGM  
83 and drier mid-Holocene climate by using palynology, radiocarbon dating and Nitrogen  
84 and Carbon elemental and isotope analysis.

85 Understanding response to LGM and mid Holocene climate change will help to  
86 test the performance of vegetation/climate models and the identification of priority areas  
87 for conservation.

88

### 89 *1.1 Regional Settings*

90 At the northern coast of Espírito Santo state, Brazil, between Doce and São  
91 Mateus rivers, two ecological reserves of Atlantic Rainforest, Vale Nature Reserve

92 (VNR) and Sooretama Biological Reserve (ReBio Sooretama) cover an area of  
93 approximately 50,000 ha of preserved vegetation (Fig 1).

94 The sampling point, known as Brejo do Louro (BL), comprises an herbaceous  
95 slightly depressed bog surrounded by dense Atlantic Rainforest, ~33km far from the  
96 current coastline, ~45 metres above sea-level (m.a.sl), and located at 19°06'32.2''S/  
97 40°01'53.8''W. The topographic difference between the bog and the forest adjacent is  
98 ~4-5m, and the area becomes flooded during the rainy season, presenting a water column  
99 around 0.5 m that preserves plant remains in an anoxic environment, developing a suitable  
100 place to peat preservation.

101 Underneath the peat, the substrate contains coarse-grained sand, classified as  
102 Spodosol (Santos et al. 2013) based on maps of soil distribution and researches developed  
103 (Schiavo et al., 2020) in the study area. Spodosols are usually found in cold climates, as  
104 northern Europe and Central Asia, but can be present in tropical regions too. In Brazil,  
105 Spodosols are present mainly in coastal environments (Gomes et al. 2007; Oliveira et al.  
106 2010; Coelho et al. 2010) and in Amazon, upper Rio Negro basin (Mafra et al. 2002). It  
107 is composed of relatively young soils, nutrient poor and strongly influenced by water  
108 table fluctuations (Calegari et al. 2017).

109 The regional climate is strongly seasonal classified as "Aw" - tropical humid- at  
110 the Köppen System (Köppen, 1948) with an average temperature ranging between 20 -  
111 26°C. The mean annual precipitation is 1215 mm (data obtained at RNV meteorological  
112 station) highly concentrated during austral summer, controlled by the South America  
113 Monsoon System (SAMS) - the South Atlantic Convergence Zone (SACZ) (Carvalho et  
114 al. 2004; Garreaud et al. 2009). The dry season occurs during austral winter, from May  
115 to September. The other two important air masses that bring humidity to this region are  
116 the South Atlantic Trade Winds and the Atlantic Polar Front (Dominguez et al. 1992).

117 The annual rainfall increases and the seasonality decreases from Espírito Santo to  
118 Southern Bahia, sustaining warm and humid coastal rainforest (Oliveira-Filho and Fontes,  
119 2000).

120 The region presents diverse phytophysiognomies inserted at Atlantic Rainforest  
121 *latu sensu* domain (Rizzini, 1997), basically composed by *Tabuleiro's* forest (1),  
122 grasslands (2) and rare and narrow areas of mangroves at the coast;

123 (1) Characterized by a canopy around 30 m, containing emergent trees up to  
124 40m (Rizzini, 1997). It is also present a lower arboreal stratum of 20 m and a  
125 not so dense herbaceous stratum. Some typical *taxa* present disjunct distribution  
126 with the Amazon biome (Mori et al. 1981) as *Parkia pendula*, *Swartzia*  
127 *polyphylla*, *Lycania cymosa* and *Anthodiscus amazonicus*; and some elements  
128 endemics from *Tabuleiros's* forest as *Hydrogaster trinervis*; and elements  
129 widespread in other areas of Atlantic Rainforest from Southeast Brazil. This type  
130 of vegetation (i.e. *Tabuleiro's* forest) occurs from Rio de Janeiro to Pernambuco,  
131 but the central area is from northern Espírito Santo to Southern Bahia, above the  
132 Neogene deposits of *Barreiras* Formation.

133 (2) Also called *campos nativos* or *mussununga* vegetation, settled over Spodosol  
134 patches that become flooded during the rainy season (IBGE, 1987). *Campos*  
135 *nativos* ranges from grasslands to woodlands with sparse trees as a response to  
136 soil water retention (Sporetti-Junior et al., 2012). Stress tolerant and mesic  
137 species are related to being found in *campos nativos* such as *taxa* of Poaceae,  
138 Melastomataceae, Bromeliaceae, Bignoniaceae, and Myrtaceae (Candido et al.,  
139 2019).

## 140 **2. Material and Methods**

### 141 *2.1. Sampling and substrate features*



142 A 123-cm long core was collected in the middle of Brejo do Louro bog using a  
143 vibro-corer aluminum tube system. The water table was right below the bottom of the  
144 tube. At  $^{14}\text{C}$  Laboratory of CENA/USP, substrate samples were systematically taken each  
145 2 cm to perform the analyses and described according to the variation of colours, grain  
146 size, and texture. Roots, charcoal and vegetation fragments were also recorded and  
147 collected. To grain size analysis, sub-samples were sent *in natura* to the Geosciences  
148 Institute from the University of São Paulo (USP). The grain size distribution was  
149 performed using a Laser Diffraction Particle Size Analyzer Malvern Mastersizer - 2000.

150

## 151 2.2. $^{14}\text{C}$ dating and age-depth model

152

153 Fourteen substrate organic matter samples were sent to radiocarbon dating by  
154 accelerator mass spectrometer (AMS) at the University Federal Fluminense Radiocarbon  
155 Laboratory (LACUFF) and Centre for Applied Isotope Studies at the University of  
156 Georgia, USA (UGAMS). Organic bulk substrate samples were physically and  
157 chemically-treated based on Pessenda et al. (2009). Radiocarbon dates were reported as  
158  $^{14}\text{C}$  yr ( $1\sigma$ ) BP (Before 1950 AD) and in calibrated years as cal yr ( $2\sigma$ ) BP (Reimer et al.  
159 2013) and each sample normalized to isotope fractionation ( $\delta^{13}\text{C}$ ) with respect to VPDB  
160 (Vienna Pee Dee Belemnite Standard) in the conventional  $\delta$  (‰) notation, with standard  
161 deviation of  $\pm 0.2\%$ . The Bayesian age-depth model of the BL core was obtained using  
162 the Bacon R package v.2.3.5 (Blaauw and Christen, 2011) and Intcal13 calibration curve  
163 (Reimer et al., 2013). All results and discussions are based on the mean calibrated age  
164 (mean cal yr B.P.).

165

## 166 2.3. C and N analyses

167           Elemental and isotopic analyses of total carbon and nitrogen of organic matter  
168 were performed each 2 cm and bulk substrate samples pre-treated physically and  
169 chemically according to Pessenda et al. (1996). The most representative modern plant  
170 species around the sampling point were also analysed to carbon isotope. Modern plants  
171 collected around the sampling point were washed in deionized water, dried at 40°C, and  
172 grinded. Then, plants and substrate subsamples were sent to the Stable Isotope Laboratory  
173 of CENA/USP (São Paulo, Brazil), and analyses were carried out on an elemental  
174 analyser attached to a Mass Spectrometry ANCA SL 2020 of Europa Scientific. Total  
175 Carbon and Nitrogen are expressed as percentages of dry weight.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are  
176 measured with respect to VPDB and atmospheric nitrogen, respectively, using the  
177 conventional  $\delta$  (‰) notation, with standard deviation of  $\pm 0.2\text{‰}$ .

178

#### 179           2.4. Palynology

180

181           Subsamples of 2 cm<sup>3</sup> were processed each 2-cm with the addition of two spikes  
182 of exotic *Lycopodium clavatum* spores (Batch number: 177745, Lund University, 2008)  
183 to determinate pollen and spore's concentration (Colinvaux et al. 1999). The samples  
184 were sieved (0.210 mm) before the chemical treatment, due to the high concentration of  
185 coarse-grained sand. The procedure was based on the addition of HF to remove minerals,  
186 KOH and acetolysis to remove humic acids, and the organic contents of the  
187 palynomorphs. For each sample, at least 300 terrestrial pollen grains (trees, shrubs and  
188 herbs) were counted using ZEISS photomicroscopes at 1000x. Non-terrestrial taxa, fern  
189 spores and algae were not included in the total pollen sum. Identification was based on  
190 the pollen reference collection of the <sup>14</sup>C Laboratory (CENA/USP) and from the  
191 University of Reading, UK. Pollen diagrams were plotted using TILIA and TGView

192 1.7.16 and CONISS - cluster analysis by similarity index - to calculate the zone  
193 boundaries (Grimm, 1992).

194

### 195 **3. Results and Discussions**

#### 196 *3.1 <sup>14</sup>C dating*

197 The <sup>14</sup>C dating results of BL core (Table 1) revealed ages ranging from ~35,910  
198 cal yr. BP (119 cm) to ~2140 cal yr. BP (11 cm), and substrate accumulation rates ranging  
199 from 0.007 mm/yr. (49-45 cm) to 0.44 mm/yr. (53-49 cm). Fourteen radiocarbon dating  
200 in a 123 cm core provided a high resolution. Approximately the same ages were recorded  
201 for the depths 49 (~13,740 cal yr. BP) and 45 cm (~13,650 cal yr. BP), which reflects low  
202 accumulation rates (0.009 mm/yr.). Ages inversions were observed between 71 (~20,880  
203 cal yr. BP), 61 (~22,020 cal yr. BP) and 57 cm (~20,940 cal yr. BP). All the samples  
204 received the same chemical treatments, and both LACUFF and UGAMS laboratories  
205 were inter-calibrated (Macario et al. 2013).

206 Thus, the age inversions may be due to erosion processes and/or bioturbation  
207 during the soil formation (Boulet et al. 1995). Furthermore, the content of organomineral  
208 complexes in the samples may have influenced the radiocarbon dating, once organic clay  
209 complexes tend to rejuvenation the soil organic matter (Scharpenseel and Becker-  
210 Hedimann, 1992). A similar interpretation can be found at Nativo do Flamengo, 11 km  
211 from BL (Buso Junior et al. 2019). Also, we cannot discard a depositional hiatus between  
212 53 to 49 cm (19,310 to 13,740 cal yr BP), and 45 to 41 cm (13,650 to 9500 cal yr BP),  
213 probably due to erosion processes associated with the water table movements in the bog.

#### 214 *3.2 Substrate features*

215 No substrate structures were visible along the core. Medium grained sand (>50%)  
216 containing organic matter domains the profile from 123 to 20 cm, >35,910 to 7300 cal yr  
217 BP (Fig 2). The range of sand compounds varies from 83 to 90%, and from 50 to 80%  
218 along the 119 - 75 cm (35,910 to 24,260 cal yr BP – estimated age) and 75 - 0 cm (<  
219 24,620 cal yr BP – estimated age) intervals, respectively; followed by silt (5 to 30%).  
220 From ~16 cm to the top (< 4000 cal yr BP), vegetal remains and roots were preserved,  
221 probably due to the proximity to the water table most of the year.

222 Considering the depression where the sampling site is located and the relative  
223 abundance of mud along the stratigraphic profile, probably such deposit was formed by a  
224 vertical accretion in a lake during at least 36,000 years. This environment favoured the  
225 continuous accumulation and preservation of pollen grains. However, post-depositional  
226 process may have increased the ratio sand/mud along the studied core, since previous  
227 works indicate that deposits suffered podsolization (Santos et al. 2004). This process  
228 causes weathering and migration of aluminium, iron, and organic matter along the profile  
229 with the formation of cemented B spodic horizon, characteristic of Spodosols (Santos et  
230 al. 2009; Schiavo et al. 2020). The organic matter content, its quality, and mobilization  
231 play an important role in the weathering of minerals and the transfer of metal ions (Fritsch  
232 et al. 2009, 2011; Nikodem et al. 2013). This process may have favored the proportional  
233 increase in the sand fraction in the studied deposits, where kaolinite ( $\text{Si}_2\text{Al}_2\text{O}_5$ ), which  
234 constitutes the silt/clay fraction, is more easily weathered. The sandy fraction represented  
235 by quartz ( $\text{SiO}_2$ ) grains is more resistant to physical and chemical weathering. The time  
236 required for the formation of Spodosols may require between 300 and 3000 years,  
237 depending on the vegetation and climatic conditions (Nikodem et al. 2013).

238

239

240           3.3 Late Pleistocene and Holocene vegetation

241           3.3.1. Late Pleistocene

242

243           Despite the substantial concentration of organic matter and TOC values around  
244 12%, palynomorphs were not preserved in the substrate dating from ~35,900 to ~33,460  
245 cal yr BP (119-103 cm; 0.06 mm/yr; Fig. 2). The absence of palynomorphs may be due  
246 to leaching of pollen grains caused by fluctuations in the water table, as proposed for  
247 phytoliths at this site (Calegari et al. 2017).

248           Carbon isotope values ( $\delta^{13}\text{C}$ ) with a mean value of -28‰, typical of C<sub>3</sub> plants,  
249 indicates the presence of the forest and/or C<sub>3</sub> grasses sources since at least ~33,460 cal yr  
250 BP (103 cm). Trees and shrubs types (~85%) dominated the pollen spectra at the end of  
251 the early glacial (Fig. 2). *Tapirira* was the most abundant (~21%), probably due to its  
252 relatively high pollen dispersal power (Behling and Negrelle, 2006) followed by  
253 *Symplocos* (~12%) and *Ilex* (~10%). Together with *Podocarpus* (~4%), the pollen  
254 assemblage indicates the presence of plant communities very different from the present  
255 (Fig. 3). *Symplocos*, *Ilex*, and *Podocarpus* are strongly related to high altitudes and  
256 relatively low temperatures in South and Southeastern Brazil (Oliveira-Filho and Fontes,  
257 2000). Also, *Podocarpus* is a conifer indicator of cold and moist climate (Ledru et al.  
258 2009). Besides that, pollen traps from Atlantic Rainforest of Santa Catarina state  
259 (Southern Brazil), characterized as meso-thermic with no frosts and very humid without  
260 a dry season, shows similar pollen assemblage found at BL from ~33,460 to ~13,740 cal  
261 yr BP (103-49 cm; 0.04-0.44 mm/yr) as: *Tapirira* (24.9%), *Alchornea* (12%), *Rapanea*  
262 (6.8%), *Sloanea* (5.4%), *Ilex* (0.9%) and *Podocarpus* (0.8%) (Behling and Negrelle,  
263 2006).

264 Typically forest trees such as *Laplacea* (4%), *Eriotheca* (3%), *Virola* (2%)  
265 *Sloanea* (~1%) indicate the presence of the dense forest near BL (Fig. 3). The rare type  
266 *Glycidendron* (present up to ~1%), known as disjunct genera between Amazon and  
267 Atlantic Rainforest (Buso Junior et al. 2013), indicates the humid forest conditions and  
268 that genera occupied the region since at least ~25,760 cal yr BP (81 cm) (Fig. 3).

269 Despite the increase of Poaceae (from 7% to 37%) and decrease of arboreal/shrub  
270 specimens between ~25,760 and ~13,740 cal yr BP (81-49 cm; 0.02-0.44 mm/yr), the  
271 high concentration of arboreal plants (90 - 65%) and the depleted mean value of  $\delta^{13}\text{C}$   
272 (~-28‰) indicate the forest dominance associated to C<sub>3</sub> herbs during LGM, probably due  
273 to a predominantly humid climate in the period (Fig. 2).

274 Two different sections show low substrate accumulation rates (Table 1), one of  
275 almost 6000 years, where mean calibrated ages vary from 19,310 (53 cm) to 13,740 cal  
276 yr BP (49 cm), with accumulation rates of 0.007 mm/year, and another of 4000 years  
277 from 13,650 (45 cm) to 9500 (41 cm) cal yr BP, with accumulation rates around 0.009  
278 mm/year and an age inversion at 71cm (20,880 cal yr BP). Similarly, stratigraphic records  
279 indicated low sedimentation rates and age inversions for the end of the Late Pleistocene  
280 and the beginning of Holocene in Southeast Brazil, between 23 and 12 kyr (Ledru et al.  
281 1998; Behling and Negrelle, 2001; Behling et al. 2002; Pessenda et al. 2009). In the study  
282 area, the palynology and depleted mean value of  $\delta^{13}\text{C}$  ~-28‰ attest to the dominance of  
283 forest and C<sub>3</sub> grasses during these periods, signifying a humid climate (Fig. 2). Based on  
284 that climatic inference, the low accumulation rate is probably associated with the erosion  
285 processes caused by leaching of surface water and the water table movement. Despite the  
286 low activity found in similar substrates (Buurman and Jongmans, 2005), the bioturbation  
287 process (Gouveia and Pessenda, 2000) associated with the age inversion cannot be  
288 discarded.

289 3.3.2. Holocene vegetation

290

291 Between 13,740 and 7300 cal yr BP (49-21 cm; 0.009-0.02 mm/yr), herbaceous  
292 plants domain the palynological records (up to 95%), and the  $\delta^{13}\text{C}$  values ranged from ~-  
293 28‰ to ~-24‰, indicating mixture of  $\text{C}_3$  and  $\text{C}_4$  sources and isotope enrichment since  
294 ~9500 cal yr BP (41 cm) up to ~7300 cal yr BP (21 cm) (Fig. 2). Poaceae represents up  
295 to ~87%, followed by Cyperaceae (5% - 8%). Phytoliths from BL also indicate the  
296 presence of grasses (up to 43%) of  $\text{C}_4$  (Panicooid 2.4%) mixed to  $\text{C}_3$  herbaceous plants  
297 (Pooid 5.4%) during the same period (Calegari et al. 2017). The generas *Tapirira*, *Ilex*,  
298 and *Symplocos*, which were highly dominant until the end of the early glacial, between  
299 13,740 and 7300 cal yr BP (49-21 cm; 0.009-0.2 mm/yr) present lower mean percentages  
300 of 0.4, 1.4, and 6%, respectively. *Laplacea*, *Eriotheca*, *Virola*, and *Sloanea* pollen, even  
301 present in low abundance, indicate that the forest was present between 13,740 and 7300  
302 cal yr BP (49-21 cm; 0.009-0.2 mm/yr) (Fig. 3).

303 From ~7300 cal yr BP (21 cm) to present, peat formation occurred. The TOC  
304 increases (up to 66%), the  $\delta^{13}\text{C}$  ranges from -24‰ (~7300 cal yr BP; 21 cm) to ~-30‰  
305 (present) and  $\text{C}/\text{N} \times \delta^{13}\text{C}$  (Figs. 2, 4) indicates the presence of freshwater phytoplankton,  
306 due to the water layer that maintains the local humidity and creates an anoxic place,  
307 minimizing the organic carbon degradation and supporting the peat preservation.  
308 Palynology attests that Algae as *Zygnema* (6 - 58%) and *Spirogyra* (0.3 – 6.7%) were  
309 abundant (Fig. 3).

310 From estimated ~4000 (15 cm) to 970 cal yr BP (7 cm) pollen grains from  
311 herbaceous plants inside the bog as Poaceae (11%), Cyperaceae (7%), Asteraceae (7%)  
312 were less abundant (between 25 and 32%). Trees and shrubs around the bog presented a  
313 frequency of ~55 to 70%, as Melastomataceae/ Combretaceae (~16%), Myrtaceae (~9%),

314 *Alchornea* (~5%), *Tapirira* (~2%) and *Cordia* (~2%). The abundance of Moraceae/  
315 Urticaceae (4 - 23%) indicates that the forest vegetation was relatively near the bog. The  
316 abrupt abundance of *Typha* (250%), *Potamogeton* (18%), and the spore of *Salvinia* (11%)  
317 indicate its local colonization (Fig. 3).

318 From estimated ~970 cal yr BP (7 cm) to present, composed by small trees and  
319 shrubs (~50 to 73%) sparsely distributed with abundance of Melastomataceae/  
320 Combretaceae (15 - 42%), *Alchornea* (4 - 22%), Myrtaceae (3 - 8%), *Tapirira* (1 - 4%)  
321 and *Cordia* (0 -1%). These families and genera are found around BL, as transitional  
322 vegetation between the bog and the dense forest. Poaceae (13 - 25%) and Cyperaceae (2  
323 - 7%) mainly from C<sub>3</sub> photosynthetic cycle and some aquatic (70 - 90%) plants as *Typha*  
324 (55 - 76%), *Potamogeton* (6 - 10%) and *Echinodorus* (1 - 6%) that occurs during the rainy  
325 season shows a very local signal. Despite the presence in low abundance, pollen genera  
326 strictly from the dense forest as *Virola* (~3%) and *Chrysophyllum* (0.3%), suggests that  
327 the dense forest is near BL, as exists today (Fig. 3).

### 328 3.4 Modern vegetation

329 The modern dominant vegetation within the bog BL is mainly composed of shrubs  
330 and herbs with  $\delta^{13}\text{C}$  values varying from -20.6‰ (*Andropogon bicornis*) to -29.8‰  
331 (*Cyperus* sp.) and small trees as *Alchornea triplinervia*,  $\delta^{13}\text{C}$  -29.3‰ (Fig 5). Only  
332 dominant grass *Andropogon bicornis* presents C<sub>4</sub> photosynthetic cycle ( $\delta^{13}\text{C}$ : -20.6‰).  
333 The values range of C<sub>3</sub> plants may be attributed to the water layer present in the bog, since  
334 the high humidity is suitable for its development and establishment.

335

### 336 3.5 Paleoenvironmental Interpretation

#### 337 3.5.1 Late Pleistocene



338 Palynology and carbon isotope indicate the presence of a typically cold and  
339 dense forest near the BL bog in a terrestrial organic matter sources domain from ~33,460  
340 cal yr BP to ~25,760 cal yr BP (103-81 cm; 0.06-0.02 mm/yr). In Colônia crater, São  
341 Paulo State, Ledru et al. (2009) recorded a pollen assemblage associated with a cold forest  
342 during the time interval between 30 and 23k cal yr BP, which reflect forest expansion and  
343 a cold and wet climate. Similar climate conditions were also characterized in Salitre,  
344 Minas Gerais State (Ledru et al. 1996), and in the marine core GeoB3202-1  
345 (21°37'S/39°58'W; Behling et al. 2002) for the same period, and those data are  
346 comparable to BL.

347 From ~25,760 and ~13,740 cal yr BP (81-49 cm; 0.04-0.44 mm/yr) the slight  
348 increase of herbs probably occurred due to C<sub>3</sub> Poaceae/Cyperaceae locally occupying the  
349 bog, once the carbon isotope is around ~-28‰ (Fig. 2). In the Colônia crater, the  
350 biodiversity index decreased, and open vegetation dominated by Poaceae replaced the  
351 rainforest between 23 and 12k yr BP. During the LGM dry and erosive climatic conditions  
352 were predominant (Ledru et al. 2009). Such climatic conditions were also characterized  
353 by other palynological records in southeastern Brazil (Ledru et al. 1996, 1998; Behling et  
354 al. 2002).

355 Despite the differences in floristics composition comparing the vegetation from  
356 LGM to present in the BL, it is possible to assume that the forest was stable in a  
357 predominantly humid climate during the end of the Late Pleistocene. The maintenance of  
358 forest vegetation since the Late Pleistocene in northern Espírito Santo was also noted by  
359 Buso Junior et al. (2013). According to the authors,  $\delta^{13}\text{C}$  analysis of soil organic matter  
360 at the forest and grassland sites suggest the dominance of C<sub>3</sub> plants and humidity  
361 conditions since ~17,000 cal yr BP.

362           The BL data for Late Pleistocene is consistent with data obtained from noble gases  
363 from Piauí state (Stute et al. 1995), which suggests a cooling of 5°C during the LGM  
364 across the Americas between 40°N and 40°S. Studies in speleothems refer to LGM, as  
365 wet period in Southeastern Brazil (Cruz Junior et al. 2005, 2006, 2007; Cheng et al. 2012),  
366 due to the expansion of Ice sheets in Northern Hemisphere, causing a southward shift in  
367 the Intertropical Convergence Zone (ITCZ) (Wang et al. 2004) and the strengthened of  
368 the South America monsoon system. In agreement with moister conditions indicated by  
369 speleothem data, Ledru et al. (2016) cited the presence of semideciduous and evergreen  
370 forests at low latitudes during the late glacial, however, with a floristic composition  
371 different from actual.

372           Similar data was also recorded for the Serra do Mar State Park – Curucutu and the  
373 Cardoso Island (Pessenda et al. 2009, 2012), São Paulo state, southeastern Brazilian coast.  
374 Between 22,780 and 12,000 cal yr BP Curucutu site was characterized by a forested  
375 landscape with montane species such as *Araucaria*, *Podocarpus*, and *Weinmannia*, an  
376 increase of algal spores and a more significant contribution of C<sub>3</sub> grasses, which suggest  
377 a cold and humid climate (Pessenda et al. 2009). The same line of reasoning applies to  
378 Cardoso Island, ~170 km of Curucutu, where the pollen record indicated a cool climate  
379 forest in the period from ~29,500 to ~23,000 cal yr BP (Pessenda et al. 2012).

380           Speleothems at the Botuverá cave, southern Brazil, recorded higher  $\delta^{13}\text{C}$  and low  
381 stalagmite growth rates between 116 and 19k cal yr BP and reflect a significant cooling  
382 during the glacial period, probably due to incursions of polar cold air over south  
383 hemisphere (Cruz et al. 2006). In the Linhares region, northern Espírito Santo, Buso  
384 Junior et al. (2013) postulated that polar air masses may have reached the studied area  
385 during the Late Pleistocene and early Holocene, which allowed the maintenance of the  
386 forest due to frontal precipitation and a humid climate.

387

### 3.5.2 Holocene

388 From 13,740 to 7300 cal yr BP (49-21 cm; 0.44-0.02 mm/yr), the herbaceous  
389 plants domain and the carbon isotope enrichment (up to  $\sim$ -24‰) (Fig. 2) together with  
390 the phytoliths results (Calegari et al. 2017) indicating the presence of C<sub>3</sub> and C<sub>4</sub> grasses  
391 probably due to a less humid climate. Although, the presence of *Zygnema* and *Spirogyra*  
392 algae during the same period (Fig. 3) may be indicative of a high seasonal system, with  
393 wet and dry seasons well defined. Even so, this opening of vegetation recorded at the bog  
394 probably did not occur at the forest, once it is possible to find dense forest specimens at  
395 the pollen records such as *Virola*, *Laplacea* and *Sloanea*, even in low abundance (Fig. 3).

396 A palynological study by Buso Junior (2015) of Lake Canto Grande, north of  
397 Espirito Santo and 13 km far from BL, revealed that the species composition of the forest  
398 around the lake between 11000 and 7700 cal yr BP presented differences in relation with  
399 the modern *Tabuleiro's* forest, probably due to a less humid period. The relatively dry  
400 period in the region may have influenced the sedimentation of sand-rich sediments and  
401 alluvial processes (Lorente et al. 2018). The same context was observed by Garcia et al.  
402 (2004) at Jacareí deposits, São Paulo State, where the authors recorded Poaceae pollen  
403 increase and drop in the sedimentation rate between  $\sim$ 8000 and  $\sim$ 5000 cal yr BP,  
404 reflecting a less humid climate.

405 At Nativo do Flamengo, 11 km from BL, herbs-dominated record and pollen of  
406 *Rheedia brasiliensis*, a typical species which occur on sandy soils of dry and seasonally  
407 flooded areas, may indicate a less humid climate at the region before 7000 yr BP (Buso  
408 Junior et al. 2019). In addition, depleted  $\delta^{13}\text{C}$  values, the dominance of C<sub>3</sub> plants, and the  
409 presence of freshwater sponge spicules suggest that a more humid climate and the  
410 establishment of the wetland may have occurred around 7000 years BP, which is also  
411 comparable to BL.

412 A transgressive sea level was recorded in Brazil during Holocene, starting to rise  
413 at ~6500 <sup>14</sup>C yr BP (~ 7400 cal yr BP) with a peak at ~5000 <sup>14</sup>C yr B.P (~5700 cal yr BP)  
414 (Suguio and Martin, 1981; Suguio et al. 1985; Angulo et al. 2006). This record is in  
415 accordance with the peat formation and the presence of freshwater phytoplankton found  
416 at BL around ~7300 cal yr BP. As the bog is placed at ~45 m.a.sl, located far away from  
417 the coast (~33 km) and has no link to the tidal channel, all the water source comes from  
418 rain and the water table, probably mainly driven by climatic conditions and influenced by  
419 the water base level during Holocene sea-level rise.

420 Climate changes reported during Late Holocene have contributed to the local  
421 moisture due to the intensification of the South America Monsoon System for the last  
422 ~4000 cal yr BP, caused by the increase of summer insolation (Cruz Junior et al. 2005)  
423 corroborated by many authors throughout Atlantic Rainforest (Behling et al. 1997; Ledru  
424 et al. 2005; Pessenda et al. 2009, 2010). According to Buso Junior et al. (2013), the  
425 modern climate in the Linhares region was established in the last 4000 years. The  
426 abundance of *Typha*, *Potamogeton*, and the spore of *Salvinia*, together with the  
427 correlation C/N x  $\delta^{13}\text{C}$ , probably indicates flooding episodes at BL mainly from ~2140  
428 (11 cm) to ~970 (estimated age; 7 cm) cal yr BP (Figs. 3, 4).

429 Since ~823 cal yr BP (5 cm – estimated age) the pollen testifies the establishment  
430 of current vegetation inside the bog, composed by small trees and shrubs sparsely  
431 distributed between Poaceae and Cyperaceae, aquatic plants that occurs during the rainy  
432 season and the *Tabuleiro's* forest surrounding the area. Pollen traps implanted for 20  
433 months at Nativo da Gavea, whose vegetation structure is similar to BL, 13 km southeast  
434 (19°12'29''S/ 39°57'46''W), presented similar pollen percentages and assembly when  
435 compared to surface samples from BL. Trees and shrubs were well represented (60%)  
436 and herbs (31%) while aquatic herbs were absent, probably because Nativo da Gavea does

437 not become flooded as BL during the rainy season (Buso Junior, 2015). At Nativo do  
438 Flamengo pollen, and sponge spicules analysis also attested the current condition since  
439 ~950 cal yr BP (Buso Junior 2015; Buso Junior et al. 2019).

440 Paleodata obtained from BL has shown the long-term stability of the rainforest  
441 biome under LGM condition, confirming the modeling and phylogenetic studies, despite  
442 the differences in its floristic composition. Our data reflect a forest with cold and humid  
443 adapted species during the last glacial period, and a bog herb-dominated probably due to  
444 a less humid climate in the early and mid-Holocene. The current floristic composition  
445 only established since the Late Holocene.

446 In contrast to the refugium model (Haffer and Prance, 2002) and the “Historically  
447 stable forest” (Carnaval and Moritz, 2008), results indicate that the patterns of  
448 biodiversity are not an ancient refuge from Pleistocene, but have undergone a significant  
449 change, with no analog assemblage in the Pleistocene. Due to its resilience to climate  
450 change, this complex tropical ecosystem in the north of Espirito Santo state can be  
451 considered a biodiversity hotspot and an important area for conservation priorities.

#### 452 **4. Conclusions**

453 Based on pollen and isotopes records obtained since Late Pleistocene and LGM  
454 at BL, it is possible to assume that the dense forest was stable, but the floristics has  
455 changed through time, from cold to warm specimens, since the pollen assemblage is  
456 significantly distinct in its pollen zones. During the Early and Mid- Holocene, occurred  
457 probably a vegetation opening recorded inside the bog, maybe due to a less humid period,  
458 but did not affect the *Tabuleiro*'s forest drastically. The current floristic composition was  
459 established since the Late Holocene. Considering the past environmental changes in the  
460 Atlantic forest, our data can highlight the importance of forest conservation in the area to  
461 maintain the biodiversity in the face of future climate changes.

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729 **Figure captions**

730

731 **Figure 1.** Study area. A) Map of Brazil emphasizing biomes distribution and the study  
732 area. The numbers indicate paleoenvironmental reconstruction studies on south and  
733 southeastern Brazil. 1. Linhares (ES): Buso Junior et al. 2013, 2019; Buso Junior, 2015.  
734 2. Marine Core GeoB3202-1 (ES): Behling et al. 2002. 3. Salitre (MG): Ledru, 1996. 4.  
735 Jacareí (SP): Garcia et al. (2004). 5. Colônia Crater (SP): Ledru et al. (2009). 6. Curucutu  
736 (SP): Pessenda et al. (2009). 7. Cardoso Island (SP): Pessenda et al. (2012). 8. Botuverá  
737 Cave (SC): Cruz Junior et al. 2005, 2006. The red dot indicates the Brejo do Louro's  
738 location. B) Image obtained from Google Earth showing BL bog surrounded by dense  
739 forest. C) Modern photograph from BL.

740 **Figure 2.**  $^{14}\text{C}$  age-depth model (mean cal yr BP), grain size (%), pollen and spores groups  
741 percentage, total organic carbon (TOC), total nitrogen (TN), C/N, and  $\delta^{13}\text{C}$  values.

742 **Figure 3.**  $^{14}\text{C}$  ages, grain size (%), and taxa percentage from BL core. White and gray  
743 horizontal bars indicate zones generated by CONISS.

744 **Figure 4.** Correlation between  $\delta^{13}\text{C}$  and C/N and their meaning (Meyers, 2003): C<sub>4</sub> Land  
745 plants, C<sub>3</sub> Land plants, and Lacustrine algae.

746 **Figure 5.** Most representative plants collected around the sampling point, the isotopic  
747 value ( $\delta^{13}\text{C}$ ), and habit.

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