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Abstract

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

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

1. Introduction

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

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

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

In central and western regions of Atlantic Forest, the Last Glacial Maximum (LGM) was characterized by the expansion of grasslands and savannas elements and decrease of arboreal pollen (Behling and Lichte, 1997; Stevaux, 2000; Ledru et al. 2005; Ledru et al. 2009) or isotopic variations from C_3 to C_4 plants recorded in soil organic matter (Gouveia et al. 2002; Pessenda et al. 2004; Saia et al. 2008) in the Late

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

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

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

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

1.1 Regional Settings

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

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

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

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

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

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

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

(1) Characterized by a canopy around 30 m, containing emergent threes up to 40m (Rizzini, 199730). It is also present a lower arboreal stratum of 20 m and a not so dense herbaceous stratum. Some typical *taxa* present disjunct distribution with the Amazon biome (Mori et al. 19813) as *Parkia pendula*, *Swartzia polyphylla*, *Lycania cymosa* and *Anthodiscus amazonicus*; and some elements endemics from *Tabuleiros's* forest as *Hydrogaster trinervis*; and elements widespread in other areas of Atlantic Rainforest from Southeast Brazil. This type of vegetation (i.e. *Tabuleiro's* forest) occurs from Rio de Janeiro to Pernambuco, but the central area is from northern Espirito Santo to Southern Bahia, above the Neogene deposits of *Barreiras* Formation.

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

2. Material and Methods

2.1. Sampling and substrate features

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

2.2. ^{14}C dating and age-depth model

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

2.3. C and N analyses

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

2.4. Palynology

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

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

3. Results and Discussions

3.1 ^{14}C dating

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

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

3.2 Substrate features

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

Considering the depression where the sampling site is located and the relative abundance of mud along the stratigraphic profile, probably such deposit was formed by a vertical accretion in a lake during at least 36,000 years. This environment favoured the continuous accumulation and preservation of pollen grains. However, post-depositional process may have increased the ratio sand/mud along the studied core, since previous works indicate that deposits suffered podsolization (Santos et al. 2004). This process causes weathering and migration of aluminium, iron, and organic matter along the profile with the formation of cemented B spodic horizon, characteristic of Spodosols (Santos et al. 2009; Schiavo et al. 2020). The organic matter content, its quality, and mobilization play an important role in the weathering of minerals and the transfer of metal ions (Fritsch et al. 2009, 2011; Nikodem et al. 2013). This process may have favored the proportional increase in the sand fraction in the studied deposits, where kaolinite ($Si_2Al_2O_5$), which constitutes the silt/clay fraction, is more easily weathered. The sandy fraction represented by quartz (SiO_2) grains is more resistant to physical and chemical weathering. The time required for the formation of Spodosols may require between 300 and 3000 years, depending on the vegetation and climatic conditions (Nikodem et al. 2013).

3.3 Late Pleistocene and Holocene vegetation

3.3.1. Late Pleistocene

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

Carbon isotope values ($\delta^{13}C$) with a mean value of -28‰, typical of C_3 plants, indicates the presence of the forest and/or C_3 grasses sources since at least ~33,460 cal yr BP (103 cm). Trees and shrubs types (~85%) dominated the pollen spectra at the end of the early glacial (Fig. 2). *Tapirira* was the most abundant (~21%), probably due to its relatively high pollen dispersal power (Behling and Negrelle, 2006) followed by *Symplocos* (~12%) and *Ilex* (~10%). Together with *Podocarpus* (~4%), the pollen assemblage indicates the presence of plant communities very different from the present (Fig. 3). *Symplocos*, *Ilex*, and *Podocarpus* are strongly related to high altitudes and relatively low temperatures in South and Southeastern Brazil (Oliveira-Filho and Fontes, 2000). Also, *Podocarpus* is a conifer indicator of cold and moist climate (Ledru et al. 2009). Besides that, pollen traps from Atlantic Rainforest of Santa Catarina state (Southern Brazil), characterized as meso-thermic with no frosts and very humid without a dry season, shows similar pollen assemblage found at BL from ~33,460 to ~13,740 cal yr BP (103-49 cm; 0.04-0.44 mm/yr) as: *Tapirira* (24.9%), *Alchornea* (12%), *Rapanea* (6.8%), *Sloanea* (5.4%), *Ilex* (0.9%) and *Podocarpus* (0.8%) (Behling and Negrelle, 2006).

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

Despite the increase of Poaceae (from 7% to 37%) and decrease of arboreal/shrub specimens between ~25,760 and ~13,740 cal yr BP (81-49 cm; 0.02-0.44 mm/yr), the high concentration of arboreal plants (90 - 65%) and the depleted mean value of $\delta^{13}C$ (~28‰) indicate the forest dominance associated to C_3 herbs during LGM, probably due to a predominantly humid climate in the period (Fig. 2).

Two different sections show low substrate accumulation rates (Table 1), one of almost 6000 years, where mean calibrated ages vary from 19,310 (53 cm) to 13,740 cal yr BP (49 cm), with accumulation rates of 0.007 mm/year, and another of 4000 years from 13,650 (45 cm) to 9500 (41 cm) cal yr BP, with accumulation rates around 0.009 mm/year and an age inversion at 71cm (20,880 cal yr BP). Similarly, stratigraphic records indicated low sedimentation rates and age inversions for the end of the Late Pleistocene and the beginning of Holocene in Southeast Brazil, between 23 and 12 kyr (Ledru et al. 1998; Behling and Negrelle, 2001; Behling et al. 2002; Pessenda et al. 2009). In the study area, the palynology and depleted mean value of $\delta^{13}C$ ~-28‰ attest to the dominance of forest and C_3 grasses during these periods, signifying a humid climate (Fig. 2). Based on that climatic inference, the low accumulation rate is probably associated with the erosion processes caused by leaching of surface water and the water table movement. Despite the low activity found in similar substrates (Buurman and Jongmans, 2005), the bioturbation process (Gouveia and Pessenda, 2000) associated with the age inversion cannot be discarded.

3.3.2. Holocene vegetation

Between 13,740 and 7300 cal yr BP (49-21 cm; 0.009-0.02 mm/yr), herbaceous plants domain the palynological records (up to 95%), and the $\delta^{13}C$ values ranged from ~-28‰ to ~-24‰, indicating mixture of C_3 and C_4 sources and isotope enrichment since ~9500 cal yr BP (41 cm) up to ~7300 cal yr BP (21 cm) (Fig. 2). Poaceae represents up to ~87%, followed by Cyperaceae (5% - 8%). Phytoliths from BL also indicate the presence of grasses (up to 43%) of C_4 (Panicooid 2.4%) mixed to C_3 herbaceous plants (Pooid 5.4%) during the same period (Calegari et al. 2017). The generas *Tapirira*, *Ilex*, and *Symplocos*, which were highly dominant until the end of the early glacial, between 13,740 and 7300 cal yr BP (49-21 cm; 0.009-0.2 mm/yr) present lower mean percentages of 0.4, 1.4, and 6%, respectively. *Laplacea*, *Eriotheca*, *Virola*, and *Sloanea* pollen, even present in low abundance, indicate that the forest was present between 13,740 and 7300 cal yr BP (49-21 cm; 0.009-0.2 mm/yr) (Fig. 3).

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

From estimated ~4000 (15 cm) to 970 cal yr BP (7 cm) pollen grains from herbaceous plants inside the bog as Poaceae (11%), Cyperaceae (7%), Asteraceae (7%) were less abundant (between 25 and 32%). Trees and shrubs around the bog presented a frequency of ~55 to 70%, as Melastomataceae/ Combretaceae (~16%), Myrtaceae (~9%), *Alchornea* (~5%), *Tapirira* (~2%) and *Cordia* (~2%). The abundance of Moraceae/ Urticaceae (4 - 23%) indicates that the forest vegetation was relatively near the bog. The abrupt abundance of *Typha* (250%), *Potamogeton* (18%), and the spore of *Salvinia* (11%) indicate its local colonization (Fig. 3).

From estimated ~970 cal yr BP (7 cm) to present, composed by small trees and shrubs (~50 to 73%) sparsely distributed with abundance of Melastomataceae/ Combretaceae (15 - 42%), *Alchornea* (4 - 22%), Myrtaceae (3 - 8%), *Tapirira* (1 - 4%) and *Cordia* (0 -1%). These families and genera are found around BL, as transitional vegetation between the bog and the dense forest. Poaceae (13 - 25%) and Cyperaceae (2 - 7%) mainly from C_3 photosynthetic cycle and some aquatic (70 - 90%) plants as *Typha* (55 - 76%), *Potamogeton* (6 - 10%) and *Echinodorus* (1 - 6%) that occurs during the rainy season shows a very local signal. Despite the presence in low abundance, pollen genera strictly from the dense forest as *Virola* (~3%) and *Chrysophyllum* (0.3%), suggests that the dense forest is near BL, as exists today (Fig. 3).

3.4 Modern vegetation

The modern dominant vegetation within the bog BL is mainly composed of shrubs and herbs with $\delta^{13}C$ values varying from -20.6‰ (*Andropogon bicornis)* to -29.8‰ (*Cyperus* sp.) and small trees as *Alchornea triplinervia*, $\delta^{13}C$ -29.3‰ (Fig 5). Only dominant grass *Andropogon bicornis* presents C_4 photosynthetic cycle ($\delta^{13}C$: -20.6‰). The values range of C_3 plants may be attributed to the water layer present in the bog, since the high humidity is suitable for its development and establishment.

3.5 Paleoenvironmental Interpretation

3.5.1 Late Pleistocene

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

From ~25,760 and ~13,740 cal yr BP (81-49 cm; 0.04-0.44 mm/yr) the slight increase of herbs probably occurred due to C_3 Poaceae/Cyperaceae locally occupying the bog, once the carbon isotope is around ~-28‰ (Fig. 2). In the Colônia crater, the biodiversity index decreased, and open vegetation dominated by Poaceae replaced the rainforest between 23 and 12k yr BP. During the LGM dry and erosive climatic conditions were predominant (Ledru et al. 2009). Such climatic conditions were also characterized by other palynological records in southeastern Brazil (Ledru et al. 1996, 1998; Behling et al. 2002).

Despite the differences in floristics composition comparing the vegetation from LGM to present in the BL, it is possible to assume that the forest was stable in a predominantly humid climate during the end of the Late Pleistocene. The maintenance of forest vegetation since the Late Pleistocene in northern Espirito Santo was also noted by Buso Junior et al. (2013). According to the authors, $\delta^{13}C$ analysis of soil organic matter at the forest and grassland sites suggest the dominance of C_3 plants and humidity conditions since ~17,000 cal yr BP.

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

Similar data was also recorded for the Serra do Mar State Park – Curucutu and the Cardoso Island (Pessenda et al. 2009, 2012), São Paulo state, southeastern Brazilian coast. Between 22,780 and 12,000 cal yr BP Curucutu site was characterized by a forested landscape with montane species such as *Araucaria*, *Podocarpus*, and *Weinmannia*, an increase of algal spores and a more significant contribution of C_3 grasses, which suggest a cold and humid climate (Pessenda et al. 2009). The same line of reasoning applies to Cardoso Island, ~170 km of Curucutu, where the pollen record indicated a cool climate forest in the period from ~29,500 to ~23,000 cal yr BP (Pessenda et al. 2012).

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

3.5.2 Holocene

From 13,740 to 7300 cal yr BP (49-21 cm; 0.44-0.02 mm/yr), the herbaceous plants domain and the carbon isotope enrichment (up to ~-24‰) (Fig. 2) together with the phytoliths results (Calegari et al. 2017) indicating the presence of C_3 and C_4 grasses probably due to a less humid climate. Although, the presence of *Zygnema* and *Spirogyra* algae during the same period (Fig. 3) may be indicative of a high seasonal system, with wet and dry seasons well defined. Even so, this opening of vegetation recorded at the bog probably did not occur at the forest, once it is possible to find dense forest specimens at the pollen records such as *Virola*, *Laplacea* and *Sloanea*, even in low abundance (Fig. 3).

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

At Nativo do Flamengo, 11 km from BL, herbs-dominated record and pollen of *Rheedia brasiliensis*, a typical species which occur on sandy soils of dry and seasonally flooded areas, may indicate a less humid climate at the region before 7000 yr BP (Buso Junior et al. 2019). In addition, depleted $\delta^{13}C$ values, the dominance of C_3 plants, and the presence of freshwater sponge spicules suggest that a more humid climate and the establishment of the wetland may have occurred around 7000 years BP, which is also comparable to BL.

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

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

Since ~823 cal yr BP (5 cm – estimated age) the pollen testifies the establishment of current vegetation inside the bog, composed by small trees and shrubs sparsely distributed between Poaceae and Cyperaceae, aquatic plants that occurs during the rainy season and the *Tabuleiro's* forest surrounding the area. Pollen traps implanted for 20 months at Nativo da Gavea, whose vegetation structure is similar to BL, 13 km southeast (19°12'29''S/ 39°57'46''W), presented similar pollen percentages and assembly when compared to surface samples from BL. Trees and shrubs were well represented (60%) and herbs (31%) while aquatic herbs were absent, probably because Nativo da Gavea does not become flooded as BL during the rainy season (Buso Junior, 2015). At Nativo do Flamengo pollen, and sponge spicules analysis also attested the current condition since ~950 cal yr BP (Buso Junior 2015; Buso Junior et al. 2019).

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

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

4. Conclusions

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

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Figure captions

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

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

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

Figure 4. Correlation between $\delta^{13}C$ and C/N and their meaning (Meyers, 2003): C_4 Land plants, C_3 Land plants, and Lacustrine algae.

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