

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

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- 2 Atlantic forest of Southeastern Brazil based on palynology of a waterlogged sandy
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Abstract

29 Mineral soils are usually considered inappropriate for pollen analysis because of the poor quality of pollen and spore preservation and the disturbed stratigraphy. However, 30 31 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 32 33 pollen and spores since ~7000 cal. BP, both in organic and in mineral horizons. By the 34 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, δ^{13} C and δ^{15} N). Mid-35 Holocene palaeoclimate inferences from this study are in accordance with climate 36 fluctuations presented in previous studies for Central, Southeastern and Southern Brazil, 37 when a change to more humid climate occurred at ~7000 cal BP. The process 38 39 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 40 41 subsequent decomposition of the litter. Ultimately, this process led to the vertical 42 accretion of the sand with the more resistant organic structures preserved in stratigraphic sequence. The preservation of pollen and spores along the profile is 43 probably caused by low pH and redoximorphic conditions due to water saturation. This 44 study suggests the potential for retrieving useful palaeoecological information from 45 mineral and organic horizons of tropical waterlogged sandy soils, which is especially 46 47 useful for those regions where traditional pollen archives (lakes and peat bogs) are absent. 48

1. Introduction

- 51 1.1 Palynology of mineral soils
- Mineral soils are generally considered unsuitable for pollen and spore analysis due to
- 53 the poor preservation of these microfossils due to oxidation, as well as disturbed
- stratigraphy caused by bioturbation and/or pollen translocation down-profile (Dimbleby,
- 55 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
- 57 may be well preserved in some mineral soil profiles (Dimbleby, 1952; Guillet, 1970,
- 1971a, 1971b; Larocque and Campbell, 1998; Bałaga and Chodorowski, 2006). The
- 59 study soil pollen would allow the reconstitution of the local vegetation changes, which
- 60 could be related with local vegetation processes and human interferences (Larocque and
- 61 Campbell, 1998).
- 62 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,
- 65 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
- 68 middle Holocene in Southeastern Brazil (Gouveia et al., 2002; Pessenda et al., 2004,
- 69 Saia et al., 2008).
- 70 This climate change during mid- to late-Holocene may reflect an intensification of the
- 71 austral summer insolation, which led to the strengthening of the South American
- Summer Monsoon system (SASM) (Prado et al., 2013). Based on δ^{18} 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.,
- 76 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
- 80 period during the austral winter and a rainy season during the austral summer.
- 81 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
- 87 of the Neotropical vegetation.

89 2. Study site

- 90 Vale Nature Reserve (VNR) is placed at the northern coast of Espírito Santo State,
- 91 Southeastern Brazil (Figure 1a, b). It comprises ~25,000 ha of pristine environments in
- 92 the Atlantic Forest hotspot.
- 93 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
- 96 grassland and forest vegetation are interspersed among the Oxisol/Ultisol matrix (Figure
- 97 1b). Small patches of Entisols Ouartzipsamments are found under *restinga* vegetation.
- 98 Wetland soils occur along watercourses, sustaining marshes and swamps.

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

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

according to Santos et al. (2004), presents a thin layer (2 cm) of litter overlying the grey

across the site and around its margins, including Ocotea pulchella (Lauraceae), 148 149 Tibouchina urceolaris (Melastomataceae), Myrsine rubra (Myrsinaceae), Campomanesia sp. (Myrtaceae) and Aeschynomene fluminensis (Fabaceae). 150 151 Paepalanthus tortilis (Eriocaulaceae), Poaceae and Bromeliaceae are common herbs. 152 153 3. Materials and methods 154 A 57 cm soil core was collected from the NF site with a 7-cm diameter aluminium 155 cylinder. The core was X-rayed, split longitudinally and cut into two centimetres increments. Selected samples were analysed for: ¹⁴C dating, C and N elemental and 156 157 isotopic composition, grain size distribution, soil pH, and biological proxies (pollen, spores, and freshwater sponge spicules). This multiproxy approach was undertaken to 158 determine the full potential of waterlogged sandy soil as an archive for 159 160 palaeoenvironmental reconstruction – pollen for vegetation history, C and N analyses to 161 determine the origin of organic matter in reduced environments (Table 1), and 162 freshwater sponge spicules to determine local hydrological changes. 163 3.1 ¹⁴C dating Five samples were selected for ¹⁴C dating. Pre-treatments included the removal of 164 modern roots fragments and cold/hot hydrolysis with diluted HCl (Table 2). The 165 hydrolysis of peat samples (11-13 cm and 05-07 cm) was more aggressive than the 166 hydrolysis of sandy and friable samples (21-23 cm, 47-49 cm and 49-51 cm). Samples 167 were combusted at the ¹⁴C Laboratory, and the purified CO₂ was sent to the University 168 169 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 170 171 present (BP) and calibrated ages (cal. BP, 2 σ), according to the SHCal13 curve (Hogg et al., 2013), using the software CALIB Rev 7.0.4 (Stuiver and Reimer, 1993) for ¹⁴C age 172

calibration. For post-bomb samples, ¹⁴C activity was expressed as the percentage of 173 modern carbon (pMC), while calibrated ages were expressed as cal. AD, 2σ, according 174 to the Brazil curve (Santos et al., 2015) and the CALIBomb software 175 176 (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 177 178 core. 179 3.2 C and N analyses 180 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 181 sand grains. All samples were dried at 50 °C. Analyses were carried out at the Stable 182 Isotope Laboratory (CENA/USP) using an elemental analyzer attached to an ANCA SL 183 2020 mass spectrometer. Total organic C (TOC) and total N (TN) are expressed as 184 185 percentage of dry weight, with an analytical precision of 0.09% and 0.07%, respectively. Stable isotopes (δ^{13} C and δ^{15} N) were measured with respect to VPDB and 186 187 atmospheric N as standards, respectively, and are expressed as per mil (%) with a 188 standard deviation of 0.2%. 3.3 Grain size 189 190 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 191 192 natura samples. Grain size distribution of the fraction < 1 mm was determined by laser 193 diffraction analysis. Samples were processed using H₂O₂ to eliminate organic matter 194 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 195 196 Wentworth (1922). 3.4 Soil pH

Five intervals were selected for the determination of pH in water and in KCl 1 mol.L⁻¹ (198 199 in weight soil: solution = 1:2.5) by means of a potentiometer (Teixeira et al., 2017). 3.5 Biological proxies 200 201 A qualitative analysis of siliceous sponge spicules was carried out in 6 samples. To 202 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 10 203 204 minutes, and washed in distilled water. Residues were stored in distilled water and then 205 mounted on light microscope slides with Naphrax or Entellan. Sponge taxa (gemmoscleres and microscleres) were identified using the following references: 206 207 Tavares et al. (2003), Volkmer-Ribeiro et al. (2006), Volkmer-Ribeiro and Machado (2007) and Buso Junior et al. (2012). 208 Pollen and spore analysis was carried out on 11 samples of 2 cm³. Samples were sieved 209 210 (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 211 212 Lycopodium spores to determine pollen and spore concentrations, dissolution of silica 213 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 214 215 each sample, at least 200 tree or shrub pollen grains were counted in at least 3 slides. 216 The total terrestrial pollen sum includes trees, shrubs, terrestrial herbs and indeterminate/reworked pollen grains, and is the basis for calculation of percentages. 217 Identification was based on the pollen reference collection of the CENA/USP ¹⁴C 218 219 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 220 221 and spore diagrams. CONISS software (Grimm, 1987) was used for constrained cluster 222 analysis to produce pollen assemblage zones.

4. Results	and	discussion
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225	4.1 Core description, grain size distribution and soil pH
226	The X-ray image allows differentiation of mineral and organic intervals in the NF core.
227	Furthermore, the X-ray image evidences the absence of sedimentary structures and
228	stratification (Figure 2), indicating that some of the changes in the content and in the
229	characteristics of the organic matter in NF core are originated from post-depositional
230	processes related with pedogenesis. Both mineral and organic intervals present low pH
231	in H ₂ O (4.5 to 5.7), moreover pH values in KCl (3.2 to 3.9) are always lower than in
232	H ₂ O (Table 3). These pH values are in agreement with studies in Spodosols of the
233	Barreiras Formation, reflecting the acid characteristic and the predominance of negative
234	charges in these soils (Oliveira et al., 2010; Secretti, 2013).
235	The mineral interval (57-17 cm depth) is composed predominantly of sand (Figure 2),
236	and may be subdivided into five sub-intervals based upon gradations of grayscale: (i)
237	from 57-52 cm, hardened and dark brownish-grey sand with some silt; (ii) from 52 to 48
238	cm, dark grey, friable sand; (iii) from 48 to 35 cm, light grey, friable sand; (iv) from 35
239	to 21 cm, dark grey, friable sand; (v) from 21 to 17 cm, black and friable sand.
240	The organic interval (17 to -5 cm) is composed of organic matter (17-00 cm) and
241	modern litter (0 to -5 cm). The humus layer contains decomposed organic matter,
242	Salvinia microsporangia, lots of modern roots and some sand. We attribute the presence
243	of sand in the organic interval to the surface transport of sand grains from the
244	surrounding mussununga forest by water runoff, as proposed by Calegari et al. (2017),
245	based on a study of soil phytoliths at the NF site.
246	The presence of peat from 17 to -5 cm is the result of the accumulation of litter,
247	reflecting vegetation productivity, relatively low organic matter decomposition, caused

by anoxic conditions that prevail during the rainy season, and low pH, which decreases 248 249 the rate of decomposition (van Breemen and Buurman, 1998). Conversely, the stratification of the carbon-enriched layers (litter – humus – black 250 251 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. 252 (1989), the below-ground decomposition of the organic matter is influenced mainly by 253 254 environmental factors such as temperature, moisture and soil texture. At the study site, 255 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 256 257 incorporation into the mineral interval. Macroscopic characteristics of NF core presented above differs markedly from the 258 description of the deep Spodosol patch that occurs around NF site (Subsection 2.3). 259 260 Similar situation was found by Dubroeucq and Volkoff (1998) in Podzolic plains in northern Amazonia. The authors suggested that small patches of waterlogged shallow 261 262 Spodosols with peat occurring in the middle of deep Spodosol areas would have 263 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 264 development of a secondary argillic horizon within the E horizon of the deep Spodosol. 265 266 Furthermore, according to Dubroeucq and Volkoff (1998), under these conditions the dissolution of quartz increases, leading to the lowering of the relief. This model may 267 help to explain the differences observed between NF profile and the surrounding deep 268 269 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 270 271 such mechanism occurred in NF site, probably a wetter climate event may be associated 272 with it and will be discussed later (Subsections 4.5 and 4.6).

4.2 ¹⁴C dating

275 AMS dates ranged from 6672 cal. BP at 47-49 cm to 1852 cal. BP at 21-23 cm and 276 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 277 278 measurements because both LACUFF and UGAMS laboratories were recently 279 intercompared and showed very good agreement for all data sets (Macario et al., 2013). 280 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 281 of sample 47-49 cm was more aggressive (60 °C, 1h hydrolysis, Table 2) than that 282 applied to sample 49-51 cm (hydrolysis at room temperature), probably resulting in a 283 more efficient removal of fulvic acids and, consequently, an older age for sample 47-49 284 285 cm. According to Scharpenseel and Becker-Heidmann (1992), clay organic complexes 286 have lower tendency towards rejuvenation of the soil organic matter. Consequently, a 287 concurrent cause of the age inversion is the higher content of organomineral complexes 288 in sample 47-49 cm, which presents a higher clay content than sample 49-51 cm (17%) and 9%, respectively). 289 290 According to Melillo et al. (1989) and Ejsackers and Zehnder (1990), less than 20% of 291 organic matter remains after four years of litter deposition. Consequently, AMS ages 292 obtained for the organic interval probably reflect both the fast organic matter deposition 293 and the fast decay dynamics at the organic layer. Ages obtained for the upper humus 294 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 22 295 296 cm (1852 cal. BP) versus 12 cm (1957 cal. AD) reflects the reduction in thickness of the 297 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 298 299 organic matter during the dry season, leading to incorporation of older, decayed humus into the top of the mineral layer (Ejsackers and Zehnder, 1990). 300 301 4.3 C and N analyses 302 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 303 304 interval, from the base to 50 cm shows slightly elevated TOC (4.9 to 8.9%) and TN 305 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 306 307 interval, from 18 cm upwards, shows increased concentrations of organic matter, with 308 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 309 310 the process of podzolization. The deficient drainage and the low pH of the studied soil imped the fast decomposition of plant litter (van Breemen and Buurman, 1998) causing 311 312 the accumulation of peat and high TOC and TN concentrations in the upper interval. 313 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 314 315 Breemen and Buurman, 1998), leading to the leaching of the intermediary interval 316 (which presents the lowest TOC and TN values) and to the accumulation of organic matter in the deepest interval. 317 C/N ratios vary between 16.3 and 211.6 (Figure 3). The following four intervals can be 318 319 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 320 321 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 322 C/N ratios are indicative of organic matter originating from vascular plants (Table 1). 323 δ^{13} C values vary from -30.3% to -25.8%, in the range of C3 plants (Table 1), which 324 325 were likely locally dominant during the entire record. Slightly enriched values occur 326 from 34-20 cm (from ~4000 to ~1700 cal BP), which may reflect compositional changes to the local plant community. Alternatively, however, fluctuations in δ^{13} C 327 along the NF core may instead reflect the decomposition and translocation of soil 328 329 organic matter through the profile. Enrichment of δ^{13} C with depth (~2.5% from 0 to 26 cm) may be related to isotopic fractionation during decomposition (Macko and Estep, 330 1984; Melillo et al., 1989), while $\delta^{13}C$ depletion between 28 and 48 cm may be related 331 to illuvial and humified material (Kramer et al., 2003). 332 δ^{15} N varied from -1.2% to +3.3% (Figure 3), showing a tendency to more enriched 333 334 values from the base to 26 cm (>7000 to ~2600 cal. BP), and relatively stable values 335 through the organic layer. Considering the influence of decomposition and translocation 336 processes upon the characteristics of the soil organic matter, it is very likely that changes in δ^{15} N reflect these processes as well. Depleted δ^{15} N in deeper NF samples 337 may result from organic matter with low N content and low aliphaticity (Kramer et al., 338 339 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, 340 341 signifying humified organic matter translocated down-profile. 342 4.4 Siliceous sponge spicules 343 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 344 345 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 346

megascleres and gemmoscleres of Racekiela sheilae. Based on a survey of modern 347 348 coastal environments in southern Brazil, Volkmer-Ribeiro and Machado (2007) concluded that R. sheilae colonizes swampy fields or shallow seasonal ponds, close to 349 350 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 351 gemmoscleres of R. sheilae and gemmoscleres of Anheteromeyenia vitrea, the latter 352 353 identified by Buso Junior et al. (2012) based on live specimens collected at the NF site. 354 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, 355 356 which are marked by very short periods of flooding. 4.5 Palynology 357 Mineral and organic horizons in the NF core contain well-preserved pollen; only one 358 sample at 54 cm depth was devoid of pollen and spores. Eighty-nine pollen and spores 359 360 types were identified and classified as aquatic herbs, trees/shrubs, terrestrial herbs and 361 terrestrial spores. Total pollen and spore concentrations varied from 3400 to 98,400 362 grains cm⁻³ (Figure 5a), with concentrations increasing above 36 cm depth. Indeterminate and reworked pollen grains varied from 5% to 20%, with higher 363 frequencies found in the mineral substrate (50 to 20 cm). The cluster analysis allowed 364 365 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 366 in each sample, and Supplementary File 2 presents pollen and spore counts in each 367 368 sample. *Pollen Zone NF-I (7043 – 2037 cal. BP; 50 – 23 cm):* 369 370 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 371

(7-27%; 209-7458 grains cm⁻³) and terrestrial spores (5-14%; 209-3919 grains cm⁻³) 372 (Figure 5a). Indeterminate and reworked pollen grain frequencies varied from 14% to 373 20% (437-9481 grains cm⁻³). The most frequent terrestrial herbs are Poaceae (32-54%; 374 1108-31,161 grains cm⁻³) and Asteraceae (5-6%; 139-2971 grains cm⁻³). The most 375 376 frequent trees/shrubs are Myrtaceae (7-17%; 456-4881 grains cm⁻³), Melastomataceae/Combretaceae (5-10%; 203-3097 grains cm⁻³), *Rheedia* (= *Garcinia*) 377 brasiliensis (6%; 177 grains cm⁻³), Anacardiaceae (2-7%; 209-1705 grains cm⁻³) and 378 379 Alchornea/Aparisthmium (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). 380 Based on the presence of a temporary freshwater pond inferred from the *R. sheilae* 381 spicules, and based on the depleted δ^{13} C values, the Poaceae pollen grains represent C3 382 terrestrial and semiaguatic species that inhabited the freshwater pond, or swampy field, 383 384 and its margins. Some of the tree and shrub taxa (Myrtaceae, Melastomataceae, 385 Alchornea, and Anacardiaceae) would be expected to have colonized the margins and 386 more elevated areas around this pond. Despite the low frequencies, pollen types such as Caryocar, Chrysophyllum, Eriotheca, Pachira, Pseudobombax, Sapium, Sapotaceae, 387 Senefeldera and Parkia indicate that the tabuleiros forest vegetation occurred close to 388 the study site. 389 390 The availability of the pollen reference collection from plants of the study region 391 allowed the identification of pollen grains of *Rheedia brasiliensis* at the species level 392 (Figure 5c). R. brasiliensis is a generalist species occurring in mesic mussununga 393 forests of the VNR (Simonelli et al., 2008; Siqueira et al., 2014). Elsewhere in 394 Southeastern Brazil, this species occurs mainly on sandy soils of dry and seasonally 395 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, 396

and its exclusive occurrence at the onset of this pollen zone (Figure 5b), may indicate 397 that a less humid environment occurred at the NF site prior to pollen zone NF-I, 398 probably a mesic *mussununga*. The absence of *Rheedia brasiliensis* in the subsequent 399 400 samples may be the result of the local displacement of this species due to the 401 establishment of the wetland around 7000 cal. BP. 402 The change of NF site from a mesic mussununga to a wetland at ~7000 cal BP is in accordance with previous pollen, δ^{13} C and δ^{18} O based studies, which indicate the onset 403 404 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; 405 406 Behling and Negrelle, 2001; Garcia et al., 2004; Pessenda et al., 2004, 2009; Cruz et al., 407 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. 408 409 *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 410 aquatic herbs (5-76%; 1977-41,329 grains cm⁻³), terrestrial herbs (14-58%; 5008-21,331 411 grains cm⁻³) and terrestrial spores (5-16%; 1129-5931 grains cm⁻³). Indeterminate and 412 destroyed pollen grains comprise 5-16% (1832-5352 grains cm⁻³) (Figure 5a). The most 413 frequent trees/shrubs are Alchornea/Aparisthmium (7-43%; 1129-15,684 grains cm⁻³), 414 415 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%; 589-416 2379 grains cm⁻³), Urticaceae/Moraceae (2-5%; 514-1933 grains cm⁻³), Arecaceae, (0-417 11%; 132-5798 grains cm⁻³) and *Cecropia* (1-4%; 174-1570 grains cm⁻³). Aquatic herbs 418 are represented mainly by Potamogetom (0-66%; 0-35,828 grains cm⁻³), Salvina (5-419 27%; 1713-8179 grains cm⁻³), Typha (1-7%; 262-1129 grains cm⁻³) and Echinodorus (0-420 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 422 Asteraceae (3-6%; 868-1933 grains cm⁻³) (Figure 5b). 423 424 Among the most important trees/shrubs in the NF-II pollen zone are 425 Alchornea/Aparisthmium and Myrsine, which are pioneer trees that may be associated with gallery forests and seasonally flooded lowlands (Marchant et al., 2002). Myrsine 426 rubra is a frequent species in the modern environment of the NF site, colonizing its 427 margins in particular. The depleted δ^{13} C values of the organic matter (Figure 3) indicate 428 429 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 430 well as higher numbers of pollen types from trees/shrubs (from 37 types in NF-I to 48 in 431 NF-II) and terrestrial herbs (from 9 to 13, respectively). Furthermore, unlike NF-I, 432 433 where aquatic herbs are dominated by Salvinia spores, NF-II has high percentages of 434 Potamogetom, Salvinia, Typha and Echinodorus. These features of the NF-II pollen 435 zone suggest a change toward a wetland characterized by more closed and diverse 436 vegetation, indicating the onset of the modern environment at the study site. 437 Some studies of modern plant communities show that the heterogeneity of hydrologic conditions favours floristic diversity in wetlands, sand dune slacks and restingas 438 (Castellani et al., 1995; Vivian-Smith, 1997; Magnago et al., 2013). These studies found 439 440 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 441 442 of flood-tolerant species. Consequently, the change to a more diverse and closed 443 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. 444 445 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 *mussununga* 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.

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The transition to a wetland ~7000 cal. BP may be due to the onset of wetter climatic 471 472 conditions in Central, Southern and Southeastern Brazil during the middle Holocene, according with the studies summarized in subsection 1.2. This wetter interval, probably 473 474 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. 475 However, an alternative, or contributory, cause may be the mid-Holocene rise in 476 477 eustatic sea-level, especially because the beginning of pollen zone NF-I (7043 cal. BP) 478 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 479 groundwater level. 480 The onset of pollen zone NF-II at ~2000 cal. BP, with more diverse and structurally 481 482 complex vegetation, may be due to a decrease in intensity and frequency of flooding, in 483 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 484 485 deposition of sand, and regional base-level lowering due to the late-Holocene relative 486 sea-level fall). 487 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 488 downwashing of pollen through the profile, bioturbation by soil fauna (Davidson et al., 489 490 1999), and pollen degradation by oxidation (Larocque and Campbell, 1998). However, the distinct assemblages of well preserved pollen and spores in the sandy soil 491 492 at NF site demonstrate clear palynological stratigraphy, both in organic and in mineral horizons, demonstrating that any down-core pollen translocation, bioturbation, or pollen 493 494 oxidation must have been relatively insignificant. Good pollen preservation can be 495 attributed to the low pH and deficient drainage, which reduce bioturbation and

microbial activity and hence pollen degradation (Larocque and Campbell, 1998; van 497 Breemen and Buurman, 1998). We have tested some Spodosol profiles in our study area regarding pollen and spore 498 499 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 cannot have been transported along with the organic matter. We suggest that the 504 505 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 for the present study, where local conditions have an important role in the maintenance 512 513 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 regionallysmoothed pollen catchments. Furthermore, pollen records from tropical waterlogged 518 519 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

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523 5.1. Distribution and characteristics of organic matter C and N data from the NF core indicate that organic matter has originated 524 predominantly from vascular C3 plants since 7000 cal. BP. However, decomposition 525 526 and translocation processes have influenced the characteristics and the distribution of 527 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. . 528 Small enrichments of δ^{13} C likely reflect isotopic fractionation during decomposition. 529 Down-core depletion of $\delta^{15}N$ may reflect translocation of humified organic matter to 530 lower soil horizons. 531 532 5.2. Biological proxies in the waterlogged sandy soil 533 The waterlogged sandy soil at NF site has well preserved biological proxies (pollen, 534 spores and sponge spicules), both in organic and mineral intervals. Clear stratigraphic 535 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 536 537 conditions prevented the degradation of pollen and spores. 538 These biological proxies indicate the transition from a mesic mussununga to a wetland 539 ~7000 cal. BP. Between ~7000 and ~2000 cal. BP this wetland was a swamp or freshwater pond, colonized mainly by aquatic and semiaguatic C3 plants and the 540 541 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. 542 543 The transition from the mesic *mussununga* to a wetland ~7000 cal. BP suggests a 544 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 $1 - \delta^{13}C$, $\delta^{15}N$ and C/N of different organic matter sources

Organic matter source	δ ¹³ C (‰)	δ ¹⁵ N (‰)	C/N
Vascular C3 plants	-33 to -20	≈ +1	≥ 20
Vascular C4 plants	-17 to -9	≈ +1	≥ 20
Freshwater phytoplankton	-37 to -25	≈ +8	4 to 10
Marine phytoplankton (1)	≈ -21	≈ +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)

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

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

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

Fluminense.

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Table 3 – pH of selected intervals in NF core

1		
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

^a ¹⁴C activity in pMC.

^b Calibrated age in cal AD.

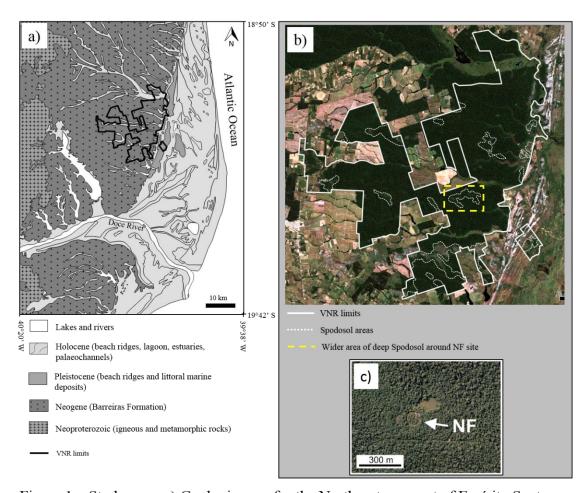


Figure 1 – Study area. a) Geologic map for the Northeastern coast of Espírito Santo State. b); Landsat 7 RGB123 composition and the Spodosol areas delimited by Santos et al. (2004) in the VNR; c) NF site.

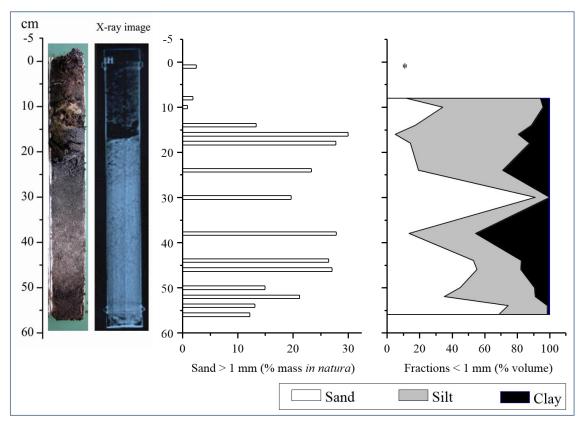


Figure 2 - NF core: photograph, X-ray image and grain size distribution. (*) sample 03-00 cm was lost during laser diffraction analysis.

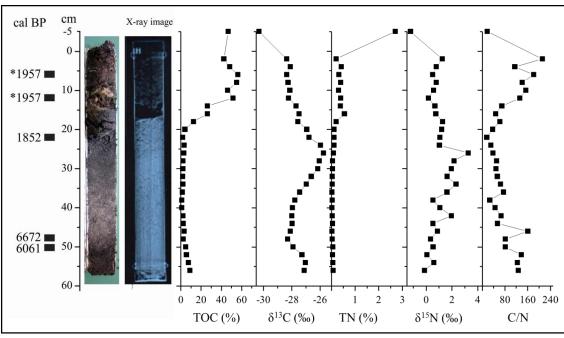


Figure 3 – C and N results from NF core. *ages in cal AD.

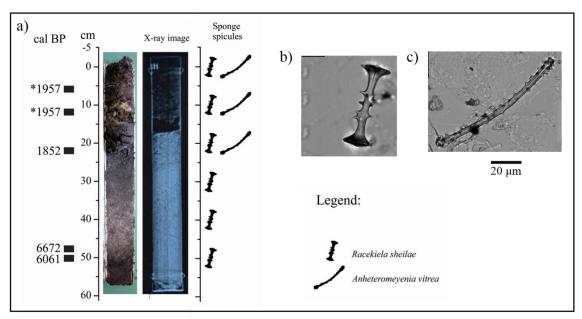


Figure 4 - a) Presence of siliceous sponge spicules. Gemmoscleres of *Racekiela sheilae* (b) and *Anheteromeyenia vitrea* (c). *age in cal AD.

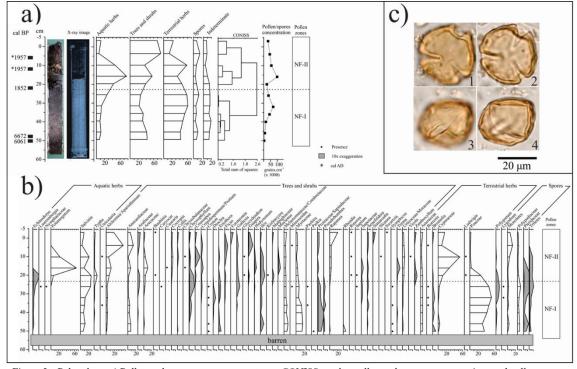


Figure 5 – Palynology. a) Pollen and spores groups percentages, CONISS results, pollen and spores concentrations and pollen zones. b) Percentage diagram of selected taxa and pollen zones. c) Photographs of *Rheedia brasiliensis* pollen grain (1-2: polar view; 3-4: equatorial view).