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HAL Authorization

1 **Pollen rain-vegetation relationship along an elevational gradient in the Serra dos Órgãos**  
2 **National Park, southeastern Brazil**

3  
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14  
15 **Abstract** We analyzed modern pollen deposition along an altitudinal gradient in the Brazilian  
16 southeastern coastal mountains between 1600 and 2200 m elevation in order to investigate  
17 the relationship between modern vegetation and pollen rain, within vegetation composed of  
18 montane and upper montane forest in a mosaic with campos de altitude (CDA). The results  
19 revealed that the CDA pollen assemblage represents a much larger source area than the  
20 forest pollen assemblage, which is comprised of more local taxa. Anemophilous pollen from  
21 vegetation at lower elevations is overrepresented in the higher elevation pollen traps.  
22 Although arboreal taxa dominate the pollen assemblages – even in the grassland pollen  
23 traps – the composition of the pollen traps can be confidently related to the vegetation  
24 surrounding the collection site. To improve distinction between grassland and forest  
25 dominance in a complex environmental mosaic subject to temporal dynamism, we selected  
26 a suite of arboreal pollen taxa aiming to reduce the influence of over- and under-  
27 representation of some pollen taxa in such kind of environment. Our findings permit more  
28 robust interpretation of palaeo-ecological and -geographical relationships between forest  
29 and CDA and build a firmer foundation for understanding how future climatic change may  
30 impact montane vegetation in SE Brazil.

31 **Key words:** modern pollen rain, campos de altitude (high elevation grassland), upper  
32 montane forest, tropical mountains, tropical South America.

33 **1. Introduction**

34 The Atlantic Forest biome stretches along Brazil's east coast for more than 4000 km, with the  
35 Brazilian Highlands as its geographic backbone. The Atlantic Forest, which once covered as  
36 much as 1.3 million km<sup>2</sup>, has been drastically reduced in area since European settlement in  
37 the 16<sup>th</sup> century (Fundação SOS Mata Atlântica/ INPE, 2017) and is considered one of the  
38 world's most threatened biomes as well as one of its most important biodiversity hotspots  
39 (Myers et al., 2000). Today, some of the largest remaining fragments of the Atlantic Forest  
40 are inside national and state protected areas found on the steep slopes of the Serra do Mar  
41 and Serra da Mantiqueira in the states of Rio de Janeiro, Minas Gerais, and São Paulo  
42 (Ribeiro et al., 2009). Among the ecosystems covered by these protected areas, some of the  
43 most important are upper montane forest and campos de altitude (CDA, or named high  
44 elevation grasslands), due to their rarity in eastern Brazil and the high numbers of endemic  
45 species they support (Martinelli and Bandeira, 1989; Safford and Martinelli, 2000; Spehn et  
46 al., 2010). These ecosystems share the summits of eastern Brazil's highest mountains, with  
47 upper montane forest often occupying concavities and protected sites and campos de  
48 altitude covering mountaintops and convex slopes (Safford, 1999a). Their geographic  
49 relationship is dynamic, with forests dominating in the absence of disturbance and when and  
50 where climates are warmer and wetter, and campos dominating after fire and in colder and  
51 drier periods (Safford, 1999a, 2001; Portes et al., 2018).

52 Over the last two decades palaeoecological studies based on fossil pollen and charcoal  
53 records have been carried out in the southeastern Brazilian highlands in order to better  
54 understand past, current, and potential future trends in vegetation, climate, and  
55 disturbance, as well as to discern synergies between these factors in driving ecological  
56 conditions (e.g. Behling, 1995, 1997a, 1997b, 2007; Scheel-Ybert, 2001; Ledru et al., 2005;  
57 Behling et al., 2007; Behling and Safford, 2010; Veríssimo et al., 2012; Raczka et al., 2013;  
58 Portes et al., 2018). This work has also provided information important to improve the  
59 design of conservation and management strategies that aim for sustainability in the face of  
60 rapid global change. However, because pollen production, dispersal, and preservation vary  
61 widely among plant species, the relationship between pollen rain, local vegetation and  
62 environment is not straightforward, which limits the interpretation of the fossil pollen  
63 record (e.g. Prentice, 1988). Studies that relate modern vegetation and environment to  
64 pollen rain – especially studies carried out along elevational and ecological gradients – can

65 help to better discern pollen production and dispersal patterns, as well as habitat and  
66 elevational relationships among species and ecological communities in order to improve  
67 interpretation of fossil pollen records (e.g. Bartlein et al., 2011; Cárdenas et al., 2014; Jantz  
68 et al., 2014; Markgraf et al., 2002; Montade et al., 2016; Niemann et al., 2010; Rodrigues et  
69 al., 2016; Schüler et al., 2014; Tonello et al., 2009; Weng et al., 2004).

70 Montade et al. (2019) recently developed the first modern pollen dataset for the full Atlantic  
71 Forest biome, describing regional vegetation and climate patterns. Based on this dataset, the  
72 authors were able to discern four broad “eco-physiognomies” from modern pollen samples,  
73 including northeastern Atlantic rain forest, semi-deciduous and riverine forests, lowland rain  
74 forest, and high elevation vegetation consisting of forests and grasslands. In the case of the  
75 high elevation vegetation group, the authors pointed out that the fine-spatial scale of  
76 intercalation of forest and grassland vegetation posed a challenge to further differentiation  
77 that only well-designed, local sampling could resolve. Due to the reduced number of modern  
78 pollen samples, several sampling methods had to be combined in this regional dataset.  
79 Nonetheless, different sampling methods can present different results which could explain  
80 this local scale limitation in differentiating vegetation physiognomies. Surface samples may  
81 be considered more representative of the pollen production as pollen rain composition  
82 commonly varies over 2 and three 3 as well as according to plant specific systems and  
83 changing in climatic conditions (Niemann et al., 2010; Montade et al., 2019). In contrast,  
84 pollen traps not only provide the representation and distribution patterns of pollen spectra  
85 but also the accumulation rates. Moreover, pollen traps present better pollen preservation,  
86 diminishing the difficulty and uncertainties in determination of pollen types and allowing to  
87 distinguish similar pollen that normally are classified together, and registering pollen with  
88 fragile exine that rarely appear in surface samples or in fossil records (Jantz et al., 2014).

89 The dynamic relationship between CDA and forest is of major ecological, conservation, and  
90 management interest in southeastern Brazil (Martinelli and Bandeira 1989; Safford, 1999a;  
91 2001; Aximoff 2011; Portes et al., 2018). In order to understand how these ecosystems  
92 interact over space and time, we require a robust discrimination of their signal in the fossil  
93 pollen record, but to this point such a discrimination had been lacking. To fill this gap, we  
94 installed a series of pollen traps along a high elevation transect through areas dominated by  
95 montane forest, upper montane forest and CDA in Serra dos Órgãos National Park  
96 (PARNASO; Fig. 1). We used pollen traps rather than surface samples so as to better preserve

97 fragile pollen types that rarely appear in soil surface samples, to diminish identification  
98 errors and to allow the calculation of pollen accumulation rates. Our principal purposes were  
99 to (1) investigate the relationship between the modern pollen assemblage and local modern  
100 vegetation cover; (2) try to better discriminate between grassland and forest dominance in a  
101 complex environmental mosaic subject to temporal dynamism; and (3) augment the modern  
102 pollen database of the Brazilian Atlantic Forest biome.

103

## 104 **2. Environmental settings**

### 105 *2.1 Study site*

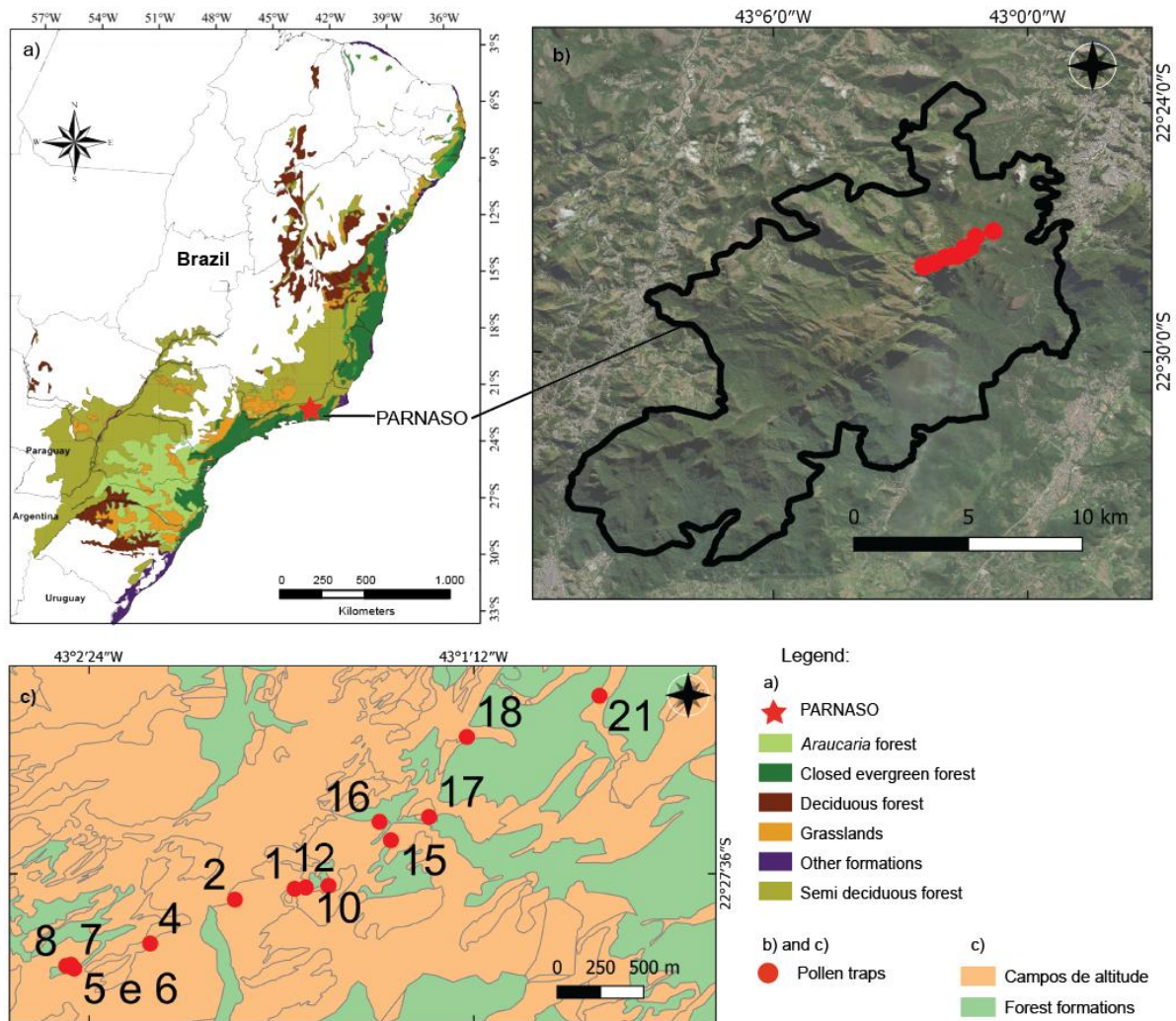
106 Our pollen traps were located along an elevational gradient in the Serra dos Órgãos, a  
107 subrange of the Serra do Mar, within PARNASO (Fig. 1). Founded in 1939 as the third  
108 national park in Brazil, PARNASO protects 20,024 ha of lower montane, montane and upper  
109 montane forest and campos de altitude of the Brazilian Atlantic Forest biome (ICMBio,  
110 2008). The park is famous for its spectacular landscape and extraordinary levels of  
111 biodiversity. Ironically, it is found in one of the most densely populated areas of Brazil, less  
112 than 50 km from downtown Rio de Janeiro.

113 In the Serra dos Órgãos, basement rocks are mostly Late Proterozoic granite and granitoid  
114 gneisses. Topographic relief is associated with late Cenozoic reactivation of faults that  
115 originally arose during the opening of the Atlantic Ocean in the late Mesozoic (Machado  
116 Filho et al., 1983). Soils in the study area are generally shallow, poorly developed, acidic and  
117 highly organic with a deep litter layer (Falkenberg and Voltolini, 1995). As a rule, the Serra  
118 dos Órgãos follows a SW-NE orientation parallel to the coastline (Riccomini et al., 1989;  
119 Safford, 1999a; ICMBio, 2008).

120

### 121 *2.2 Climate*

122 In the broader region, the climate is mostly controlled by the South Atlantic Convergence  
123 Zone (SACZ), with most precipitation falling between November and April (Safford, 1999a).  
124 Although the climate for the region has been classified as mesothermic with mild and wet  
125 summers and moderate winters without a marked dry season (ICMBio, 2008), a winter dry  
126 season (months with <50 mm precipitation) of two to three months occurs most years in the  
127 southeastern Brazilian mountains (Nimer, 1977; Safford, 1999b). The annual average  
128 temperature at the nearest long-term meteorological station at Teresópolis (22°25.980'S,



129

130 **Fig. 1.** Location of the study site and the pollen traps. a) national location of Parque Nacional  
 131 da Serra dos Órgãos (PARNASO) (adapted from Fundação SOS Mata Atlântica/ INPE, 2017),  
 132 b) regional location of PARNASO and c) location of the pollen traps collected in PARNASO.

133

134 42°58.980'W, 1100 m a.s.l.) is 17.6 °C, ranging from 8.6 °C (mean of the coldest month –  
 135 July) to 27.2 °C (mean of the warmest month – February). Mean average precipitation at  
 136 Teresópolis is 1800 mm, with less than 40 mm in the driest month (July) and 270 mm in the  
 137 wettest (January) (Hijmans et al., 2005). Orographic effects play an important role in  
 138 modifying the Serra dos Órgãos climate, and elevations higher than Teresópolis are cooler,  
 139 wetter, and characterized by frequent fog. PARNASO installed temperature data loggers at  
 140 sites near our transect between September 2012 and February 2014 (C. Cronemberger,  
 141 PARNASO, pers. comm.). In montane forest at 1600 m elevation (near pollen trap site 21),  
 142 the mean overall temperature was 15.4 °C, with an absolute maximum of 30.7 °C and a  
 143 minimum of 3.1 °C. In upper montane forest at 2012 m elevation, mean, maximum and

144 minimum temperatures were 12.7 °C, 25.6 °C, and 1 °C, respectively. Temperatures in the  
145 campos de altitude at 1954 m elevation showed a similar mean temperature (12.5 °C), but  
146 temperatures were more extreme due to the lack of trees and the valley bottom position:  
147 max = 27 °C, min = -5.2 °C). Safford (unpub. data) measured -9.8 °C during a July night in  
148 1997 at this same campos de altitude site. Safford (1999b) measured soil temperatures from  
149 depths of >75 cm in deep soil pockets on the summit of Pedra do Sino and obtained an  
150 estimate of mean annual temperature of approximately 10.2 °C at 2260 m a.s.l.. Annual  
151 precipitation in the Serra dos Órgãos at 2000 m elevation is >2500 mm (Safford, 1999b).

152

### 153 2.3 *Vegetation*

154 The vegetation encountered at the study sites is classified as montane Atlantic rain forest  
155 (ARF), upper montane ARF, and campos de altitude (CDA) (ICMBio, 2008). Montane ARF  
156 occurs from c. 700 to c. 1600 m a.s.l. It typically presents three strata, within the canopy  
157 reaching 25-30 m height. Common overstory tree families include Myrtaceae, Lauraceae,  
158 Melastomataceae, Fabaceae, Solanaceae, Asteraceae, Rubiaceae, and Euphorbiaceae.  
159 Important epiphyte families include Orchidaceae, Bromeliaceae, Gesneriaceae and various  
160 ferns. The palm *Euterpe edulis*, tall *Chusquea* bamboos, and tree ferns are common in the  
161 midstory. Lianas are dominated by Asteraceae, Malpighiaceae, Fabaceae, and Sapindaceae,  
162 and shrubs are represented by Rubiaceae, Melastomataceae, Piperaceae, and Begoniaceae,  
163 among many other families (Lima and Guedes-Bruni, 1997; Pardo et al., 2007; ICMBio, 2008).  
164 Montane habitats grade gradually into upper montane habitats starting above 1300 m a.s.l.,  
165 with upper montane ARF prevailing at elevations >1600 m a.s.l. (ICMBio, 2008). Due to the  
166 common presence of fog, constant winds and other microclimatic conditions, upper  
167 montane ARF is characterized by twisted and dwarfed trees and shrubs distributed usually in  
168 one stratum <10 m height. A salient feature is the abundance and diversity of epiphytes –  
169 especially Orchidaceae, Bromeliceae, Cactaceae, ferns and mosses – as a result of the high  
170 air humidity (Falkenberg and Voltolini, 1995; Safford, 1999a). The most frequent tree and  
171 shrub families are Myrtaceae, Proteaceae, Melastomataceae and Malpighiaceae (ICMBio,  
172 2008). Important tree genera include *Myrsine*, *Clethra*, *Piptocarpha*, *Myrceugenia*,  
173 *Daphnopsis*, *Roupala*, *Weinmannia*, *Symplocos*, *Ilex*, and *Ocotea* (Behling and Safford, 2010;  
174 Gomes, 2015).

175 CDA vegetation dominates above 1800 m a.s.l., covering hilltops and convex slopes as well as

176 poorly-drained valley bottoms that are affected by cold air drainage (Safford, 1999a; ICMBio,  
177 2008). The CDA is dominated by tall bunchgrasses and sedges (especially *Cortaderia* and  
178 *Machaerina*), montane bamboo (*Chusquea*) and a heterogeneous mixture of sclerophyllous  
179 shrubs, particularly from the genera *Baccharis* and *Escallonia*, and the families Asteraceae,  
180 Ericaceae, Melastomataceae, and Myrtaceae. Frequent herbs are *Eryngium*, *Paepalanthus*,  
181 *Plantago* and *Xyris*, and lycopods and cool-weather bryophytes are widespread (Behling and  
182 Safford, 2010).

183

### 184 **3. Material and Methods**

#### 185 *3.1 Pollen trap design and sampling*

186 For collection of the modern pollen assemblage of the mountain vegetation of PARNASO, 23  
187 pollen traps were placed along a 4-km section of the Pedra do Sino trail, ranging from 1600  
188 m to 2200 m a.s.l., between the coordinates 22°26'53"S, 43°00'28"W and 22°27'53"S,  
189 43°02'28"W (Fig. 1). Each pollen trap was classified according to their respective local  
190 vegetation in the field (CDA, upper montane ARF and montane ARF). The trap model used  
191 was developed by Behling and formally described in Behling et al. (2001) and tested by Jantz  
192 et al. (2013). Each trap was installed about 10 cm above the soil surface in October, 2015  
193 and collected in October, 2016 (Table 1).

194

#### 195 *3.2 Pollen analysis*

196 The pollen grains were extracted from each trap as described in Jantz et al. (2013). Before  
197 processing, one tablet of *Lycopodium clavatum* spores (20,848 1546, batch 3862) was  
198 added as exotic marker to each sample for influx calculation. Acetolysis was carried out to  
199 dissolve cellulose material and to stain the pollen residues. The pollen residue obtained was  
200 kept in distilled water until mounted in slides with glycerine for pollen analysis. Samples  
201 were counted to a minimum of 300 pollen grains and identification of pollen and spores was  
202 based on the reference collection of Brazil and Ecuador at the Department of Palynology and  
203 Climate Dynamics, University of Goettingen (Germany). Further support was obtained from  
204 literature and electronic pollen keys (Behling, 1993; Melhem et al., 2003; Bush and Weng,  
205 2006; Neotropical Fossil Pollen Search Tool developed by Dr. Hermann Behling and Dr.  
206 Chengyu Weng, unpublished). Nomenclature follows the Flora do Brasil 2020  
207 (<http://floradobrasil.jbrj.gov.br>). Pollen percentages were calculated excluding aquatics,

208 exotics, unidentified and spores. Pollen diagrams were plotted using the C2 software  
 209 (Juggins, 2007) and clustered according to the habit and the ecology of the taxa.

210

211 **Table 1.** List of 23 pollen traps grouped by vegetation zone where each trap was installed,  
 212 with their geographic coordinates and elevation. In black the recovered traps and in gray the  
 213 unfounded ones.

Vegetation	Sample	Coordinate S	Coordinate W	Altitude (m)
Campos de altitude (CDA)	SOPT1	22°27'38.48"	43°01'45.66"	2188
	SOPT10	22°27'38.23"	43°01'43.57"	2180
	SOPT2	22°27'40.50"	43°01'56.86"	2169
	SOPT11	22°27'37.87"	43°01'36.44"	2148
	SOPT15	22°27'29.41"	43°01'27.66"	2128
	SOPT13	22°27'33.08"	43°01'43.46"	2126
	SOPT14	22°27'31.78"	43°01'40.81"	2115
	SOPT3	22°27'44.86"	43°02'4.27"	2107
Upper montane ARF	SOPT4	22°27'48.70"	43°02'12.70"	2086
	SOPT16	22°27'25.96"	43°01'29.78"	2157
	SOPT12	22°27'37.90"	43°01'39.36"	2134
	SOPT9	22°27'46.30"	43°02'6.97"	2113
	SOPT17	22°27'25.06"	43°01'20.53"	2031
	SOPT7	22°27'52.67"	43°02'27.52"	2013
	SOPT8	22°27'52.88"	43°02'28.39"	2008
	SOPT5	22°27'53.40"	43°02'26.91"	2003
Montane ARF	SOPT6	22°27'53.40"	43°02'26.91"	2003
	SOPT18	22°27'10.12"	43°01'13.44"	1923
	SOPT19	22°27'18.18"	43°01'3.40"	1844
	SOPT20	22°27'8.17"	43°0'53.60"	1671
	SOPT21	22°27'02.41"	43°00'48.67"	1597
	SOPT22	22°26'54.49"	43°00'49.36"	1439
	SOPT23	22°26'53.27"	43°00'28.15"	1287

214

### 215 3.3 *Vegetation cover analysis and multivariate analysis*

216 The modern vegetation surrounding each pollen trap was analyzed using the software QGIS  
 217 (QGIS Developing Team, 2019) based on a Bing aerial image (2019) with support of  
 218 geographical information from 2008 provided by PARNASO. We delimited buffers of 0.79 ha  
 219 (50 m radius), 3.14 ha (100 m radius), and 78.6 ha (500 m radius) for each trap (see  
 220 supplementary material) and identified the percentage of the area dominated by two  
 221 different components: forest and CDA. The CDA component includes CDA *sensu stricto*, rock

222 vegetation, and rock outcrops. A coefficient of correlation ( $r$ ) was calculated between  
223 percentage values of vegetation cover and pollen data for the forest and CDA components  
224 within each of the buffer areas.

225 A correspondence analysis (CA) was applied with R-packages ADE4 (Dray and Dufour, 2007)  
226 and VEGAN (Orkansen et al., 2019) in R-Studio (R-Studio Team, 2016) to investigate  
227 correlations between pollen spectra from the pollen traps and the representative  
228 vegetation. We focused on the CDA and upper montane forest groups and excluded the  
229 montane forest group from the CA as it was characterized by only one sample (SOPT21). In  
230 order to reduce noise, the CA was performed with the major pollen taxa (with percentages  
231  $\geq 1\%$  occurring in at least three samples). Percentage values were square-root transformed  
232 before performing the CA to stabilize the variance.

233 To better reconstruct the local changes of ARF in this mosaic of grassland and forest, we  
234 defined a group of most distinctive pollen taxa of upper montane ARF composed by  
235 *Weinmannia*, *Myrsine*, *Clethra*, and Myrtaceae based on the results of the CA and  
236 considering pollen assemblages, habit and ecological features. We also considered the  
237 facility in distinguishing these taxa (important when comparing several sites involving  
238 different palynologists) as well as their abundance and well preservation in fossil samples.

239 This restricted group of ARF and the ARF group were passively projected on the first and  
240 second axes of the CA bi-plot.

241

## 242 **4. Results**

### 243 *4.1 Modern pollen rain*

244 Of the original 23 pollen traps only 14 were recovered. A total of 98 pollen types and 24  
245 spores were identified from the recovered traps. The most abundant and important taxa are  
246 displayed in the pollen diagrams (Figs. 2 and 3). A list of all palynomorphs identified can be  
247 found in the supplementary material. The pollen taxa were classified into the following  
248 ecological groups based on their habit and ecology: CDA including subgroups herbs and  
249 shrubs and Asteraceae; upper montane ARF; montane ARF; sub-aquatics, exotics, tree ferns,  
250 and ferns. The separation of the groups follows Safford (1999a), Behling and Safford (2010),  
251 Gomes (2015) and Montade et al. (2019).

252 According to their respective local vegetation and elevation, the pollen sampling sites were  
253 separated into three ecological zones: CDA, upper montane ARF, and montane ARF (Table 1).

254 Each zone is typified by a characteristic pollen assemblage composition and abundance.  
255 Overall, arboreal taxa predominate in the pollen rain, even in samples taken from CDA  
256 vegetation. The five most abundant taxa in all pollen spectra are *Myrsine*, Melastomataceae,  
257 Poaceae, Moraceae/Urticaceae, and *Weinmannia*. Asteraceae, Myrtaceae, *Cecropia*, and  
258 *Alchornea* were present in all samples, along with the introduced taxon *Pinus*.

259

#### 260 4.1.1 Campos de altitude (5 samples)

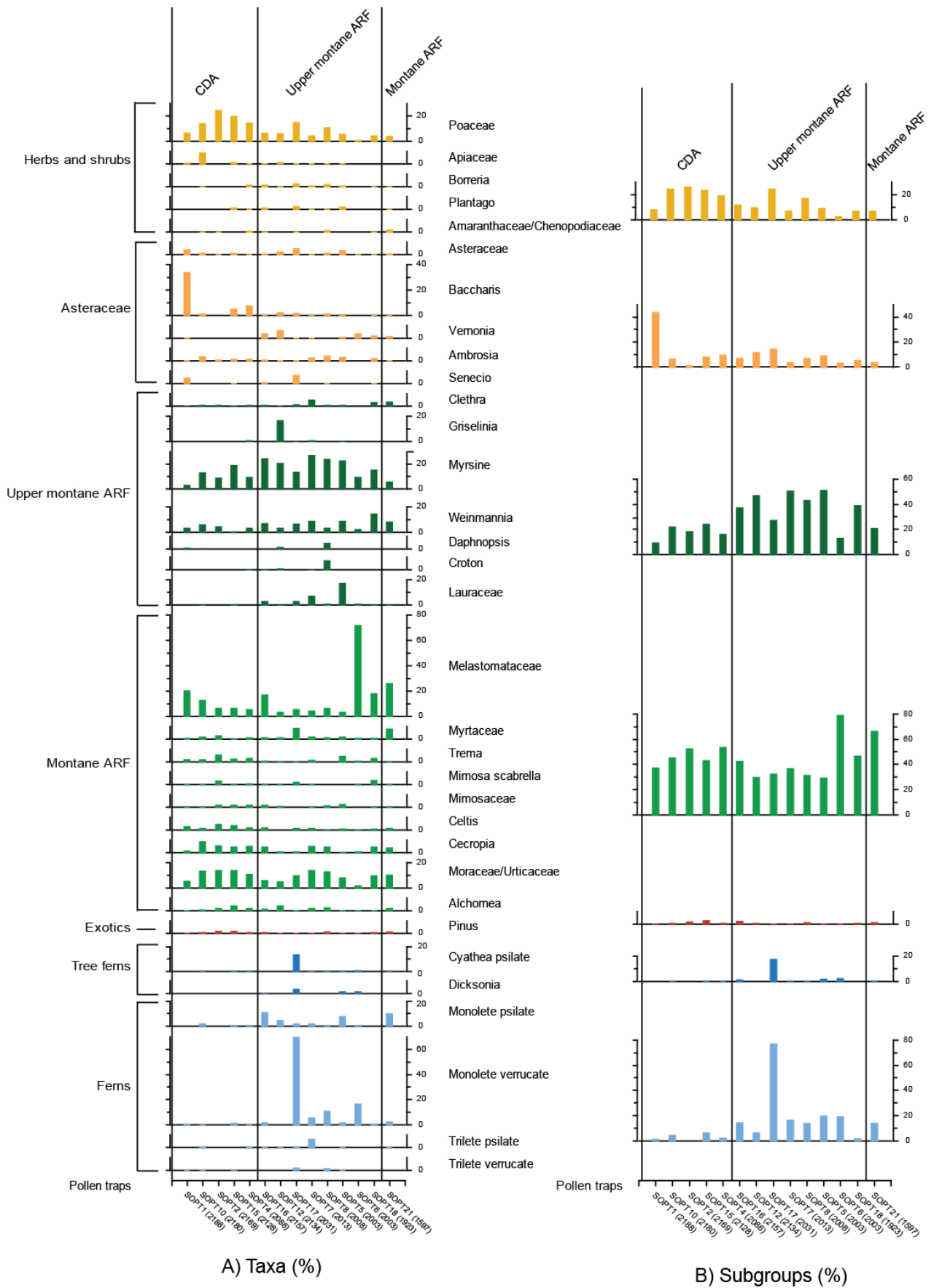
261 Although this vegetation zone is characterized principally by herbs, shrubs, and Asteraceae,  
262 forest pollen types are up to 65% of all pollen; that is, pollen from the CDA ecological group  
263 only contributed an average of 35% of the pollen collected in the traps. In this vegetation  
264 type, pollen of Poaceae (16%) and *Baccharis* (c.10%, separated from other Asteraceae pollen  
265 types due to its relatively high number of small and long echini (Behling, 1993)) are the best  
266 indicators. Pollen taxa of upper montane ARF (*Myrsine* > 10%, *Weinmannia* c. 4% and *Clethra*  
267 1%) and montane ARF (Moraceae/Urticaceae c. 12%, Melastomataceae c. 10%, *Cecropia* 5%,  
268 *Celtis* c. 3%, Myrtaceae 2%, and *Alchornea* c. 2%) are also abundant. There is high variability  
269 among samples for some pollen taxa. For example, *Baccharis* represents c. 34% and  
270 Melastomataceae c. 20% in sample SOPT1 and Cyperaceae almost 12% in SOPT2. Although  
271 *Eryngium* type 2 is generally rare, it occurs at a high percentage in a single sample (SOPT10 >  
272 9%). *Mimosa scabrella* reaches c. 3% in SOPT2 with average of c. 1% in this zone. Spores of  
273 tree ferns are almost absent in CDA, the average sum of other spores reaches 3% while the  
274 exotic *Pinus* is about 1% in this zone.

275 Pollen influx is very low in traps in CDA, the mean value is <2000 pollen grains cm<sup>-2</sup>, varying  
276 from 920 to 3055 pollen grains cm<sup>-2</sup>. In the CDA zone, the sum of characteristic CDA taxa  
277 produces an average influx of c. 700 pollen grains cm<sup>-2</sup>, while upper montane ARF average  
278 influx is 335 pollen grains cm<sup>-2</sup> and the montane ARF average is 945 pollen grains cm<sup>-2</sup>.

279

#### 280 4.1.2 Upper montane ARF (8 samples) and montane ARF (1 sample)

281 Upper montane vegetation is well represented by its pollen assemblage. The upper  
282 montane/montane ARF zone (they are combined here due to similar pollen spectra and the  
283 existence of only one sample in the montane ARF zone) is characterized by higher spore  
284 sums than the CDA zone. *Myrsine*, *Weinmannia*, Lauraceae, *Griselinia*, and *Clethra* are the  
285 most important upper montane ARF indicator taxa with averages of c. 18%, 7%, 4%, 2%, and

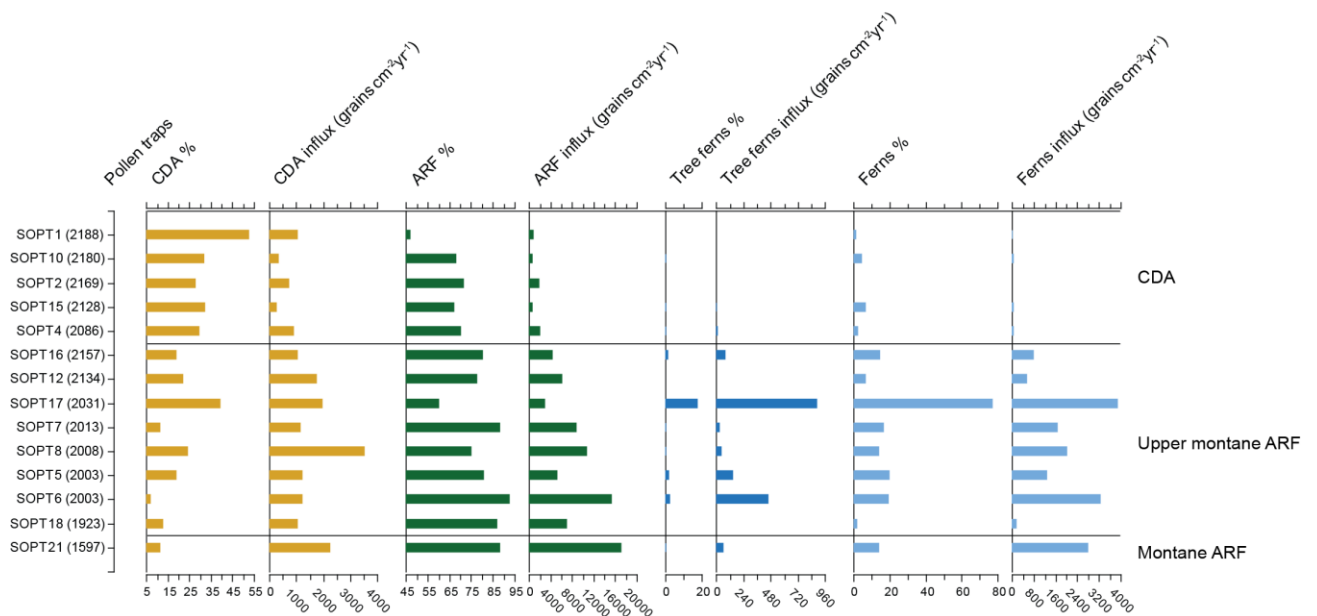


289

290 respectively. The main montane ARF pollen taxa are Melastomataceae 18%,  
291 Moraceae/Urticaceae 9%, *Cecropia* c. 3% and Myrtaceae 3%. Pollen traps from SOPT17 and  
292 SOPT18 have higher values of *Mimosa scabrella*, 2% and 4% respectively, and  
293 Melastomataceae represents 72% of all pollen in the trap SOPT6. Pollen types from the CDA  
294 ecological group contribute about 19% of all pollen in the ARF zone, mainly from Poaceae (c.  
295 7%), *Vernonia* (c. 2%), and other Asteraceae types (c. 2%). Two outlying samples are SOPT6  
296 (7% CDA pollen) and SOPT17 (c. 40% CDA pollen). The average for tree ferns reaches c. 3%,  
297 but SOPT17 shows very high values: *Cyathea* with 14% and *Dicksonia* with c. 4%. The group  
298 of sub-aquatic taxa is represented by c. 2% and exotics by c. 1% pollen.

299 Regarding pollen influx in these zones, the average sum is 10,400 pollen grains  $\text{cm}^{-2}$ , varying  
300 from 5000 in SOPT17 to 20,000 in SOPT21. The influx of taxa from the upper montane ARF  
301 ecological group ranges from 1400 to 6250 pollen grains  $\text{cm}^{-2}$  and taxa correlated with the  
302 montane ARF ecological group range from 1700 to 13000 pollen grains  $\text{cm}^{-2}$ . Pollen influx  
303 from the CDA ecological group averages 1700 pollen grains  $\text{cm}^{-2}$ .

304



305

306 **Fig. 3.** Percentage and influx diagram of groups sorted by vegetation types and altitude.

307

#### 308 4.2 Vegetation cover and multivariate analysis

309 Table 2 shows the percentage of CDA and forest vegetation surrounding each pollen trap  
310 using spatial buffers of 50 m radius (0.79 ha total area), 100 m radius (3.14 ha) and 500 m

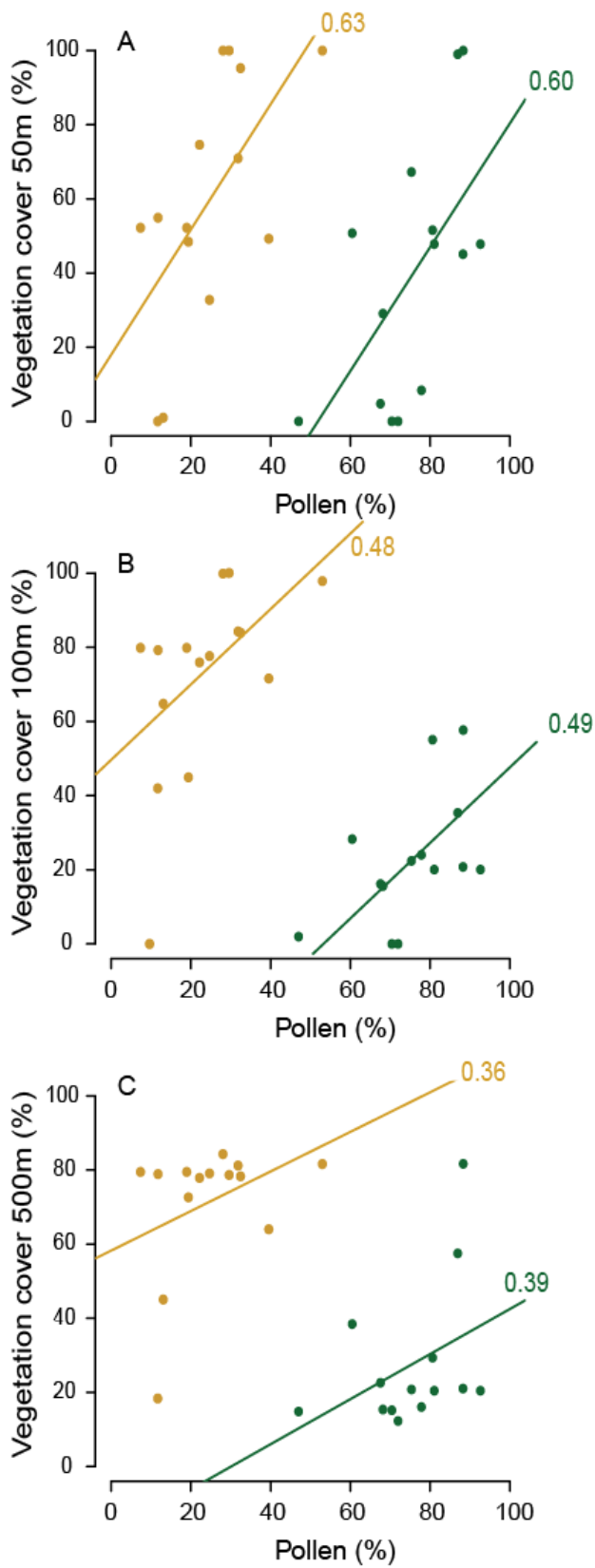
311 (78.6 ha) radius, combined with pollen percentage of the CDA and ARF ecological groups.  
312 Applying a smaller buffer would have been interesting if the satellite image presented higher  
313 resolution however, with the resolution available, the surrounded vegetation was the same  
314 as in the pollen traps classification. Pollen traps installed in CDA are mostly surrounded by  
315 CDA vegetation (mean = >70% CDA vegetation) in all sizes of buffer, although the percentage  
316 of forest vegetation is higher at the 500 m radius. With buffer at 50 m, the highest % of  
317 forest is shown in SOPT10 (c. 30%) and with buffer at 100 m both SOPT10 and SOPT15 reach  
318 c. 16%. On the other hand, the area surrounding the pollen traps in upper montane forest  
319 only averaged 55% of forest in the small buffer (excluding SOPT21) and <70% in the two  
320 larger buffers. The one recovered trap installed in montane forest (SOPT21) at lower altitude  
321 is dominated by forest vegetation at all buffer sizes, although the 78.6 ha buffer included a  
322 number of patches of open canopy where rock and herbaceous vegetation dominated. The  
323 correlation coefficient ( $r$ ) between the pollen assemblages and the respective vegetation  
324 groups dropped as buffer size increased. The coefficients for the CDA group are 0.63 for 50  
325 m radius, 0.48 for 100 m and 0.36 for 500 m radius, while in the ARF group the coefficients  
326 are 0.60, 0.49, and 0.39 for 50, 100, and 500 m radius, respectively (Fig. 4).

327 A preliminary correspondence analysis using 13 samples clearly separated a group that  
328 includes all samples from SOPT6 (supplementary material). This sample is characterized by a  
329 high value of Melastomataceae (>70%) due to a local signal. We therefore considered this  
330 sample as an outlier and performed a new CA with 12 samples to provide an understanding  
331 of the relationships among pollen assemblages and vegetation groups (Fig. 5). The first two  
332 axes explain 54.6% of the total variation. Axis 1 clearly separates CDA from forest pollen trap  
333 samples (Fig. 5a). The most robust CDA indicators include *Baccharis* (displaced upward along  
334 ordination Axis 2 by its strong association with sample SOPT1), Melastomataceae, and  
335 Poaceae, as well the woody genera (trees and lianas) *Celtis*, *Trema*, and *Cecropia*, all of  
336 which are pioneer taxa in disturbed forest (Fig. 5b). Mimosaceae, *Alchornea*, and  
337 Moraceae/Urticaceae (also largely pioneer/secondary taxa) are located very close to the Axis  
338 1 origin line and are not very robust indicators of CDA sites as they occur in all vegetation  
339 groups (see Fig. 2). Indicators of forest habitats have a stronger signal in the ordination. The  
340 most robust forest indicators according to the results of the CA are Lauraceae, *Vernonia*,  
341 *Plantago* and *Borreria* (excluding Lauraceae, they are weedy, mostly herbaceous genera,  
342 *Plantago* is cosmopolitan and *Vernonia* and *Borreria* are found mostly in warm, tropical

343 habitats), followed by the upper montane forest taxa *Myrsine*, *Clethra*, *Weinmannia*, and  
344 Myrtaceae (Fig. 5b).

345 To present an assemblage approach whereby associations of pollen taxa are better  
346 indicative of a particular vegetation type, we defined a restricted group representing the  
347 ARF. For this restricted group of forest habitat, we considered several aspects to select the  
348 taxa. We only considered arboreal pollen taxa. Although evidenced as robust indicators  
349 based on the CA (Fig. 5b), we for example excluded *Plantago*, *Vernonia*, and *Borreria* which  
350 represent mostly herbaceous genera and which can also be characteristic of CDA. Among the  
351 arboreal pollen taxa, we excluded taxa which are abundant in CDA pollen traps, e.g. *Celtis*,  
352 *Alchornea*, *Trema*, *Cecropia*, Mimosaceae, Moraceae/Urticaceae (Fig. 2 and 5b). Their high  
353 relative abundances in CDA pollen traps is certainly due to high pollen productivity of these  
354 taxa (Gosling et al., 2009; Jantz et al., 2013; Schüler et al., 2014) and their occurrence as  
355 dwarfed trees in or near CDA habitats. The representativeness of the taxa in fossil records  
356 was also considered for the selection of taxa. For example, although Lauraceae is one of the  
357 best indicators of forest in modern pollen rain (Fig. 2 and 5b), this pollen taxon is generally  
358 not well preserved in the fossil pollen records due to its thin exine (Behling, 1993) and it was  
359 excluded from the restricted forest group. We finally settled our choice on *Weinmannia*,  
360 *Myrsine*, *Clethra*, and Myrtaceae, which are good indicators of upper montane ARF since  
361 they are morphologically distinct arboreal pollen taxa and easily distinguished, they are  
362 significantly more abundant in upper montane forest than in CDA (Figures 2 and 5b) and  
363 they are generally well preserved and abundant in fossil pollen records (Behling, 1997a;  
364 Behling et al., 2007; Behling and Safford, 2010; Niemann et al., 2010; Veríssimo et al., 2012).  
365 The correlation between the restricted ARF group and the forest vegetation cover at 50 m ( $r$   
366 = 0.74) shows a higher correlation than the correlation calculated between the ARF group  
367 and forest vegetation cover at 50 m ( $r$  = 0.55) in figure 5c. We also try to select taxa to better  
368 discriminate CDA, however this was discarded because this group is mostly composed of  
369 Poaceae which pollen grains are extremely difficult to be identified to species or genera level  
370 due to the rather uniform morphology, and may be over-represented in some fossil records  
371 according to the study site (e.g. Gosling et al., 2009).

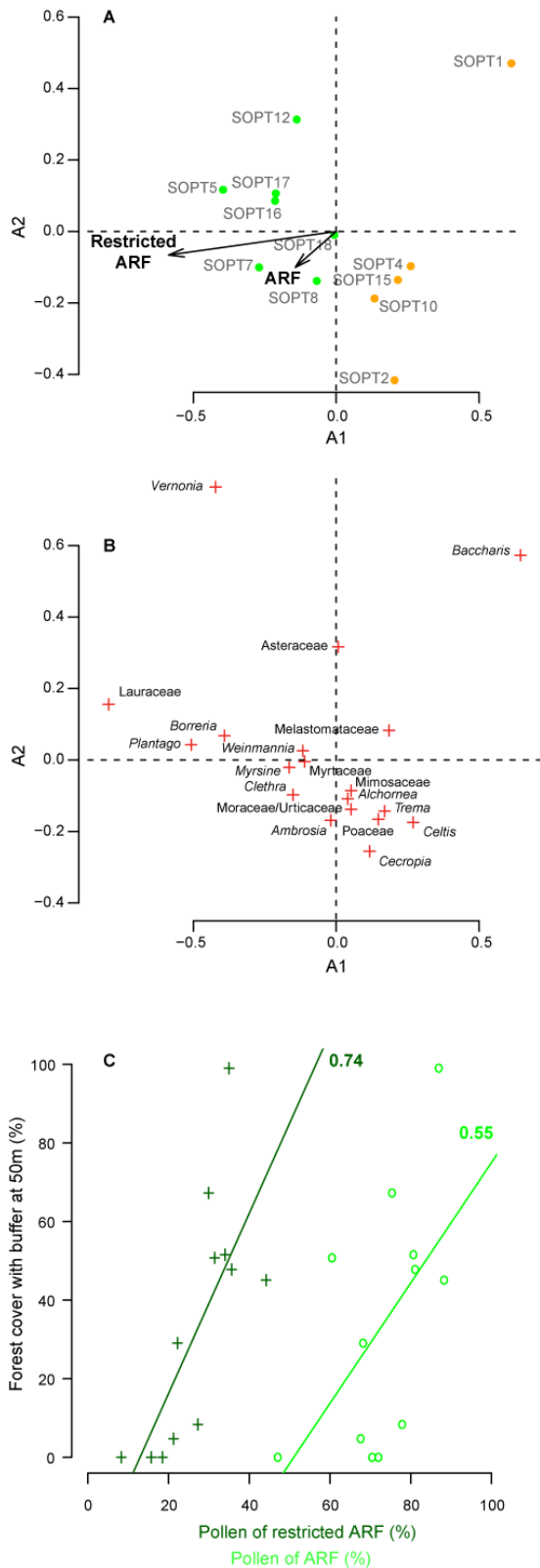
372



373

374 **Fig. 4.** Correlation coefficient (r) between pollen group and modern vegetation for spatial

375 buffers of 50, 100 and 500 m radius. Pollen traps of CDA are in orange and ARF in green.



376  
 377 **Fig. 5.** Correspondence Analysis (CA) for axes 1 and 2 using pollen taxa  $\geq 1\%$  in at least three  
 378 samples. A - distribution of pollen traps (CDA in orange and ARF in green) with the projection  
 379 of the ARF restricted group and ARF group, B - distribution of pollen taxa, C –correlation  
 380 between ARF restricted group and forest vegetation cover with buffer at 50 m (dark green)  
 381 and correlation between ARF and forest vegetation cover with buffer at 50 m (light green).

382 **Table 2.** Percentages of total vegetation cover comprised by campos (CDA) and forest (ARF)  
 383 vegetation within areas of 0.79 ha (50 m radius), 3.14 ha (100 m radius) and 78.6 ha (500 m  
 384 radius) surrounding each pollen trap, and pollen % of CDA group and ARF group in each  
 385 pollen trap. Table organized by vegetation type found at the pollen trap site.

Sample	Buffer 50 m		Buffer 100 m		Buffer 500 m		Pollen	
	Campos	Forest	Campos	Forest	Campos	Forest	CDA	ARF
CDA (mean)	93.2	6.8	93.2	6.8	80.8	16.07	34.98	65.02
SOPT1	100.00	0.00	97.89	1.97	81.61	14.85	52.98	47.02
SOPT10	70.95	29.05	84.29	15.60	81.20	15.39	31.83	68.17
SOPT2	100.00	0.00	99.90	0.00	84.29	12.29	28.04	71.96
SOPT15	95.26	4.74	83.93	16.17	78.30	22.60	32.45	67.55
SOPT4	100.00	0.00	100.08	0.00	78.66	15.19	29.59	70.41
ARF (mean)	40.6	59.4	63.8	36.2	66.0	34.0	18.73	81.27
SOPT16	48.44	51.56	44.93	55.08	72.62	29.38	19.38	80.63
SOPT12	74.60	25.40	75.95	24.03	77.87	16.07	22.16	77.84
SOPT17	49.25	50.75	71.61	28.28	64.01	38.44	39.54	60.46
SOPT7	54.91	45.09	79.26	20.78	78.90	21.04	11.75	88.25
SOPT8	32.75	67.25	77.67	22.40	79.08	20.79	24.67	75.33
SOPT5	52.20	47.80	79.87	20.06	79.48	20.46	18.95	81.05
SOPT6	52.20	47.80	79.87	20.06	79.48	20.46	7.36	92.64
SOPT18	0.99	99.01	64.79	35.37	45.06	57.50	13.07	86.93
SOPT21	0.00	100.00	0.40	99.60	18.36	81.66	11.68	88.32

386

## 387 5. Interpretation and discussion

388 The pollen rain collected by our traps permitted a relatively robust discrimination of campos  
 389 de altitude (CDA) and upper montane forest (ARF) habitats, even though there was notable  
 390 overlap between the pollen assemblages. With respect to the CDA, our pollen trap data  
 391 show that the pollen taxa most indicative of the CDA environment are Poaceae and  
 392 *Baccharis*. Other common taxa in the CDA pollen traps represent (mostly small tree/shrub)  
 393 taxa shared with ARF, or pioneer or secondary tree/liana taxa associated with disturbed  
 394 forest habitats at lower elevations. The upper montane ARF pollen traps were characterized  
 395 by a suite of taxa that are common to all eastern and southern Brazilian studies of mountain  
 396 forests (e.g. Portes et al., 2001; Koehler et al., 2002; Sheer and Mocoichinski, 2009; Gomes;  
 397 2015). These include, most prominently, Melastomataceae, *Myrsine*, and *Weinmannia*, but  
 398 also *Clethra*, *Symplocos*, *Drimys*, *Croton*, Myrtaceae, *Ilex*, and the tree ferns *Cyathea* and  
 399 *Dicksonia*. In addition, as pollen traps allow better pollen preservation than surface samples,  
 400 we recorded a high percentage of Lauraceae, which, although very characteristic of upper  
 401 montane ARF, have thin exine therefore are not commonly found in fossil pollen records  
 402 (see also Cardenás et al., 2019).

403 These results are strikingly similar to those of Montade et al. (2019), who carried out a broad  
404 geographic meta-analysis of 125 modern pollen samples across the Atlantic Forest biome.  
405 Montade et al. (2019) also found high levels of pollen taxa overlap between neighboring  
406 high elevation vegetation types, including campos de altitude, *Araucaria* forest, and upper  
407 montane Atlantic Forest. They ascribed at least some of this palynological concordance to  
408 the mosaic pattern of habitats that characterizes the higher Brazilian mountains (Safford,  
409 1999a), where patches of grassland and forests occur in such close proximity that typical  
410 pollen sampling methods cannot discern a completely “clean” pollen signature from either  
411 habitat. We found the same pattern of pollen “pollution” happening between our CDA and  
412 ARF traps. This was especially pronounced in the CDA traps, where upper montane ARF taxa  
413 comprised almost 2/3 of the captured pollen. This was due to at least three factors. First, the  
414 Brazilian Highlands do not reach the elevations of climatic treeline (Safford, 1999b),  
415 therefore the presence and distribution of high-elevation páramo-like grasslands is driven by  
416 local-scale environmental and disturbance gradients that lead to a very fine-grained  
417 intercalation of grassland and forest patches (Safford, 1999a, 2001). Second, many taxa from  
418 the upper montane ARF – such as the prodigious pollen producers *Myrsine* and *Weinmannia*,  
419 as well as various species of Myrtaceae, Melastomataceae, *Croton*, *Drimys*, *Clethra*, and  
420 *Symplocos* – occur as shrubs or small scattered trees in the campos de altitude (Safford,  
421 2007). These are usually interpreted as either remnants of burned forest stands, or pioneers  
422 of forest expansion. Third, CDA vegetation is characterized by a much lower pollen  
423 production and accumulation rate than the montane or upper montane ARF. The same  
424 pattern was recognized by Bush (2000) in a study of páramo vs treeline forests in Central  
425 America and by Gosling et al. (2009) in an ecotonal area of tropical forest, semi-deciduous  
426 forest and savannah in Colombia. Even though Poaceae is wind-pollinated, most of the  
427 genera in the CDA require a pollen vector (c. 71% are insect-pollinated and 5% bird or bat  
428 pollinated according to Safford, 2007), and such taxa are always under-represented in the  
429 pollen rain. There are also relatively few wind-pollinated taxa in the ARF, but a number of  
430 pioneer or secondary forest taxa are anemophilous – examples include  
431 Moraceae/Urticaceae, *Cecropia*, *Trema*, *Celtis*, and *Alchornea* – and their high levels of  
432 pollen production, combined with the often up-slope nature of mountain winds, lead to  
433 over-representation of these montane taxa in many higher elevation pollen rain studies in  
434 the neotropics (e.g. Weng et al., 2004; Niemann et al., 2010; Urrego et al., 2011; Montade et

435 al., 2019). The relative paucity of CDA pollen in the lower elevation forest traps is driven  
436 probably by the combination of predominantly upslope winds with the very high local  
437 production of pollen in ARF, which masks the downslope movement of CDA pollen (see also  
438 Bush, 2000; Schüler et al., 2014).

439 Another important difference between the CDA and ARF pollen assemblages is the size of  
440 the pollen source area. Pollen samples from open areas dominated by Poaceae and subject  
441 to high influence of wind transport will necessarily represent larger geographic areas than  
442 samples from close canopy forests, where local pollen production strongly dominates  
443 (Tauber, 1967; Schüler et al., 2014). This explains why, although our ARF traps were found  
444 mostly in forest patches surrounded by CDA vegetation (almost 64% of vegetation within  
445 100 m of the ARF traps was CDA), they still recorded an average of >80% ARF pollen (Table  
446 2). In some cases, forest pollen rain can be strongly influenced by individual trees beneath  
447 which the traps are located (Cheng et al., 2020; Niemann et al., 2010; Weng et al., 2004).  
448 One obvious case in our study is sample SOPT6, which registered >70% Melastomataceae  
449 pollen, while the adjacent sample SOPT5 (only 10 m distant) registered only 3% of this pollen  
450 type.

451 A few unexpected results are worth briefly mentioning. The low percentages of *Celtis* and  
452 *Trema* pollen in the lower montane sample SOPT21 – which are typically characteristic of  
453 lower montane ARF – are anomalous and may represent masking by Melastomataceae.  
454 SOPT21 also recorded a high percentage of *Weinmannia* which, although it produces large  
455 amounts of pollen and is usually overrepresented in upper montane environments, is not  
456 normally present in lower elevation forest samples. In an arboreal floristic inventory of a  
457 montane forest in the PARNASO, Pardo et al. (2007) registered the occurrence of all the  
458 arboreal taxa we found in the pollen rain, except for *Weinmannia*. Cárdenas et al. (2019),  
459 studying the modern pollen-vegetation relationship in *Araucaria* forest in southern Brazil  
460 also remarked that although *Weinmannia* is normally cited as evidence of *Araucaria* forest, it  
461 is much more floristically important at higher elevations.

462 In order to develop a reasonably accurate process by which fossil pollen records might be  
463 used to better discriminate between grassland and forest habitats in such a complex  
464 environmental mosaic, we proposed a suite of distinctive upper montane ARF taxa  
465 composed of *Weinmannia*, *Myrsine*, *Clethra*, and Myrtaceae.

466 Calculated with more specific taxa than the pollen groups usually used to distinguish forest

467 from CDA, this discrimination group excludes over-represented taxa (e.g. *Celtis*, *Cecropia*,  
468 Moraceae/Urticaceae as observed in the pollen traps) as well as under-represented taxa  
469 (e.g. Lauraceae in fossil samples). Within vegetation cover buffer at 50 m of the sampling  
470 site, it reflects better proportion of forest cover (Fig. 5c). We believe this group is more  
471 appropriate to discriminate vegetation change between forest habitats and CDA and can be  
472 applied to fossil pollen data in order to support palaeo records interpretation. However, as  
473 each region presents a different species occurrence pattern, its replication should be treated  
474 with caution. It can be transferred to historical pollen data for the given region or other CDA  
475 and forest mosaic in similar altitude and in the same mountain range in southeastern Brazil.  
476 Moreover, data from a sediment core and a pollen trap from the same vegetation type may  
477 lead to slightly different results with regard to pollen diversity (Jantz et al., 2013) as the  
478 catchment area from which samples are taken may be different. For example, fossil samples  
479 from lake sediments represent a large source area and high proportions of Poaceae and  
480 Cyperaceae (Gosling et al., 2009). Sediments collect in the mosaic of CDA and forest in the  
481 Highlands from southeastern Brazil are basically peats but also bogs, within a more local  
482 catchment area (but probably also larger than the pollen trap source area) and the  
483 contribution of these taxa are quite well representative of local diversity. Application of our  
484 restricted ARF might be therefore more relevant for sites with local catchment area (e.g.  
485 peats and bogs) than for site with large source area (e.g. lakes). Other point to consider is  
486 that our study was based on 1 year of pollen rain, and probably there is variability in pollen  
487 productivity according to changes in climatic conditions through the years. A long-term  
488 investigation with pollen traps could be interesting to verify this possible variation.

489

## 490 **6. Conclusion**

491 Our study of the modern pollen rain along an elevational gradient was focused on  
492 supporting palaeo-studies of vegetation and climate dynamics in southeastern Brazil by  
493 helping to refine the pollen taxa and spectra that most robustly differentiate CDA and forest  
494 habitats. Our assemblages indicated that vegetation distribution is closed related with  
495 altitude, even with occurrence of low montane taxa in higher elevations. Although arboreal  
496 taxa dominated all of our pollen assemblages, pollen traps located in CDA captured a  
497 characteristic mix of grass, herbs, and shrub pollen. The results indicate that the CDA pollen  
498 spectra represent much larger geographic areas than forest pollen spectra, which sample

499 local taxa more heavily. Nonetheless, the pollen assemblages accurately reflected the  
500 vegetation zone in which they were found, and we were able to specify a characteristic  
501 group of taxa for each elevation. Our results underlined that special care must be taken with  
502 pollen trap location, as samples can be strongly influenced by a few individual plants if they  
503 dominate the trap area. Pioneer tree and liana species with anemophilous pollen dispersal  
504 dispersion produce copious pollen and were over-represented in CDA pollen traps from  
505 higher elevation, these included Melastomataceae, Moraceae/Urticaceae, *Cecropia*, *Trema*,  
506 and *Celtis*. As found in other tropical montane studies as well, the main direction of wind-  
507 driven pollen dispersal seems to be uphill in our study area, although the low presence of  
508 CDA pollen in lower elevation forest traps is probably also influenced by masking due to high  
509 local pollen production in the study area forests. Finally, we proposed the use of a suite of  
510 distinctive taxa which more confidently differentiate CDA and forest habitats from pollen  
511 data. We believe that will prove useful to efforts to reconstruct and model climate and  
512 vegetation dynamics in such kind of specific environment, with important applications to  
513 conservation and management (e.g., developing the natural range of variation of CDA vs.  
514 forest areas as a function of landscape and climate) and climate and vegetation science (e.g.,  
515 developing a more quantitative idea of the dependence of CDA vegetation on climate  
516 variability vs. natural disturbances like fire).

517

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527

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698

699 **Supplementary Material**

700 List of taxa identified in the pollen rain.

Taxa	Group	Vegetation
Poaceae	Herbs and shrubs	Campos de altitude (CDA)
Apiaceae		
<i>Eryngium</i> type 1		
<i>Eryngium</i> type 2		
Lamiaceae		
Fabaceae		
<i>Borreria</i>		
Ericaceae		
<i>Plantago</i>		
Amaranthaceae/Chenopodiaceae		
Malpighiaceae		
<i>Valeriana</i>		
Cactaceae <i>Rhipsalis</i>		
Cactaceae		
<i>Amaryllis</i>		
Menispermaceae		
Malvaceae		
<i>Verbena</i>		
Scrophulariaceae		
Ochnaceae		
<i>Polygonum</i>		
<i>Polygala</i>		
Convolvulaceae		
Asteraceae	Asteraceae	
<i>Baccharis</i>		
<i>Vernonia</i>		
<i>Ambrosia</i>		
<i>Senecio</i>		

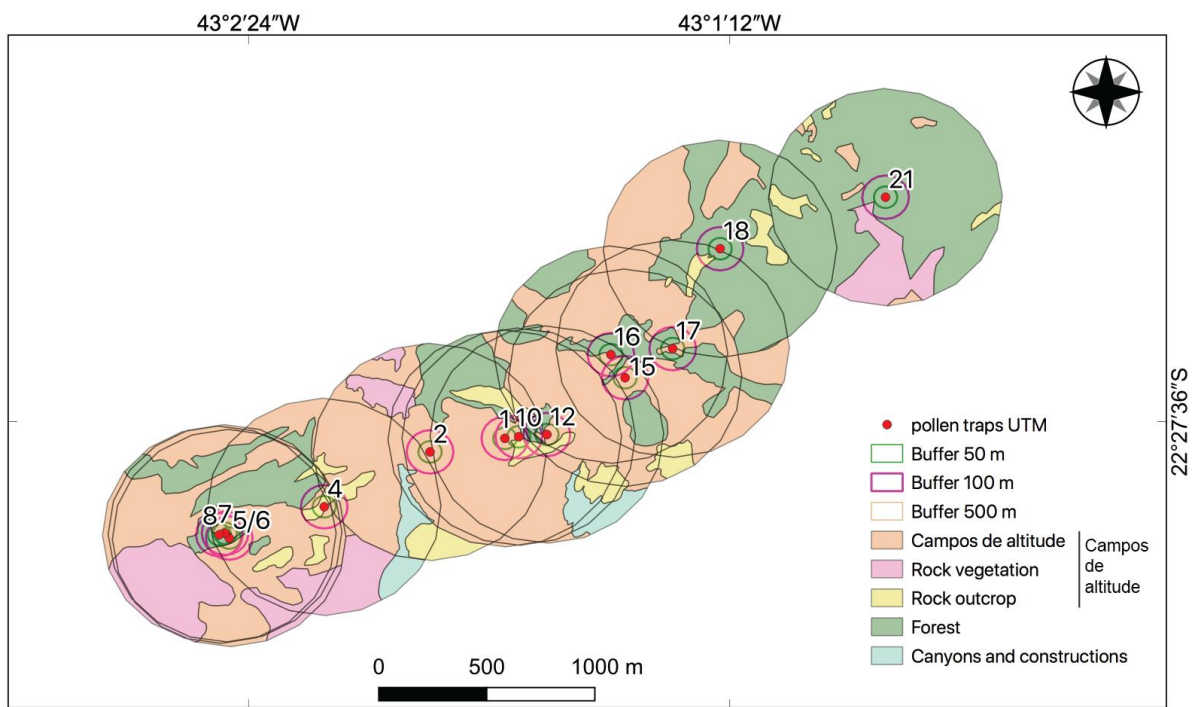
Taxa	Group	Vegetation
Cyperaceae <i>Hydrocotyle</i> <i>Xyris</i> <i>Typha</i> Liliaceae	Sub-aquatics	Sub-aquatics
<i>Clethra</i> <i>Griselinia</i> <i>Myrsine</i> <i>Weinmannia</i> <i>Symplocos tenuifolia</i> type <i>Symplocos lanceolata</i> type <i>Hedyosmum</i> <i>Drimys</i> <i>Daphnopsis</i> <i>Croton</i> <i>Roupala</i> Lauraceae <i>Lamanonia</i> <i>Fuchsia</i> <i>Begonia</i> <i>Euphorbia</i> <i>Laplacea</i> <i>Struthanthus</i>	Upper Montane ARF	Atlantic rain forest (ARF)
<i>Podocarpus</i> <i>Araucaria</i> <i>Mimosa scabrella</i> Melastomataceae Melastomataceae (small) Flacourtiaceae Myrtaceae <i>Ilex</i>	Montane ARF	
Taxa	Group	Vegetation
Mimosaceae <i>Mimosa</i> (small) <i>Schefflera</i> <i>Oreopanax</i> <i>Sebastiania commersoniana</i> <i>Sebastiania brasiliensis</i> <i>Piper</i> <i>Trema</i> <i>Celtis</i> <i>Schinus</i>	Montane ARF	Atlantic rain forest (ARF)

*Zanthoxylum*  
*Meliosma*  
*Allophyllus*  
*Luehea*  
*Pera*  
*Parapiptadenia*  
*Matayba*  
 Bignoniaceae  
 Anacardiaceae  
*Bauhinia*  
*Cordia*  
 Rubiaceae  
 Rubiaceae *Bridelia*  
*Lythraea*  
*Dadonea*  
 Solanaceae  
*Prunus* type  
*Euterpe/Geonoma*  
*Cecropia*  
 Moraceae/Urticaceae  
*Alchornea*

Taxa	Group	Vegetation
<i>Sloanea</i> <i>Schizolobium</i> <i>Rhamnus</i> <i>Tetrorchilium</i>	Montane ARF	Atlantic rain forest (ARF)
<i>Pinus</i> <i>Casuarina</i>	Exotics	Exotics
<i>Cyathea</i> psilate <i>Cyathea</i> reticulate <i>Cyathea</i> verrucate <i>Dicksonia</i> <i>Lophosoria quadripinnata</i>	Tree ferns	
<i>Lycopodium</i> foveolate <i>Lycopodium</i> clavatum Monolete psilate Monolete psilate large (> 40 cm) Monolete scabrate Monolete echinate Monolete verrucate Monolete verrucate large <i>Osmunda</i> Polypodiaceae Monolete with perispore type 2	Ferns	Ferns

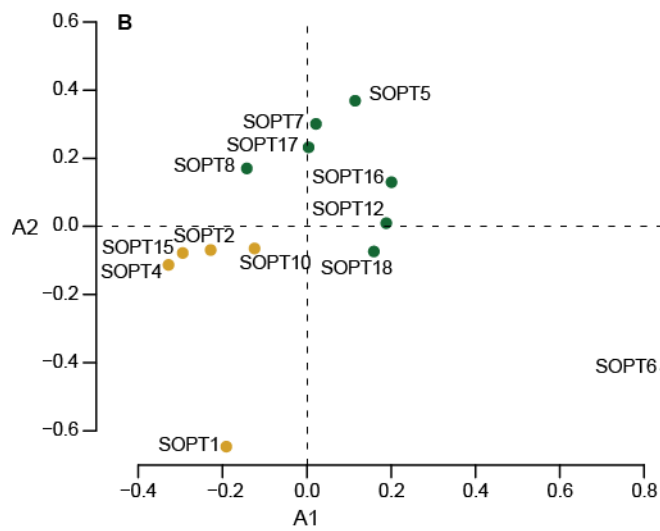
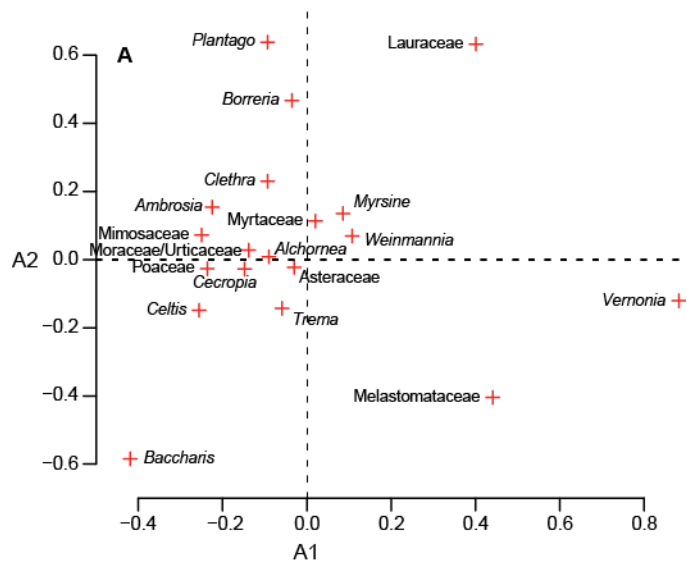
*Pteris* type  
*Schizaea*  
 Trilete psilate  
 Trilete verrucate  
 Trilete scabrata  
 Pteridophyta type 6  
 Pteridophyta type 4  
 Trilete with perispore  
 Trilete striate

701



702

703 Figure S1: Interpretation of the vegetation surrounding each pollen trap and limit of the  
 704 spatial buffers of 50 m radius (0.79 ha total area), 100 m radius (3.14 ha total area) and 500  
 705 m radius (78.6 ha total area).



706

707 Figure S2: Correspondence Analysis (CA) for axes 1 and 2 using pollen taxa >1% in at least  
 708 three samples, including sample SOPT6. A – distribution of pollen taxa, B - distribution of  
 709 pollen traps.

710