

*Palaeovegetation and palaeoclimate
dynamics during the last 7000 years in the
Atlantic forest of Southeastern Brazil
based on palynology of a waterlogged
sandy soil*

Article

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Palaeovegetation and palaeoclimate dynamics during the last 7000 years in the Atlantic forest of Southeastern Brazil based on palynology of a waterlogged sandy soil.

BUSO JUNIOR, Antonio Alvaro^(a); PESSENDA, Luiz Carlos Ruiz^(a); MAYLE, Francis Edward^(b); LORENTE, Flávio Lima^(a); VOLKMER-RIBEIRO, Cecília^(c); SCHIAVO, Jolimar Antonio^(d); PEREIRA, Marcos Gervasio^(e); BENDASSOLLI, José Albertino^(f); MACARIO, Kita Chaves Damasio^(g); SIQUEIRA, Geovane Souza^(h)

^(a)University of São Paulo, ¹⁴C Laboratory, Avenida Centenário 303, 13400-970, Piracicaba, São Paulo, Brazil

^(b)University of Reading, Centre for Past Climate Change and Department of Geography & Environmental Science, Reading RG6 6DW, Berkshire, UK

^(c)Fundação Zoobotânica do Rio Grande do Sul, Museu de Ciências Naturais, Rua Dr. Salvador França 1427, 90690-000, Porto Alegre, Rio Grande do Sul, Brazil

^(d)State University of Mato Grosso do Sul, Unidade Universitária de Aquidauana, Rodovia Aquidauana, km 12, Aquidauana, Mato Grosso do Sul, Brazil.

^(e)Federal Rural University of Rio de Janeiro, Instituto de Agronomia, Departamento de Solos, BR-465, Seropédica, Rio de Janeiro, Brazil.

^(f)University of São Paulo, Stable Isotope Laboratory, Avenida Centenário 303, 13400-970, Piracicaba, São Paulo, Brazil

^(g)Universidade Federal Fluminense, Instituto de Física, Av. General Milton Tavares de Souza S/N, 24210-346, Niterói, Rio de Janeiro, Brazil

^(h)Vale Nature Reserve, BR 101 Highway, km 122, Linhares, Espírito Santo, Brazil

Corresponding author: BUSO JUNIOR, Antonio Alvaro (alvaro.buso.jr@gmail.com)

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Abstract

Mineral soils are usually considered inappropriate for pollen analysis because of the poor quality of pollen and spore preservation and the disturbed stratigraphy. However, here we present a 57 cm core, collected from a waterlogged sandy soil in the lowland Atlantic Forest of SE Brazil, which shows good stratigraphy and good preservation of pollen and spores since ~7000 cal. BP, both in organic and in mineral horizons. By the other hand, the decomposition of the organic matter and its translocation along the soil profile led to changes of C and N results (TOC, TN, C/N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Mid-Holocene palaeoclimate inferences from this study are in accordance with climate fluctuations presented in previous studies for Central, Southeastern and Southern Brazil, when a change to more humid climate occurred at ~7000 cal BP. The process responsible for the presence of biological proxies along this sandy soil profile involves the continuous deposition of these proxies together with litter and sand, and the subsequent decomposition of the litter. Ultimately, this process led to the vertical accretion of the sand with the more resistant organic structures preserved in stratigraphic sequence. The preservation of pollen and spores along the profile is probably caused by low pH and redoximorphic conditions due to water saturation. This study suggests the potential for retrieving useful palaeoecological information from mineral and organic horizons of tropical waterlogged sandy soils, which is especially useful for those regions where traditional pollen archives (lakes and peat bogs) are absent.

1. Introduction

1.1 Palynology of mineral soils

Mineral soils are generally considered unsuitable for pollen and spore analysis due to the poor preservation of these microfossils due to oxidation, as well as disturbed stratigraphy caused by bioturbation and/or pollen translocation down-profile (Dimbleby, 1952; Jacobson and Bradshaw, 1981; Boulet et al., 1995; Davidson et al., 1999). However, despite these concerns, some mid-high latitude studies have shown that pollen may be well preserved in some mineral soil profiles (Dimbleby, 1952; Guillet, 1970, 1971a, 1971b; Larocque and Campbell, 1998; Bałaga and Chodorowski, 2006). The study soil pollen would allow the reconstitution of the local vegetation changes, which could be related with local vegetation processes and human interferences (Larocque and Campbell, 1998).

1.2 Mid- and late-Holocene climate in Central, Southeastern and Southern Brazil

Most pollen studies indicate a change to a wetter climate, beginning ca. 7000-4000 years BP in Central, Southeastern and Southern Brazil (Ledru, 1993; Behling, 1997a, 1997b, 2003; Salgado-Labouriau et al., 1998; Behling and Negrelle, 2001; Garcia et al., 2004; Pessenda et al., 2009; Veríssimo et al., 2012). Similarly, stable carbon isotopes from bulk soil organic matter also indicate a transition to wetter conditions in the middle Holocene in Southeastern Brazil (Gouveia et al., 2002; Pessenda et al., 2004, Saia et al., 2008).

This climate change during mid- to late-Holocene may reflect an intensification of the austral summer insolation, which led to the strengthening of the South American Summer Monsoon system (SASM) (Prado et al., 2013). Based on $\delta^{18}\text{O}$ of speleothems, Cruz et al. (2005, 2006) showed the increasing importance of the SASM in southern and southeastern Brazil during the middle to late Holocene.

However, pollen data from a lake in the region of the present study (Buso Junior et al., 2013a) show that humid conditions between 7000 and 4000 cal. BP were followed by less humid climatic conditions after 4000 cal. BP. The authors attribute this shift to less humid climatic conditions over the past 4000 yr to the establishment of the modern seasonal climate in the region, which is influenced by the SASM and marked by a dry period during the austral winter and a rainy season during the austral summer.

1.3 Objectives of the study

This study aims to test the palaeoenvironmental potential of a waterlogged sandy soil in the Neotropical forest. We will do this by analysis of pollen, siliceous sponge spicules, and C and N isotopes from mineral and organic horizons. Because old lakes/bogs are absent or scarce in many areas of the Neotropical region, the use of waterlogged sandy soils has the potential for improving understanding of the palaeoenvironmental history of the Neotropical vegetation.

2. Study site

Vale Nature Reserve (VNR) is placed at the northern coast of Espírito Santo State, Southeastern Brazil (Figure 1a, b). It comprises ~25,000 ha of pristine environments in the Atlantic Forest hotspot.

2.1 Soils and associated vegetation

According to Santos et al. (2004), Oxisols and Ultisols are the most representative soil orders at VNR, sustaining a dense tropical forest. Spodosols patches covered with grassland and forest vegetation are interspersed among the Oxisol/Ultisol matrix (Figure 1b). Small patches of Entisols Quartzipsamments are found under *restinga* vegetation. Wetland soils occur along watercourses, sustaining marshes and swamps.

99 The Oxisols and Ultisols at VNR developed from Neogene sediments of the Barreiras
 100 Formation (Figure 1a) and constitute a flat, smooth undulated terrain, around 20-70 m
 101 above sea level (m a.s.l.) (Moreau et al., 2006; Dominguez, 2009). Oliveira et al. (2010)
 102 studied Spodosols patches in southern Bahia (~120 km north from VNR) and suggested
 103 that Spodosols genesis in the Barreiras Formation is related with clay destruction,
 104 leading to the lateral transformation of Ultisols into Spodosols.
 105 The vegetation that overlies Oxisols and Ultisols (*tabuleiros* forest, Figure 1b) is a
 106 relatively tall tropical forest, with the most frequent trees in the Fabaceae, Annonaceae,
 107 Sapotaceae, Rubiaceae, Euphorbiaceae and Bignoniaceae families, constituting a
 108 biologically diverse ecosystem (Peixoto and Gentry, 1990; Thomas, 2003).
 109 Grassland and forest vegetation over Spodosols in the Barreiras Formation are
 110 denominated *mussununga* vegetation (Thomas, 2003; Meira Neto et al., 2005; Ferreira
 111 et al., 2014). Some authors denominate the *mussununga* grasslands as *campos nativos*
 112 (native grasslands), nonetheless studies have pointed that differences in structure and
 113 species composition relate with soil physical properties, with grassland *mussunungas*
 114 colonizing areas subjected to water stress (flooding or drying), and savanna and forest
 115 *mussunungas* colonizing mesic areas (Saporetti-Junior et al., 2012).
 116 The *restinga* vegetation is a coastal ecosystem occurring on sandy soils (Entisols
 117 Quartzipsamments and Spodosols) along the Brazilian coast. These soils are usually
 118 associated with sand ridges created during marine transgressions and regressions during
 119 the late Pleistocene and middle Holocene (Figure 1a), and some sites may present the
 120 process of podzolization (Oliveira et al., 2010). *Restinga* vegetation patches may present
 121 distinct structures and species composition, reflecting local edaphic and hydrological
 122 conditions (Magnago et al., 2013). Some authors have identified some floristic

similarities between *restinga* and *mussunungas* formations, suggestive of edaphic similarities between these two vegetation types (Ferreira et al., 2014).

2.2 Climate

The SASM controls precipitation patterns at the study site (Garreaud et al., 2009). The regional climate is strongly seasonal, with the rainy season occurring during the austral summer. The mean monthly temperature is always higher than 18 °C. The regional climate (between 1975 and 2002) is classified as the “Aw” type in the Köppen system, with mean annual precipitation of 1215 mm, mean annual temperature of 23.3 °C, and a dry season during the June-September winter months (Buso Junior et al., 2013a).

2.3 Sampling site

The Nativo do Flamengo sampling site (NF – 19°09’48.6’’S, 39°56’22.3’’W, ~25 m a.s.l.) is a circular, peat-covered wetland depression, ~100 m in diameter, occurring inside a plain area of deep Spodosol.

The Spodosol around NF is covered by a mussununga forest (Figure 1b, c) and, according to Santos et al. (2004), presents a thin layer (2 cm) of litter overlying the grey sand of the A horizon (8 cm thick) followed by a thick leached and white E horizon, with the spodic B horizon appearing at 171 cm depth.

During the dry season, NF usually lacks surface water but nonetheless has a shallow water table immediately below the peat layer and is characterized as a waterlogged place. Because of the groundwater influence, it was not possible to dig a trench in the study site to proceed with the substrate description, analysis and classification.

Remnants of *Salvinia* sp. and dried specimens of the freshwater sponge *Anheteromeyenia vitrea* at the bog surface are indicative of short-term flooding events, even during the dry season. The wetland is densely colonized by Cyperaceae species (e.g. *Cyperus distatus* and *Fuirena umbellata*), and scattered trees and shrubs grow

across the site and around its margins, including *Ocotea pulchella* (Lauraceae),
Tibouchina urceolaris (Melastomataceae), *Myrsine rubra* (Myrsinaceae),
Campomanesia sp. (Myrtaceae) and *Aeschynomene fluminensis* (Fabaceae).
Paepalanthus tortilis (Eriocaulaceae), Poaceae and Bromeliaceae are common herbs.

3. Materials and methods

A 57 cm soil core was collected from the NF site with a 7-cm diameter aluminium cylinder. The core was X-rayed, split longitudinally and cut into two centimetres increments. Selected samples were analysed for: ^{14}C dating, C and N elemental and isotopic composition, grain size distribution, soil pH, and biological proxies (pollen, spores, and freshwater sponge spicules). This multiproxy approach was undertaken to determine the full potential of waterlogged sandy soil as an archive for palaeoenvironmental reconstruction – pollen for vegetation history, C and N analyses to determine the origin of organic matter in reduced environments (Table 1), and freshwater sponge spicules to determine local hydrological changes.

3.1 ^{14}C dating

Five samples were selected for ^{14}C dating. Pre-treatments included the removal of modern roots fragments and cold/hot hydrolysis with diluted HCl (Table 2). The hydrolysis of peat samples (11-13 cm and 05-07 cm) was more aggressive than the hydrolysis of sandy and friable samples (21-23 cm, 47-49 cm and 49-51 cm). Samples were combusted at the ^{14}C Laboratory, and the purified CO_2 was sent to the University of Georgia, USA, or to the LACUFF Laboratory, Brazil, for accelerator mass spectrometry (AMS) dating. For pre-Bomb samples, ages are expressed as years before present (BP) and calibrated ages (cal. BP, 2σ), according to the SHCal13 curve (Hogg et al., 2013), using the software CALIB Rev 7.0.4 (Stuiver and Reimer, 1993) for ^{14}C age

calibration. For post-bomb samples, ^{14}C activity was expressed as the percentage of modern carbon (pMC), while calibrated ages were expressed as cal. AD, 2σ , according to the Brazil curve (Santos et al., 2015) and the CALIBomb software (<http://calib.org/CALIBomb/>). Calibrated ages were used to create an age model in the software Tilia 1.7.16 (Grimm, 1992) to interpolate ages at any undated interval in the core.

3.2 C and N analyses

Modern root fragments were manually removed from samples selected for C and N analyses. Mineral samples were sieved (350 μm) with distilled water to remove coarse sand grains. All samples were dried at 50 $^{\circ}\text{C}$. Analyses were carried out at the Stable Isotope Laboratory (CENA/USP) using an elemental analyzer attached to an ANCA SL 2020 mass spectrometer. Total organic C (TOC) and total N (TN) are expressed as percentage of dry weight, with an analytical precision of 0.09% and 0.07%, respectively. Stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were measured with respect to VPDB and atmospheric N as standards, respectively, and are expressed as *per mil* (‰) with a standard deviation of 0.2‰.

3.3 Grain size

In natura samples were sieved (mesh = 1 mm) using distilled water, and the dry mass ratio of the mineral fraction > 1 mm was calculated in relation to the original mass of *in natura* samples. Grain size distribution of the fraction < 1 mm was determined by laser diffraction analysis. Samples were processed using H_2O_2 to eliminate organic matter and HCl to eliminate carbonates. Grain size distributions of the fraction < 1 mm were divided into sand (1-0.0625 mm), silt (62.5-3.9 μm) and clay (3.9-0.12 μm), following Wentworth (1922).

3.4 Soil pH

Five intervals were selected for the determination of pH in water and in KCl 1 mol.L⁻¹ (in weight soil: solution = 1:2.5) by means of a potentiometer (Teixeira et al., 2017).

3.5 Biological proxies

A qualitative analysis of siliceous sponge spicules was carried out in 6 samples. To remove organic matter, samples were treated with H₂O₂ at 50 °C, and washed with distilled water. Subsequently, samples were treated with 10% HCl, at 50 °C for 10 minutes, and washed in distilled water. Residues were stored in distilled water and then mounted on light microscope slides with Naphrax or Entellan. Sponge taxa (gemmoscleres and microscleres) were identified using the following references: Tavares et al. (2003), Volkmer-Ribeiro et al. (2006), Volkmer-Ribeiro and Machado (2007) and Buso Junior et al. (2012).

Pollen and spore analysis was carried out on 11 samples of 2 cm³. Samples were sieved (350 µm) with 5% KOH for removal of coarse sand and coarse vegetal fragments. They were processed according to Colinvaux et al. (1999), with the addition of exotic *Lycopodium* spores to determine pollen and spore concentrations, dissolution of silica with HF, and removal of organic matter with 5% KOH and acetolysis. Residues were mounted on light microscope slides using liquid glycerin as the mounting medium. For each sample, at least 200 tree or shrub pollen grains were counted in at least 3 slides.

The total terrestrial pollen sum includes trees, shrubs, terrestrial herbs and indeterminate/reworked pollen grains, and is the basis for calculation of percentages.

Identification was based on the pollen reference collection of the CENA/USP ¹⁴C

Laboratory, which contains more than 1500 samples of the regional vegetation, and on Lorente et al. (2017). Tilia 1.7.16 software (Grimm, 1992) was used to construct pollen and spore diagrams. CONISS software (Grimm, 1987) was used for constrained cluster analysis to produce pollen assemblage zones.

4. Results and discussion

4.1 Core description, grain size distribution and soil pH

The X-ray image allows differentiation of mineral and organic intervals in the NF core. Furthermore, the X-ray image evidences the absence of sedimentary structures and stratification (Figure 2), indicating that some of the changes in the content and in the characteristics of the organic matter in NF core are originated from post-depositional processes related with pedogenesis. Both mineral and organic intervals present low pH in H₂O (4.5 to 5.7), moreover pH values in KCl (3.2 to 3.9) are always lower than in H₂O (Table 3). These pH values are in agreement with studies in Spodosols of the Barreiras Formation, reflecting the acid characteristic and the predominance of negative charges in these soils (Oliveira et al., 2010; Secretti, 2013).

The mineral interval (57-17 cm depth) is composed predominantly of sand (Figure 2), and may be subdivided into five sub-intervals based upon gradations of grayscale: (i) from 57-52 cm, hardened and dark brownish-grey sand with some silt; (ii) from 52 to 48 cm, dark grey, friable sand; (iii) from 48 to 35 cm, light grey, friable sand; (iv) from 35 to 21 cm, dark grey, friable sand; (v) from 21 to 17 cm, black and friable sand.

The organic interval (17 to -5 cm) is composed of organic matter (17-00 cm) and modern litter (0 to -5 cm). The humus layer contains decomposed organic matter, *Salvinia* microsporangia, lots of modern roots and some sand. We attribute the presence of sand in the organic interval to the surface transport of sand grains from the surrounding *mussununga* forest by water runoff, as proposed by Calegari et al. (2017), based on a study of soil phytoliths at the NF site.

The presence of peat from 17 to -5 cm is the result of the accumulation of litter, reflecting vegetation productivity, relatively low organic matter decomposition, caused

by anoxic conditions that prevail during the rainy season, and low pH, which decreases the rate of decomposition (van Breemen and Buurman, 1998). Conversely, the stratification of the carbon-enriched layers (litter – humus – black friable sand) reflects decay processes that lead to the incorporation of the organic matter into the mineral interval (Ejsackers and Zehnder, 1990). According to Melillo et al. (1989), the below-ground decomposition of the organic matter is influenced mainly by environmental factors such as temperature, moisture and soil texture. At the study site, decomposition rates are probably low, nonetheless these rates may be enhanced by oxic conditions during the dry season, causing decomposition of the organic matter and its incorporation into the mineral interval.

Macroscopic characteristics of NF core presented above differs markedly from the description of the deep Spodosol patch that occurs around NF site (Subsection 2.3). Similar situation was found by Dubroeuq and Volkoff (1998) in Podzolic plains in northern Amazonia. The authors suggested that small patches of waterlogged shallow Spodosols with peat occurring in the middle of deep Spodosol areas would have evolved in response to the rise of the groundwater level. In this sense, the onset of wetter climate led to the gradual development of peat on the surface, as well as the development of a secondary argillic horizon within the E horizon of the deep Spodosol. Furthermore, according to Dubroeuq and Volkoff (1998), under these conditions the dissolution of quartz increases, leading to the lowering of the relief. This model may help to explain the differences observed between NF profile and the surrounding deep Spodosol, especially in relation to the lowered relief of the site, the presence of peat on the surface and the hardened and dark interval from 57 to 52 cm depth. Moreover, if such mechanism occurred in NF site, probably a wetter climate event may be associated with it and will be discussed later (Subsections 4.5 and 4.6).

4.2 ¹⁴C dating

AMS dates ranged from 6672 cal. BP at 47-49 cm to 1852 cal. BP at 21-23 cm and modern ages at 11-13 and 05-07 cm (Table 2). The two lowermost dated samples showed age inversions, which can not be attributed to differences regarding ¹⁴C measurements because both LACUFF and UGAMS laboratories were recently intercompared and showed very good agreement for all data sets (Macario et al., 2013). The age inversion may be due to the distinct treatments of these two samples and distinct clay contents. Due to the low availability of sample mass, the acid pre-treatment of sample 47-49 cm was more aggressive (60 °C, 1h hydrolysis, Table 2) than that applied to sample 49-51 cm (hydrolysis at room temperature), probably resulting in a more efficient removal of fulvic acids and, consequently, an older age for sample 47-49 cm. According to Scharpenseel and Becker-Heidmann (1992), clay organic complexes have lower tendency towards rejuvenation of the soil organic matter. Consequently, a concurrent cause of the age inversion is the higher content of organomineral complexes in sample 47-49 cm, which presents a higher clay content than sample 49-51 cm (17% and 9%, respectively).

According to Melillo et al. (1989) and Ejsackers and Zehnder (1990), less than 20% of organic matter remains after four years of litter deposition. Consequently, AMS ages obtained for the organic interval probably reflect both the fast organic matter deposition and the fast decay dynamics at the organic layer. Ages obtained for the upper humus layer (~1957 cal. AD, at 12 and 6 cm) therefore likely reflect recent deposition of the upper ~20 cm of organic matter. The ~1900-yr age difference between the humus at 22 cm (1852 cal. BP) versus 12 cm (1957 cal. AD) reflects the reduction in thickness of the humus layer caused by organic matter decay. These results suggest that, under the

present-day seasonal climate of the study area, there may be enhanced oxidation of organic matter during the dry season, leading to incorporation of older, decayed humus into the top of the mineral layer (Ejsackers and Zehnder, 1990).

4.3 C and N analyses

C and N results are presented in Supplementary File 1 and in Figure 3. Three main intervals may be distinguished based on the concentration of TOC and TN. The first interval, from the base to 50 cm shows slightly elevated TOC (4.9 to 8.9%) and TN varying from 0.0 to 0.1%. In the interval from 48 cm to 20 cm TOC presents the lowest concentrations of the core (from 0.8 to 4.0%) and TN varied from 0.0 to 0.1%. The last interval, from 18 cm upwards, shows increased concentrations of organic matter, with TOC varying from 12.4 to 56.2%, and TN from 0.2 to 2.7%.

These three intervals delimited by TOC and TN concentrations are likely the result of the process of podzolization. The deficient drainage and the low pH of the studied soil impeded the fast decomposition of plant litter (van Breemen and Buurman, 1998) causing the accumulation of peat and high TOC and TN concentrations in the upper interval.

Under this condition soluble organic acids are produced causing the mobilization of the organic matter and its transport and immobilization into deeper soil horizon (van Breemen and Buurman, 1998), leading to the leaching of the intermediary interval (which presents the lowest TOC and TN values) and to the accumulation of organic matter in the deepest interval.

C/N ratios vary between 16.3 and 211.6 (Figure 3). The following four intervals can be recognized: (i) 56 to 46 cm (>7000 to ~6300 cal. BP), ratios ranging between 81.0 and 160.5 (mean = 118.6). (ii) 46 to 20 cm (5930 to 1715 cal. BP), ratios ranging between 16.3 and 74.5 (mean = 46.5). (iii) 22 to 0 cm (1578 cal. BP to modern), ratios ranging

from 47.5 to 211.6 (mean = 123.7). (iv) Modern litter (17.3). For most of the core, the C/N ratios are indicative of organic matter originating from vascular plants (Table 1). $\delta^{13}\text{C}$ values vary from -30.3‰ to -25.8‰, in the range of C3 plants (Table 1), which were likely locally dominant during the entire record. Slightly enriched values occur from 34-20 cm (from ~4000 to ~1700 cal BP), which may reflect compositional changes to the local plant community. Alternatively, however, fluctuations in $\delta^{13}\text{C}$ along the NF core may instead reflect the decomposition and translocation of soil organic matter through the profile. Enrichment of $\delta^{13}\text{C}$ with depth (~2.5‰ from 0 to 26 cm) may be related to isotopic fractionation during decomposition (Macko and Estep, 1984; Melillo et al., 1989), while $\delta^{13}\text{C}$ depletion between 28 and 48 cm may be related to illuvial and humified material (Kramer et al., 2003).

$\delta^{15}\text{N}$ varied from -1.2‰ to +3.3‰ (Figure 3), showing a tendency to more enriched values from the base to 26 cm (>7000 to ~2600 cal. BP), and relatively stable values through the organic layer. Considering the influence of decomposition and translocation processes upon the characteristics of the soil organic matter, it is very likely that changes in $\delta^{15}\text{N}$ reflect these processes as well. Depleted $\delta^{15}\text{N}$ in deeper NF samples may result from organic matter with low N content and low aliphaticity (Kramer et al., 2003). For instance, Mafra et al. (2007) found that humic acids extracted from Bh horizons of Spodosols in northern Amazonia have low N content and low aliphaticity, signifying humified organic matter translocated down-profile.

4.4 Siliceous sponge spicules

The presence of freshwater sponge spicules along the entire NF record attests to the presence of a wetland since ~7000 cal. BP. Figure 4 presents the results of the qualitative analysis of sponge spicules in NF core as well pictures of diagnostic spicules. Samples at 50, 40 and 30 cm (7000 – 3300 cal BP) show the presence of

megascleres and gemmoscleres of *Racekiela sheilae* . Based on a survey of modern coastal environments in southern Brazil, Volkmer-Ribeiro and Machado (2007) concluded that *R. sheilae* colonizes swampy fields or shallow seasonal ponds, close to dunes or palaeodunes, forming slender crusts on stems of macrophytes and on sand or gravel conglomerates. Samples at 20, 10 and 4 cm contain megascleres and gemmoscleres of *R. sheilae* and gemmoscleres of *Anheteromeyenia vitrea* , the latter identified by Buso Junior et al. (2012) based on live specimens collected at the NF site. Consequently, the presence of gemmoscleres of *A. vitrea* from 20 cm (~1500 cal. BP) upwards indicates the onset of environmental conditions similar to those of today, which are marked by very short periods of flooding.

4.5 Palynology

Mineral and organic horizons in the NF core contain well-preserved pollen; only one sample at 54 cm depth was devoid of pollen and spores. Eighty-nine pollen and spores types were identified and classified as aquatic herbs, trees/shrubs, terrestrial herbs and terrestrial spores. Total pollen and spore concentrations varied from 3400 to 98,400 grains cm⁻³ (Figure 5a), with concentrations increasing above 36 cm depth. Indeterminate and reworked pollen grains varied from 5% to 20%, with higher frequencies found in the mineral substrate (50 to 20 cm). The cluster analysis allowed the identification of two pollen assemblage zones. Figure 5a presents the percentage diagram for selected pollen and spores found in the NF core and the total concentration in each sample, and Supplementary File 2 presents pollen and spore counts in each sample.

Pollen Zone NF-I (7043 – 2037 cal. BP; 50 – 23 cm):

This interval is dominated by pollen grains from terrestrial herbs (42-61%; 2800-35,270 grains cm⁻³) followed by trees/shrubs (23-42%; 1279-13,337 grains cm⁻³), aquatic herbs

(7-27%; 209-7458 grains cm⁻³) and terrestrial spores (5-14%; 209-3919 grains cm⁻³) (Figure 5a). Indeterminate and reworked pollen grain frequencies varied from 14% to 20% (437-9481 grains cm⁻³). The most frequent terrestrial herbs are Poaceae (32-54%; 1108-31,161 grains cm⁻³) and Asteraceae (5-6%; 139-2971 grains cm⁻³). The most frequent trees/shrubs are Myrtaceae (7-17%; 456-4881 grains cm⁻³), Melastomataceae/Combretaceae (5-10%; 203-3097 grains cm⁻³), *Rheedia* (= *Garcinia*) *brasiliensis* (6%; 177 grains cm⁻³), Anacardiaceae (2-7%; 209-1705 grains cm⁻³) and *Alchornea/Aparisthium* (2-4%; 44-2023 grains cm⁻³). Aquatic herbs are represented mainly by spores of *Salvinia* (7-25%; 209-7016 grains cm⁻³) (Figure 5b).

Based on the presence of a temporary freshwater pond inferred from the *R. sheilae* spicules, and based on the depleted $\delta^{13}\text{C}$ values, the Poaceae pollen grains represent C3 terrestrial and semiaquatic species that inhabited the freshwater pond, or swampy field, and its margins. Some of the tree and shrub taxa (Myrtaceae, Melastomataceae, *Alchornea*, and Anacardiaceae) would be expected to have colonized the margins and more elevated areas around this pond. Despite the low frequencies, pollen types such as *Caryocar*, *Chrysophyllum*, *Eriotheca*, *Pachira*, *Pseudobombax*, *Sapium*, Sapotaceae, *Senefeldera* and *Parkia* indicate that the *tabuleiros* forest vegetation occurred close to the study site.

The availability of the pollen reference collection from plants of the study region allowed the identification of pollen grains of *Rheedia brasiliensis* at the species level (Figure 5c). *R. brasiliensis* is a generalist species occurring in mesic *mussumunga* forests of the VNR (Simonelli et al., 2008; Siqueira et al., 2014). Elsewhere in Southeastern Brazil, this species occurs mainly on sandy soils of dry and seasonally flooded *restingas* (Araújo and Oliveira, 1988; Silva and Oliveira, 1989; Talora and Morellato, 2000; Duarte et al., 2005). The high frequency (6%) of *Rheedia brasiliensis*,

and its exclusive occurrence at the onset of this pollen zone (Figure 5b), may indicate that a less humid environment occurred at the NF site prior to pollen zone NF-I, probably a mesic *mussumunga*. The absence of *Rheedia brasiliensis* in the subsequent samples may be the result of the local displacement of this species due to the establishment of the wetland around 7000 cal. BP.

The change of NF site from a mesic *mussumunga* to a wetland at ~7000 cal BP is in accordance with previous pollen, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ based studies, which indicate the onset of more humid climates at Southern, Central and Southeastern Brazil during the middle Holocene (Ledru, 1993; Behling, 1997a, 1997b, 2003; Salgado-Labouriau et al., 1998; Behling and Negrelle, 2001; Garcia et al., 2004; Pessenda et al., 2004, 2009; Cruz et al., 2005; Veríssimo et al., 2012). Buso Junior et al. (2013a) also inferred an interval of more humid climatic conditions in the study area between 7000 and 4000 cal. BP.

Pollen Zone NF-II (2037cal. BP – modern; 23cm – litter):

This zone is dominated by trees/shrubs (37-77%; 5963-30,327 grains cm^{-3}), followed by aquatic herbs (5-76%; 1977-41,329 grains cm^{-3}), terrestrial herbs (14-58%; 5008-21,331 grains cm^{-3}) and terrestrial spores (5-16%; 1129-5931 grains cm^{-3}). Indeterminate and destroyed pollen grains comprise 5-16% (1832-5352 grains cm^{-3}) (Figure 5a). The most frequent trees/shrubs are *Alchornea/Aparisthium* (7-43%; 1129-15,684 grains cm^{-3}), *Myrsine* (3-20%; 434-5566 grains cm^{-3}), Anacardiaceae (1-14%; 289-5140 grains cm^{-3}), Melastomataceae/Combretaceae (3-6%; 782-2230 grains cm^{-3}), Myrtaceae (2-6%; 589-2379 grains cm^{-3}), Urticaceae/Moraceae (2-5%; 514-1933 grains cm^{-3}), Arecaceae, (0-11%; 132-5798 grains cm^{-3}) and *Cecropia* (1-4%; 174-1570 grains cm^{-3}). Aquatic herbs are represented mainly by *Potamogeton* (0-66%; 0-35,828 grains cm^{-3}), *Salvina* (5-27%; 1713-8179 grains cm^{-3}), *Typha* (1-7%; 262-1129 grains cm^{-3}) and *Echinodorus* (0-2%; 0-261 grains cm^{-3}). Among the terrestrial herbs, the most frequent are Cyperaceae

(8-54%; 1679-19,761 grains cm⁻³), Poaceae (1-27%; 393-4168 grains cm⁻³) and Asteraceae (3-6%; 868-1933 grains cm⁻³) (Figure 5b).

Among the most important trees/shrubs in the NF-II pollen zone are *Alchornea/Aparisthium* and *Myrsine*, which are pioneer trees that may be associated with gallery forests and seasonally flooded lowlands (Marchant et al., 2002). *Myrsine rubra* is a frequent species in the modern environment of the NF site, colonizing its margins in particular. The depleted $\delta^{13}\text{C}$ values of the organic matter (Figure 3) indicate that Cyperaceae and Poaceae pollen grains represent C3 species. In contrast with the previous pollen zone, NF-II has higher percentages of trees/shrubs and aquatic herbs, as well as higher numbers of pollen types from trees/shrubs (from 37 types in NF-I to 48 in NF-II) and terrestrial herbs (from 9 to 13, respectively). Furthermore, unlike NF-I, where aquatic herbs are dominated by *Salvinia* spores, NF-II has high percentages of *Potamogeton*, *Salvinia*, *Typha* and *Echinodorus*. These features of the NF-II pollen zone suggest a change toward a wetland characterized by more closed and diverse vegetation, indicating the onset of the modern environment at the study site.

Some studies of modern plant communities show that the heterogeneity of hydrologic conditions favours floristic diversity in wetlands, sand dune slacks and *restingas* (Castellani et al., 1995; Vivian-Smith, 1997; Magnago et al., 2013). These studies found that permanent flooding is a stress factor for some plant species, reducing their chances of colonization and establishment in poorly drained areas, favouring the smaller group of flood-tolerant species. Consequently, the change to a more diverse and closed vegetation type during the NF-II pollen zone may be due to less frequent and less intense flooding events at the NF site from ~2000 cal. BP.

There may be several reasons for these flood-regime changes at the NF site ~2000 cal. BP which are not mutually incompatible. One possible cause is increasing seasonality

during the late Holocene, as proposed by Buso Junior et al. (2013a) for the study area. This seasonality would cause the NF site to be flooded during the rainy season and dry out during the dry season. Another possible explanation is changes in the local relief, with the reduction of habitable area due to the constant deposition of sand. As described above (Subsection 4.1), sand grains are found in the organic interval of the NF core, probably transported from the surrounding *mussumunga* forest by water runoff. The decay process would lead to the destruction of the organic matter, leaving only sand grains and more resistant organic structures. The vertical increment of the mineral interval originating from this process would result in a shallower and more ephemeral water column. Lastly, the relative sea-level fall during the late Holocene (Buso Junior et al., 2013b) may have lowered the regional base level and thus the local groundwater level, leading to less frequent flooding of the NF site. Increased frequencies of Urticaceae/Moraceae pollen in NF-II indicate closer proximity of the *tabuleiros* forest vegetation to the core site. That *tabuleiros* forest was likely close to the study site is also suggested by the presence of some tree/shrub taxa characteristic of this vegetation type (e.g. Chrysobalanaceae, *Chrysophyllum*, *Eriotheca*, *Ficus*, *Glycydendron*, *Rinorea*, *Sapium*, *Senefeldera*, *Simarouba*, *Sloanea*, *Swartzia* and *Virola*).

4.6 Palaeoclimate inferences

The presence of pollen grains of *Rheedia brasiliensis* at the beginning of pollen zone NF-I suggests a less humid environment at the NF site before ~7000 cal. BP. The subsequent absence of this species, along with the appearance of pollen and spores of aquatic and semi-aquatic plants and freshwater sponge spicules, suggests the initial establishment of a wetland around 7000 cal. BP.

The transition to a wetland ~7000 cal. BP may be due to the onset of wetter climatic conditions in Central, Southern and Southeastern Brazil during the middle Holocene, according with the studies summarized in subsection 1.2. This wetter interval, probably caused by intensification of the SASM (Cruz et al., 2005, 2006; Prado et al., 2013), could have raised the groundwater level at the NF site, causing frequent flooding. However, an alternative, or contributory, cause may be the mid-Holocene rise in eustatic sea-level, especially because the beginning of pollen zone NF-I (7043 cal. BP) is coincident with the mid-Holocene sea-level high-stand (Murray-Wallace, 2007; Buso Junior et al., 2013b), which would have elevated the base level and raised the local groundwater level.

The onset of pollen zone NF-II at ~2000 cal. BP, with more diverse and structurally complex vegetation, may be due to a decrease in intensity and frequency of flooding, in turn due to a change toward a more seasonal climate (Buso Junior et al. 2013a). Local, non-climatic, factors may also have played a role (e.g. local relief changes due to the deposition of sand, and regional base-level lowering due to the late-Holocene relative sea-level fall).

4.7 The use of tropical sandy soils for pollen studies

Important concerns over the feasibility of pollen analysis in soil are the potential for downwashing of pollen through the profile, bioturbation by soil fauna (Davidson et al., 1999), and pollen degradation by oxidation (Larocque and Campbell, 1998). However, the distinct assemblages of well preserved pollen and spores in the sandy soil at NF site demonstrate clear palynological stratigraphy, both in organic and in mineral horizons, demonstrating that any down-core pollen translocation, bioturbation, or pollen oxidation must have been relatively insignificant. Good pollen preservation can be attributed to the low pH and deficient drainage, which reduce bioturbation and

496 microbial activity and hence pollen degradation (Larocque and Campbell, 1998; van
497 Breemen and Buurman, 1998).

498 We have tested some Spodosol profiles in our study area regarding pollen and spore
499 preservation and found that profiles from sites which were not water-saturated during
500 the dry season were devoid of pollen and spores. This suggests that the redoximorphic
501 conditions, provided by water saturation during most of the year, explains the good
502 pollen preservation in the NF profile as well.

503 The preservation of the pollen stratigraphy in the NF core shows that pollen grains
504 cannot have been transported along with the organic matter. We suggest that the
505 mechanism responsible for the incorporation of pollen, spores and sponge spicules in
506 the NF core was the gradual deposition of the organic matter and sand on the soil
507 surface and the subsequent decomposition of this organic matter, leaving behind the
508 resistant pollen.

509 Pollen records from soils usually represent the local vegetation (Larocque and
510 Campbell, 1998). Consequently, interpretation of pollen data from soil samples must
511 take into account local features that may influence vegetation dynamics. This is the case
512 for the present study, where local conditions have an important role in the maintenance
513 of water saturated soil, even during the dry season. Another important factor influencing
514 the vegetation at the NF site is the change in local relief, which influences the depth of
515 the water column and the persistence of surface water. Analysis of pollen from several
516 soil profiles in a given region has the potential for reconstructing vegetation histories at
517 much higher spatial resolution than is possible from large lakes with regionally-
518 smoothed pollen catchments. Furthermore, pollen records from tropical waterlogged
519 sandy soils may be of great importance for palaeoecological studies in regions where

peat bogs and natural lakes are rare or absent; e.g. southern Bahia, northern Espírito Santo, and the white-sand vegetation of northern Amazonia.

5. Conclusions

5.1. Distribution and characteristics of organic matter

C and N data from the NF core indicate that organic matter has originated predominantly from vascular C3 plants since 7000 cal. BP. However, decomposition and translocation processes have influenced the characteristics and the distribution of the organic matter in the soil profile, with the accumulation of organic matter in the upper and lower horizons and depletion of organic matter in the intermediary horizon. . Small enrichments of $\delta^{13}\text{C}$ likely reflect isotopic fractionation during decomposition. Down-core depletion of $\delta^{15}\text{N}$ may reflect translocation of humified organic matter to lower soil horizons.

5.2. Biological proxies in the waterlogged sandy soil

The waterlogged sandy soil at NF site has well preserved biological proxies (pollen, spores and sponge spicules), both in organic and mineral intervals. Clear stratigraphic changes in these proxies demonstrate that down-core translocation and bioturbation (e.g. by soil fauna) must have been minimal, while the low pH and redoximorphic soil conditions prevented the degradation of pollen and spores. These biological proxies indicate the transition from a mesic *mussumunga* to a wetland ~7000 cal. BP. Between ~7000 and ~2000 cal. BP this wetland was a swamp or freshwater pond, colonized mainly by aquatic and semiaquatic C3 plants and the freshwater sponge *R. sheilae*. At ~2000 cal. BP the wetland began to be colonized by a more diverse flora, composed of aquatic and semiaquatic plants, trees and shrubs. The transition from the mesic *mussumunga* to a wetland ~7000 cal. BP suggests a change to wetter climate at this time, which is in accordance with previous studies from

central, southern and southeastern Brazil. The subsequent colonization of the wetland by a more diverse vegetation at ~2000 cal. BP signifies the onset of environmental conditions similar to those of today, with more frequent and intense flood events restricted to the wet season. A change to a more seasonal climate, changes in local relief, and a fall in relative sea-level are the likely drivers of these late Holocene environmental changes at the study site.

Our results suggest that useful palaeoecological information can be retrieved via analysis of pollen and spores from waterlogged sandy soils in tropical environments. Analysis of several depressions from a given region has the potential to provide palaeoecological information at much finer spatial resolution than is possible from lakes in these areas, most of which yield environmental records at much coarser spatial resolution due to their much larger pollen catchments associated with their larger areas.

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Table 1 – $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C/N of different organic matter sources

Organic matter source	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C/N
Vascular C3 plants	-33 to -20	$\approx +1$	≥ 20
Vascular C4 plants	-17 to -9	$\approx +1$	≥ 20
Freshwater phytoplankton	-37 to -25	$\approx +8$	4 to 10
Marine phytoplankton ⁽¹⁾	≈ -21	$\approx +8$	4 to 10

⁽¹⁾ At southern tropical latitudes;

According to: Rau et al. (1989); Wada et al. (1989); Boutton (1991); Matsuura and Wada (1994); Meyers (2003)

Table 2 – Hydrolysis parameters and results of samples for AMS ^{14}C analysis

Sample	Depth (cm)	Hydrolysis	Laboratory code	^{14}C (BP)	Age (cal. BP; 2 σ)	Mean (cal. BP)
NF07-05	05-07	2% HCl; 60 °C; 4 h	UGAMS28371	102.436 \pm 0.297 ^a	1957.0-1957.4 ^b	1957 ^b
NF13-11	11-13	2% HCl; 60 °C; 4 h	UGAMS28375	102.913 \pm 0.308 ^a	1957.2-1957.6 ^b	1957 ^b
NF23-21	21-23	1% HCl; 4 h	LACUFF150039	1937 \pm 51	1991-1713	1852
NF49-47	47-49	1% HCl; 60 °C; 1 h	LACUFF150040	5906 \pm 40	6788-6555	6672
NF51-49	49-51	2% HCl; 4 h	UGAMS15861	5320 \pm 30	6181-5941	6061

UGAMS: AMS Laboratory of University of Georgia; LACUFF: AMS Laboratory of Universidade Federal Fluminense.

^a ^{14}C activity in pMC.

^b Calibrated age in cal AD.

Table 3 – pH of selected intervals in NF core

Depth (cm)	pH (H ₂ O)	pH (KCl)
00-19	4.8	3.2
19-25	5.7	3.6
29-35	5.4	3.8
39-45	5.3	3.9
51-57	4.5	3.4

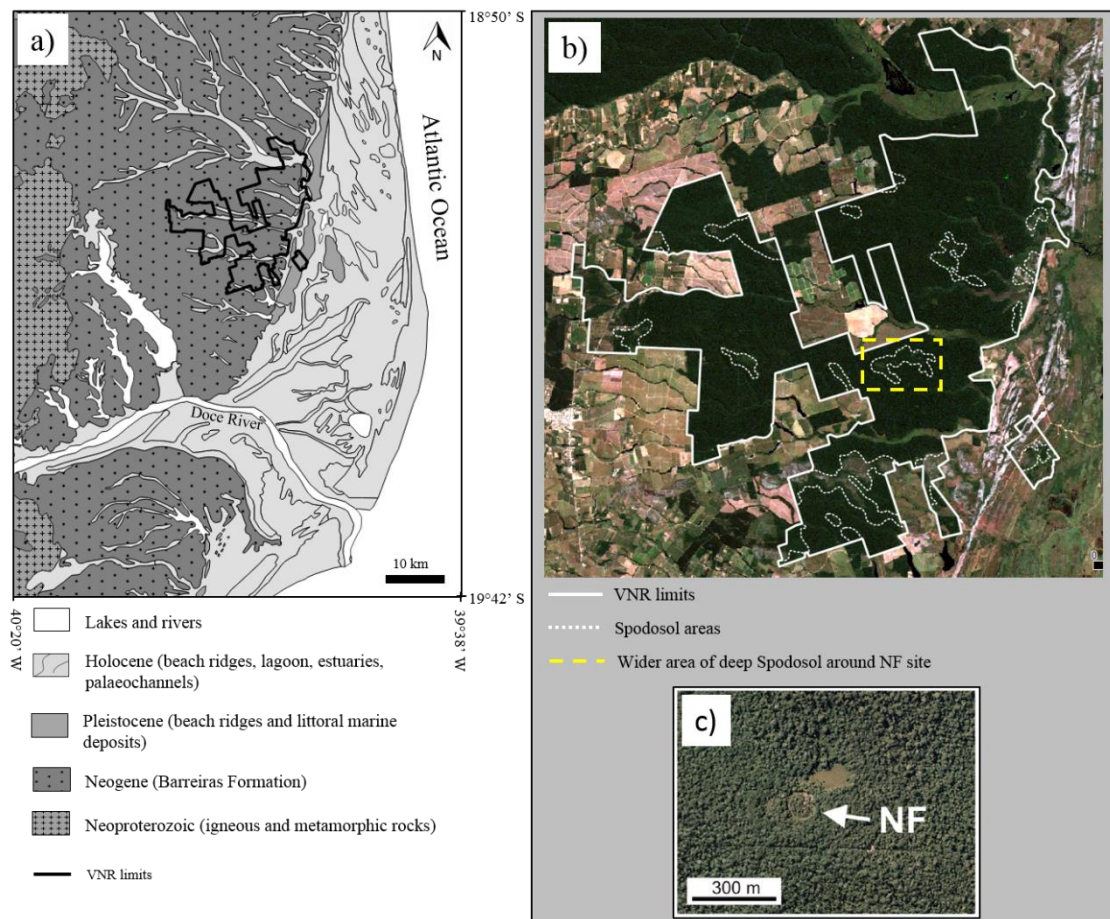


Figure 1 – Study area. a) Geologic map for the Northeastern coast of Espírito Santo State. b); Landsat 7 RGB123 composition and the Spodosol areas delimited by Santos et al. (2004) in the VNR; c) NF site.

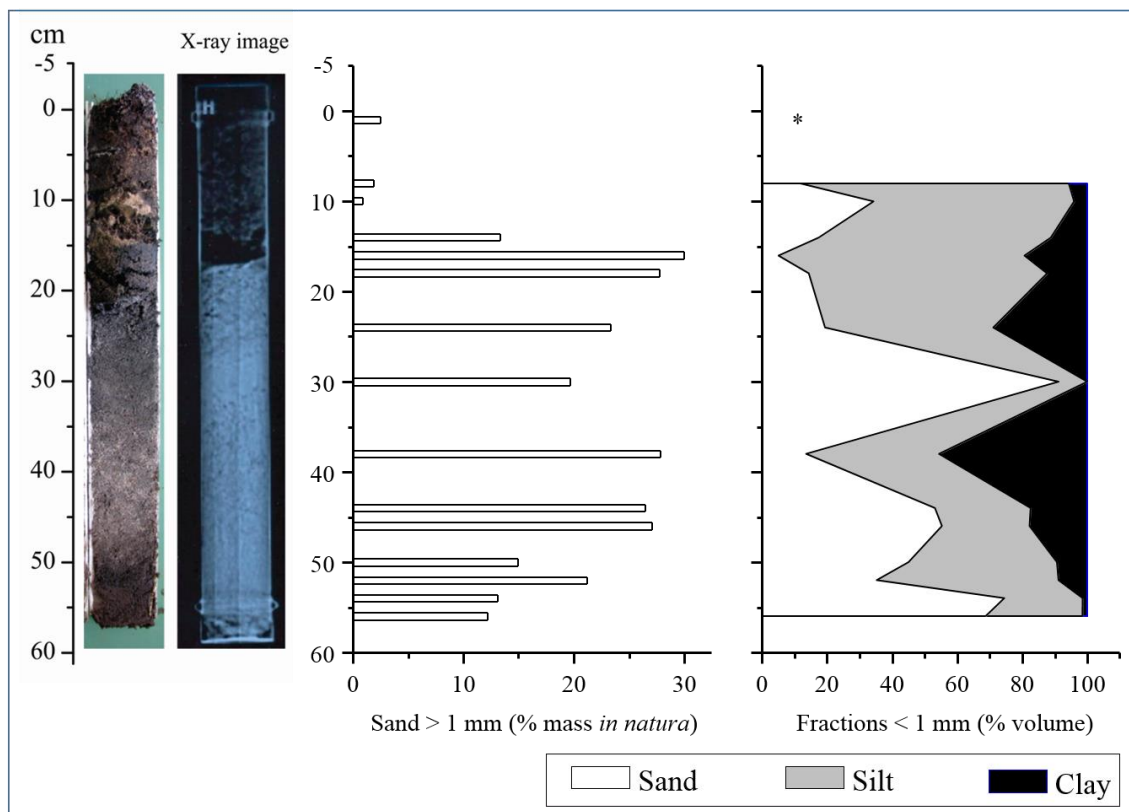


Figure 2 – NF core: photograph, X-ray image and grain size distribution. (*) sample 03-00 cm was lost during laser diffraction analysis.

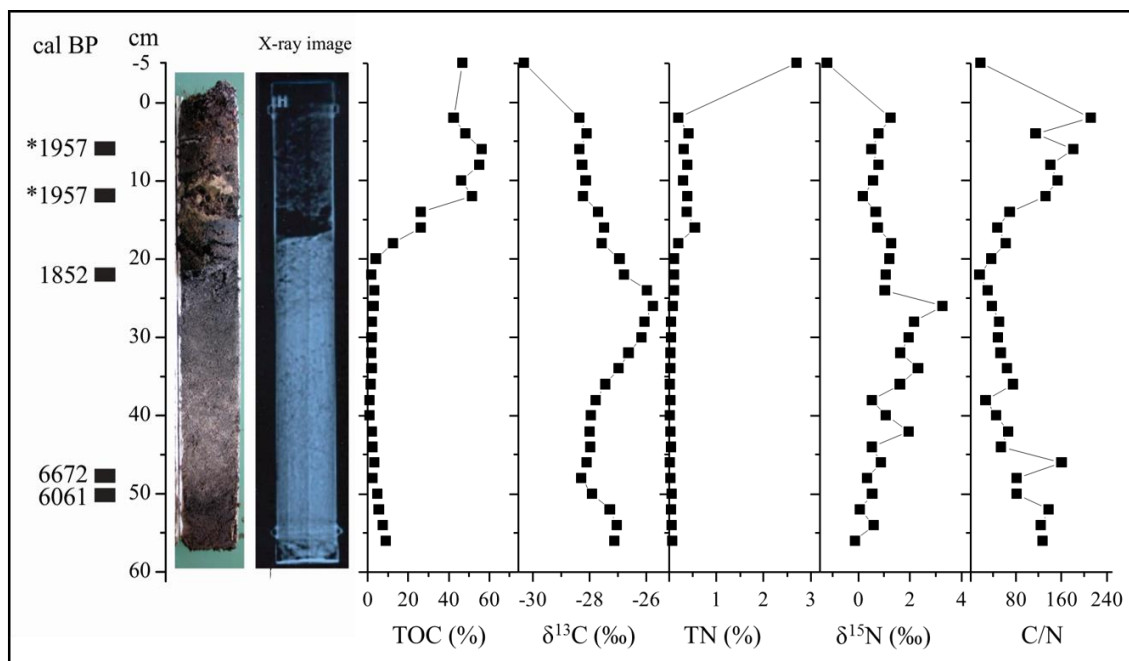


Figure 3 – C and N results from NF core. *ages in cal AD.

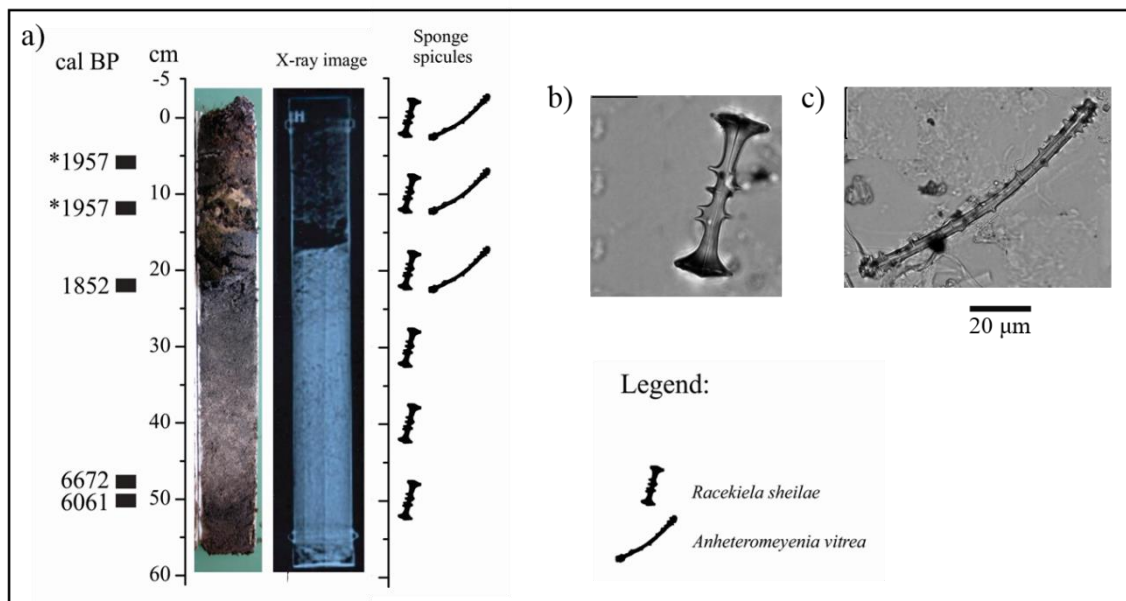


Figure 4 – a) Presence of siliceous sponge spicules. Gemmoscleres of *Racekiela sheilae* (b) and *Anheteromeyenia vitrea* (c). *age in cal AD.

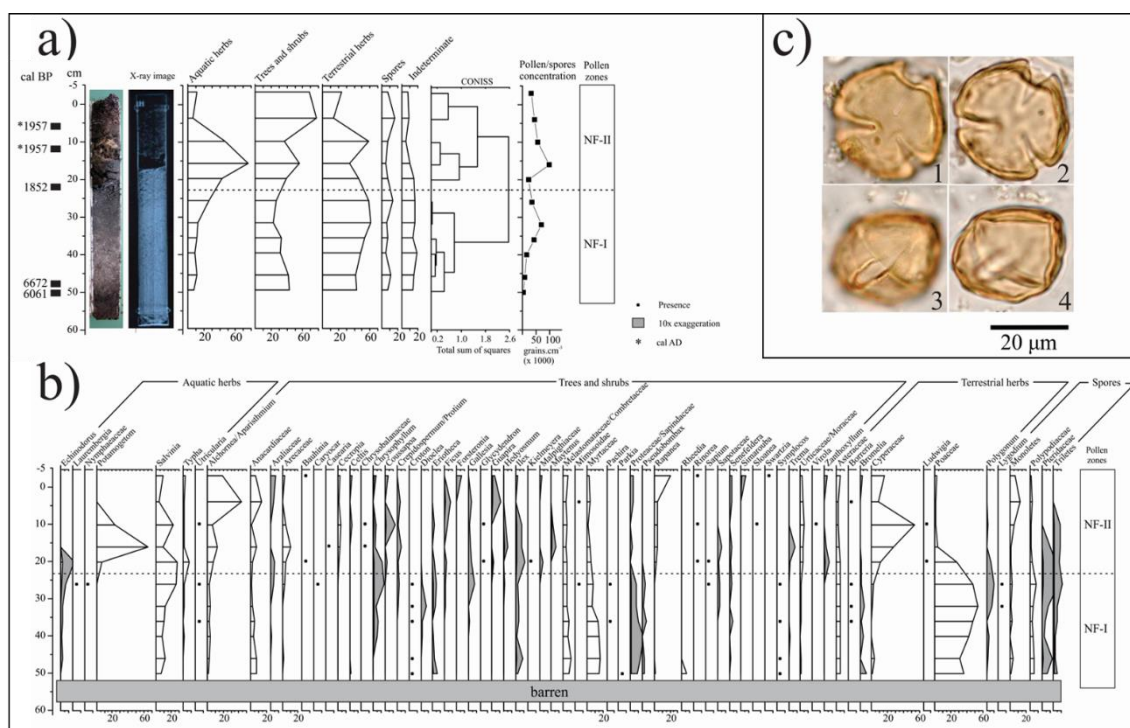


Figure 5 – Palynology. a) Pollen and spores groups percentages, CONISS results, pollen and spores concentrations and pollen zones. b) Percentage diagram of selected taxa and pollen zones. c) Photographs of *Rheedra brasiliensis* pollen grain (1-2: polar view; 3-4: equatorial view).