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

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

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

1. Introduction

The Atlantic Forest biome stretches along Brazil's east coast for more than 4000 km, with the Brazilian Highlands as its geographic backbone. The Atlantic Forest, which once covered as much as 1.3 million km², has been drastically reduced in area since European settlement in the 16th century (Fundação SOS Mata Atlântica/ INPE, 2017) and is considered one of the world's most threatened biomes as well as one of its most important biodiversity hotspots (Myers et al., 2000). Today, some of the largest remaining fragments of the Atlantic Forest are inside national and state protected areas found on the steep slopes of the Serra do Mar and Serra da Mantiqueira in the states of Rio de Janeiro, Minas Gerais, and São Paulo (Ribeiro et al., 2009). Among the ecosystems covered by these protected areas, some of the most important are upper montane forest and campos de altitude (CDA, or named high elevation grasslands), due to their rarity in eastern Brazil and the high numbers of endemic species they support (Martinelli and Bandeira, 1989; Safford and Martinelli, 2000; Spehn et al., 2010). These ecosystems share the summits of eastern Brazil's highest mountains, with upper montane forest often occupying concavities and protected sites and campos de altitude covering mountaintops and convex slopes (Safford, 1999a). Their geographic relationship is dynamic, with forests dominating in the absence of disturbance and when and where climates are warmer and wetter, and campos dominating after fire and in colder and drier periods (Safford, 1999a, 2001; Portes et al., 2018).

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

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

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

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

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

2. Environmental settings

2.1 Study site

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

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

2.2 Climate

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

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

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

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

2.3 Vegetation

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

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

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

3. Material and Methods

3.1 Pollen trap design and sampling

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

3.2 Pollen analysis

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

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

Table 1. List of 23 pollen traps grouped by vegetation zone where each trap was installed, with their geographic coordinates and elevation. In black the recovered traps and in gray the 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
	SOPT4	22°27'48.70"	43°02'12.70"	2086
Upper montane ARF	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
	SOPT6	22°27'53.40"	43°02'26.91"	2003
	SOPT18	22°27'10.12"	43°01'13.44"	1923
Montane ARF	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

3.3 Vegetation cover analysis and multivariate analysis

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

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

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

To better reconstruct the local changes of ARF in this mosaic of grassland and forest, we defined a group of most distinctive pollen taxa of upper montane ARF composed by *Weinmannia*, *Myrsine*, *Clethra*, and Myrtaceae based on the results of the CA and considering pollen assemblages, habit and ecological features. We also considered the facility in distinguishing these taxa (important when comparing several sites involving different palynologists) as well as their abundance and well preservation in fossil samples. This restricted group of ARF and the ARF group were passively projected on the first and second axes of the CA bi-plot.

4. Results

4.1 Modern pollen rain

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

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

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

4.1.1 Campos de altitude (5 samples)

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

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

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

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

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

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

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

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

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

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

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

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

Fig. 4. Correlation coefficient (r) between pollen group and modern vegetation for spatial buffers of 50, 100 and 500 m radius. Pollen traps of CDA are in orange and ARF in green.

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

Table 2. Percentages of total vegetation cover comprised by campos (CDA) and forest (ARF) vegetation within areas of 0.79 ha (50 m radius), 3.14 ha (100 m radius) and 78.6 ha (500 m radius) surrounding each pollen trap, and pollen % of CDA group and ARF group in each 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

5. Interpretation and discussion

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

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

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

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

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

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

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

6. Conclusion

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

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

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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)

<i>Zanthoxylum</i> <i>Meliosma</i> <i>Allophyllus</i> <i>Luehea</i> <i>Pera</i> <i>Parapiptadenia</i> <i>Matayba</i> Bignoniaceae Anacardiaceae <i>Bauhinia</i> <i>Cordia</i> Rubiaceae Rubiaceae <i>Bridelia</i> <i>Lythraea</i> <i>Dodonea</i> Solanaceae <i>Prunus</i> type <i>Euterpe/Geonoma</i> <i>Cecropia</i> Moraceae/Urticaceae <i>Alchornea</i>		
Taxa	Group	Vegetation
<i>Sloanea</i> <i>Schizolobium</i> <i>Rhamnus</i> <i>Tetrorchidium</i>	Montane ARF	Atlantic rain forest (ARF)
<i>Pinus</i> <i>Casuarina</i>	Exotics	Exotics
<i>Cyathea psilate</i> <i>Cyathea reticulata</i> <i>Cyathea verrucata</i> <i>Dicksonia</i> <i>Lophosoria quadripinnata</i>	Tree ferns	Ferns
<i>Lycopodium foveolatum</i> <i>Lycopodium clavatum</i> 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	

<i>Pteris</i> type		
<i>Schizaea</i>		
Trilete psilate		
Trilete verrucate		
Trilete scabrate		
Pteridophyta type 6		
Pteridophyta type 4		
Trilete with perispore		
Trilete striate		

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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).

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