



Research paper

Pollen-based characterization of montane forest types in north-eastern Brazil



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ABSTRACT

Surface soil samples were collected in three mountainous massifs in north-eastern Brazil to characterize the different vegetation types according to their respective pollen assemblages. Complementary approach between pollen and vegetation data shows that the pollen rain accurately reflects the following three main forest types: i) a dense ombrophilous forest (or tropical moist broadleaf forest) characterized by Myrtaceae associated with high percentages of *Miconia*, *Guapira*, *Ilex*, Moraceae-Urticaceae undif. or *Byrsonima*, ii) a seasonal semi-deciduous montane forest characterized by an increase of Arecaceae associated with Fabaceae-Mimosoideae, Myrtaceae, *Piper*, *Cecropia*, *Urera* and *Mitracarpus*, and iii) a seasonal deciduous forest dominated by Fabaceae-Mimosoideae and Arecaceae tree taxa associated with *Alternanthera*, Cyperaceae and *Mitracarpus*. Using of botanical data from several plots of ombrophilous forest, in which several surface soil samples have been collected, allows to roughly estimate the over- and underrepresentation of pollen taxa relative to their floristic abundance. Furthermore, distribution of surface soil samples at different altitude and mountain sides also allows to characterize vegetation variation according to several environmental parameters. The precipitation increase with altitude is confirmed as the main environmental factor controlling vegetation distribution. However, the forests located close to the crest with a proportion increase of pollen taxa characteristic of heliophilous and pioneer trees (*Alchornea*, *Miconia*, *Clusia*), are also influenced by changes of edaphic conditions. In addition to provide useful information in understanding of fossil pollen records, this approach improves our understanding of the ecosystem functioning in mountainous massifs in north-eastern Brazil. A useful knowledge for conservation or restoration purposes.

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1. Introduction

Tropical mountains which harbor a high species diversity are considered as the world's most important diversity hotspots (Barthlott et al., 2005). Indeed, interactions of an extraordinary variety of wet and dry habitats in close proximity due to local altitudinal climate gradients, allows the coexistence of different vegetation types, contributing to the high species richness in tropical mountains (Richter, 2008). In particular,

these complex landscapes generate climatically suitable habitats, that can shelter animals and plants from hostile climates, which is especially important for species conservation in periods of climate change (Shoo et al., 2011; Williams et al., 2003). In north-eastern Brazil, mountainous massifs (or “brejo de altitude”), which form islands of moisture, where tropical rainforests contrast with the dry forest (Caatinga) of the surrounding plain, could be considered as such a type of habitat. Closely related to the Caatinga in terms of floristic composition (Rizzini, 1963), these montane rainforests could be result of the evolution from this dry to a wet forest. On the other hand, these montane rainforests harbor endemics species of Atlantic and Amazonian forests showing a past connection between these two biomes (Andrade-Lima, 1982), which thus illustrates the capacity of such areas to shelter species from long-

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term climate changes. Several botanical surveys performed in mountainous massifs in north-eastern Brazil allowed describing composition, density and diversity of different forest types (e.g., Andrade et al., 2006; Araújo et al., 2007; Costa-Junior et al., 2008; Ferraz et al., 2004). The development of these forests is related to altitude increase, generating high orographic precipitation. However, no studies focused on the specific impact of environmental parameters (such as precipitation) on the distribution of these forests. Although botanical data from this region provide a representative set of different vegetation types, they arise from discontinuous sampling, and consequently they do not allow to link the observed vegetation changes to the closely altitude-related climatic gradient. In comparison to extratropical mountains, vegetation boundaries in tropical mountains are generally discrete (e.g., Ashton, 2003; Duarte et al., 2005; Fernández-Palacios and de Nicolás, 1995; Hemp, 2005; Martin et al., 2007). Discontinuities in vegetation composition may offer insights into the factors controlling the assembly of plant communities and thus may have significance for management and nature conservation. The present study aims to fill this gap by using pollen samples from different plant communities along an altitudinal gradient with discontinuous botanical data from several mountainous massifs in north-eastern Brazil. Studying modern pollen samples in the tropics allows an accurate characterization of the different vegetation types (e.g., Burn et al., 2010; Gosling et al., 2009; Jones et al., 2011). In addition, variations in the pollen assemblages along altitudinal gradients are sensitive to altitudinal climate changes (Cárdenas et al., 2014; Schüller et al., 2014; Urrego et al., 2011; Weng et al., 2004). Here we focus on several mountainous massifs from north-eastern Brazil to try to answer the following questions: Does the modern pollen rain represent the composition of different forest types? Using modern pollen data, do the present-day environmental conditions explain the spatial distribution of different vegetation types? By providing a better understanding of ecosystem functioning, the present study will be helpful in defining conservation strategies for the rainforest of north-eastern Brazil with growing human activities.

2. Environmental settings and methods

2.1. Study location

Our study was conducted in the state of Ceará of north-eastern Brazil (“Nordeste”) in three isolated mountainous massifs named Pacatuba, Maranguape and Baturité, that reach respectively up to 735 m, 920 m and 1115 m asl (Fig. 1). Located between 80 km (Baturité) and 30 km (Pacatuba and Maranguape) from the coast, mineralogy of basement rocks mainly consists in gneissic facies interpreted as the erosional remnants of an Early Cretaceous rift shoulder (Peulvast and de Claudino Sales, 2004). Characterized by steep slopes and sinuous scarps, these mountainous massifs are contrasted with the topography and climate of the surrounding plains. Climate is defined as hot and humid in mountainous massifs, semi-arid in lowlands and sub-humid close to coast (FUNCEME; <http://www.funceme.br/>). While the temperature with annual mean of c. 27 °C in the lowlands shows no seasonal variations, rainfalls, mainly from February to May, show a strong seasonality. Precipitation generated by maritime trade winds is distributed along two main gradients: (1) a precipitation decrease with the distance from the coast, and (2) a precipitation increase with the elevation. Annual precipitation ranges from c. 1400 mm in the coastal area to 700 mm in the interior and reach values higher than 1600 mm in the mountainous massifs. High evapotranspiration (generally between 2000 and 3000 mm yr⁻¹) causes an important water deficit resulting in a semi-arid climate. In mountainous massifs, altitude increase that lowers temperature, results in cloud formation and precipitation, enabling the development of a highly diversified tropical forest. From the mountain top downwards, the following vegetation types are observed: a tropical moist broadleaf forest corresponding to dense ombrophilous forest (sub-montane) according to Veloso (2012), a seasonal semi-deciduous montane forest, and a seasonal deciduous forest (Caatinga).

2.2. Field collection and data processing

Fieldwork was carried out in 2013 and 2014 and the modern pollen samples were collected from surface soils. Each pollen sample consists of 10 sub-samples collected in the upper 2 cm layer of surface soil and distributed on a plot between 1/2 and 1 ha under homogeneous vegetation cover. In order to simultaneously obtain a representative set of each vegetation type and a representative sampling of the climatic gradient, surface samples were located at different altitudes and mountainsides (Fig. 1 and Table 1). A complete altitudinal transect on the lee- and windward sides was sampled in the Pacatuba Massif with an altitude interval between each sample of c. 100 m (Fig. 1c). As the Baturité and Maranguape massifs are more disturbed by human activity, surface soil samples were collected above 600 m asl (Fig. 1b and d). To study the pollen-vegetation relationships, samples were collected close to the locations of the botanical surveys performed by Araújo et al. (2007) in Baturité Massif. In Maranguape Massif four surface soil samples (MB9, MB7, MS7a and MS7b) were collected in botanical plots performed at the same time. Each botanical plot consists of ten parallel transects of 100 m length. Following the point-centered quarter method (Cottam and Curtis, 1956), the nearest trees with at least 15 cm perimeter at breast height were identified along these transects. Surface samples were collected between two or three transects depending on the topography. For MS7, because of slight difference in altitude, species composition and vegetation structure, the plot was split in two sub-groups: a group of eight transects below 700 m asl corresponding to the surface sample MS7a and a group of two transects above 700 m asl corresponding to the surface samples MS7b.

After sampling, surface soil samples were transported to the laboratory and stored in a cold room at 5 °C. To extract pollen grains, an aliquot of 2 cm³ for each sample was chemically treated, adapting the method of Faegri and Iversen (1975). Surface samples were processed by five successive KOH (10%) at 70 °C to remove humic acids followed by HF (70%) to eliminate silicates and by the standard acetolysis method. Prior to chemical treatment, a calibrated *Lycopodium* tablet was added to each sample in order to calculate the pollen concentrations (Stockmarr, 1972). Palynomorphs were counted and identified using a light microscope (Leica) at 1000× magnification after mounting slides with residues and glycerine. At least 300 pollen grains were counted for each sample and 119 pollen and spore taxa were identified using the reference collection of M.-P. Ledru (IRD pollen collection) and several specialized publications on pollen morphology (Colinvaux et al., 1999; Leal et al., 2011; Roubick and Moreno, 1991; Rull, 2003).

All statistical analyses were performed on the pollen taxa with percentages ≥ 1% and percentages were calculated on a pollen sum excluding fern spores. Pollen spectra (Fig. 2) were plotted using PSIMPOLL 4.10 software (Bennett, 1994). Pollen-vegetation representativeness ratios were calculated for the four surface samples collected in the botanical plot of the Maranguape Massif by calculating the p/v values (% of arboreal pollen / % of total stems of all taxa in plot). Only for p/v values, pollen percentages were calculated on the arboreal pollen sum (Appendix A). As described by Gosling et al. (2009) this ratio is intended to assess the relative pollen productivity and dispersal of different pollen taxa (Fig. 3). In order to determine correlations between the spatial distribution of vegetation groups and environmental data from pollen assemblages, Correspondence Analysis (CA) was carried out (Figs. 4, 5 and Appendix B). Correspondence Analysis is a classically used ordination method to summarize the patterns of variations among a collection of pollen assemblages, as it is well suited to contingency tables. Different or more refined commonly used ordination methods were also tested (Principal Correspondence Analysis, square-root transform of percentages, Detrended Correspondence Analysis) but they lead to similar results. Environmental parameters such as slope angle and distance to the crest were calculated using QGIS software (QGIS Development Team, 2015) running the ASTER Global Digital Elevation Model (from METI and NASA). Mean annual precipitation (MAP) values for the period

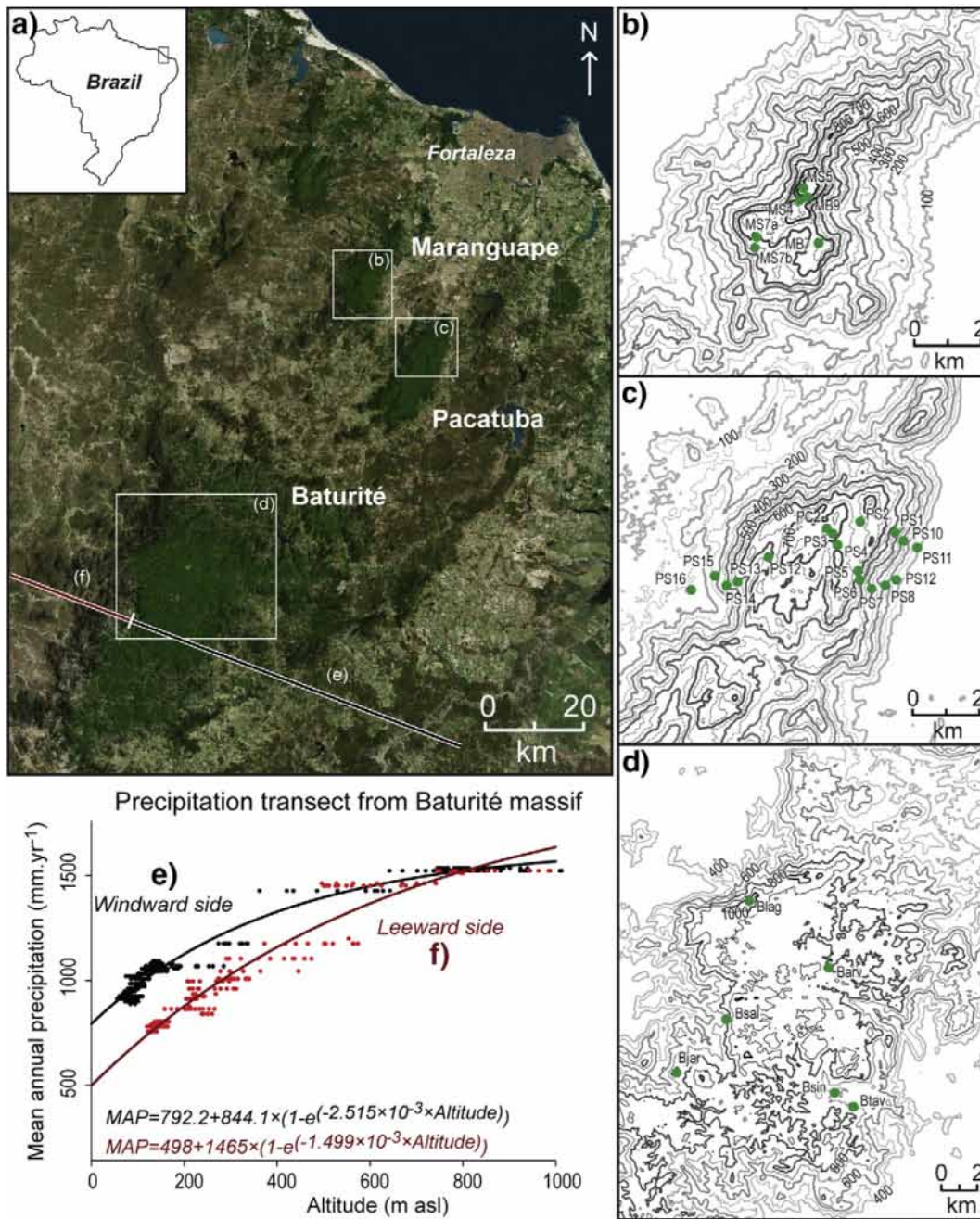


Fig. 1. General location maps of (a) mountainous massifs in north-eastern Brazil with the locations of their respective modern pollen samples (b, c and d). (e) and (f) represent the transect location performed on the mean annual precipitation values based on WorldClim database (Hijmans et al., 2005). Satellite image (from Bing maps) and elevation maps (from ASTER Global Digital Elevation Model from METI and NASA) were plotted using QGIS software (QGIS Development Team, 2015).

1950–2000 were obtained using the WorldClim database for each location of the surface samples (Hijmans et al., 2005). The first estimates of MAP is denoted hereafter MAP1 (Table 1). As the Maranguape and Pacatuba massifs occupy relatively small areas, without any meteorological stations, the climatic altitudinal gradient is not well resolved at WorldClim resolution. Contrariwise, from the Baturité Massif, being larger than the Maranguape and Pacatuba massifs, more precise meteorological data are available, which allow obtaining a realistic pattern of precipitation changes according to elevation. A second estimation of MAP (hereafter MAP2) was then obtained by assuming that altitude/precipitation patterns are the same over the three massifs. Altitude and MAP were related along an altitudinal transect between the wind- and leeward side of the Baturité Massif and two non-linear regression fits were performed to model altitudinal variations of MAP wind- and leeward (Fig. 1e and f). The

obtained equations were applied to all surface sample locations. Then, an increase of 200 mm was added for all samples of Pacatuba and Maranguape in order to take into account the observed difference in MAP recorded in rainfall stations located in the lowland at a greater proximity to the seashore.

3. Results

3.1. Modern pollen assemblages

According to their respective altitudinal ranges and their main pollen taxa based on percentage values, the different vegetation types can be characterized by the following pollen assemblages (Fig. 2 and Table 2).

Table 1
Names and locations of surface samples with their ecological and environmental parameters. Lat S and Lat W: latitude south and west; MAP: Mean Annual Precipitation; Veg: vegetation type; DF: Deciduous Forest; SDF: Semi-Deciduous Forest; OF: Ombrophilous Forest (*close to the crest).

Site	Massif	Lat S	Lon W	Altitude m asl	Side	Distance to the crest m	Slope °	MAP 1 mm	MAP 2 mm	Veg	Human disturbance
PS11	Pacatuba	-3.98	-38.62	130	Windward	2529	10	1296	1228	DF	Low
PS9	Pacatuba	-3.98	-38.63	158	Windward	2514	26	1272	1269	DF	Low
PS8	Pacatuba	-3.99	-38.63	263	Windward	2350	16	1272	1401	SDF	High
PS10	Pacatuba	-3.97	-38.62	312	Windward	2056	32	1320	1451	SDF	Low
PS7	Pacatuba	-3.99	-38.63	383	Windward	2079	27	1272	1514	SDF	Moderate
PS1	Pacatuba	-3.97	-38.63	411	Windward	1720	17	1440	1536	SDF	Moderate
PS6	Pacatuba	-3.98	-38.63	569	Windward	1633	18	1416	1635	OF	Low
PS5	Pacatuba	-3.98	-38.63	631	Windward	1432	22	1428	1664	OF	Low
PS2	Pacatuba	-3.97	-38.63	650	Windward	633	3	1428	1672	OF	Low
PS4	Pacatuba	-3.98	-38.64	724	Windward	446	19	1428	1700	OF	Undisturbed
PS3	Pacatuba	-3.97	-38.64	759	Windward	204	10	1428	1711	OF	Low
PC2*	Pacatuba	-3.97	-38.64	765	Windward	34	14	1464	1713	OF*	Undisturbed
PS12	Pacatuba	-3.98	-38.66	575	Leeward	414	18	1428	1544	SDF	Moderate
PS13	Pacatuba	-3.99	-38.66	489	Leeward	657	32	1296	1459	SDF	Moderate
PS14	Pacatuba	-3.99	-38.67	395	Leeward	986	23	1296	1353	DF	Moderate
PS15	Pacatuba	-3.99	-38.67	279	Leeward	1374	21	1284	1199	DF	Moderate
PS16	Pacatuba	-3.99	-38.67	160	Leeward	2022	5	1284	1010	DF	Moderate
Bsal	Baturité	-4.26	-38.98	735	Leeward	580	14	1548	1476	DF	Low
Bjar	Baturité	-4.29	-39.00	760	Leeward	1411	3	1512	1494	SDF	Low
Btav	Baturité	-4.30	-38.92	600	Windward	433	15	1500	1450	OF	Low
Bsin	Baturité	-4.29	-38.93	647	Windward	840	17	1524	1470	OF	Low
Barv	Baturité	-4.24	-38.93	816	Windward	350	12	1560	1528	OF	Low
Blag*	Baturité	-4.21	-38.97	940	Windward	0	31	1584	1557	OF*	Low
MB7	Maranguape	-3.91	-38.72	730	Windward	800	16	1464	1702	OF	Low
MS4*	Maranguape	-3.90	-38.72	850	Windward	37	21	1524	1737	OF*	High
MB9*	Maranguape	-3.90	-38.72	934	Windward	30	17	1524	1756	OF*	Undisturbed
MS5*	Maranguape	-3.89	-38.72	950	Windward	8	19	1524	1759	OF*	Undisturbed
MS7a	Maranguape	-3.91	-38.73	700	Leeward	1260	6	1476	1650	OF	Low
MS7b	Maranguape	-3.91	-38.73	659	Leeward	1500	12	1392	1617	OF	Low

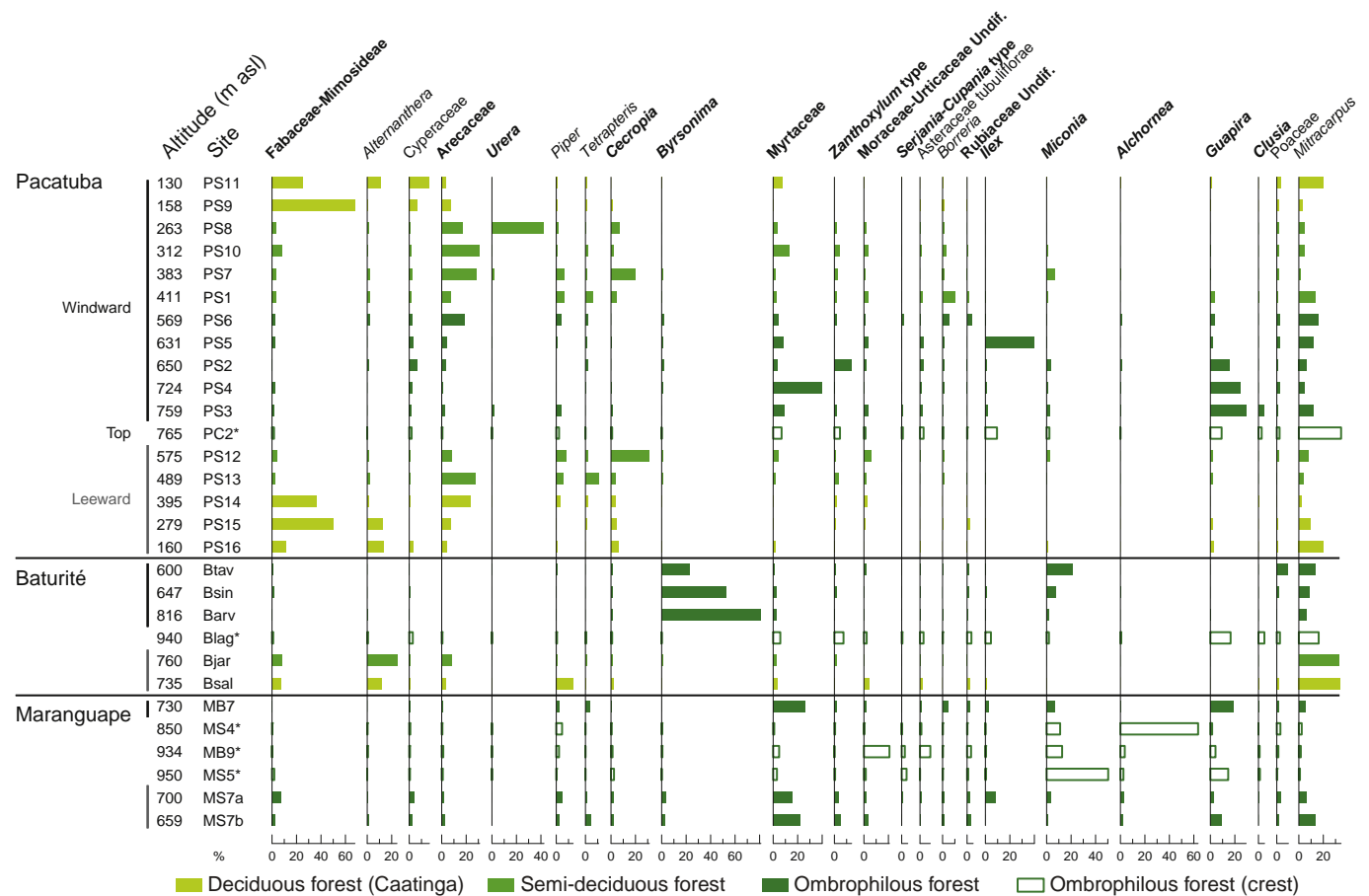


Fig. 2. Percentage pollen diagram of surface soil samples of the three mountainous massifs studied in the north-eastern Brazil. Pollen taxa in bold represent arboreal elements and the other correspond to shrubs or herbs. Samples located on the mountain top are indicated by “*”.

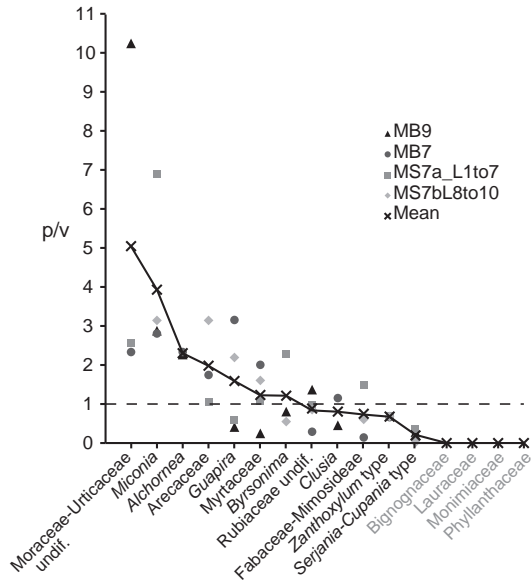


Fig. 3. p/v values according to arboreal taxa present in both the pollen rain and vegetation of the botanical plots from Maranguape Massif (in black). The p/v ratio corresponds to “% of arboreal pollen / % of total stems of all taxa in plot”. Values higher and lower than 1 respectively characterize the pollen taxa over- and underrepresented. Taxa in gray are absent in the pollen rain.

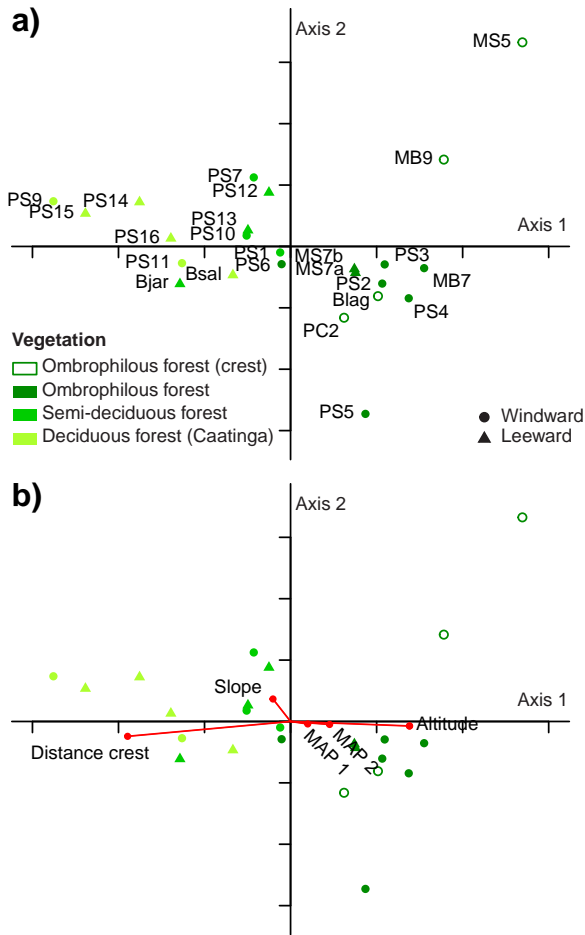


Fig. 4. Bi-plot of correspondence analysis for axes 1 and 2 with (a) distribution of surface soil samples and (b) projection of passive environmental parameters. Empty circles represent samples of ombrophilous forest located close to the crest.

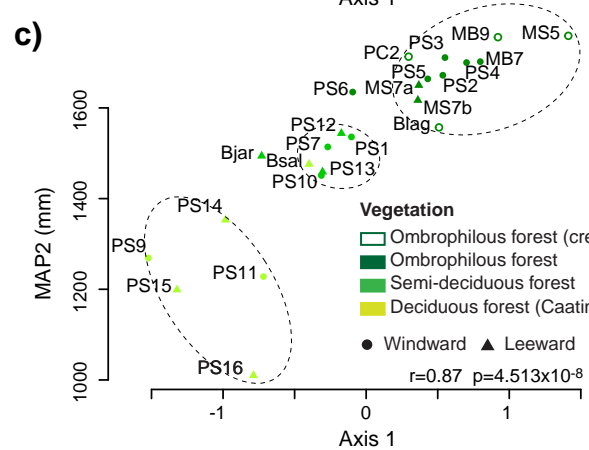
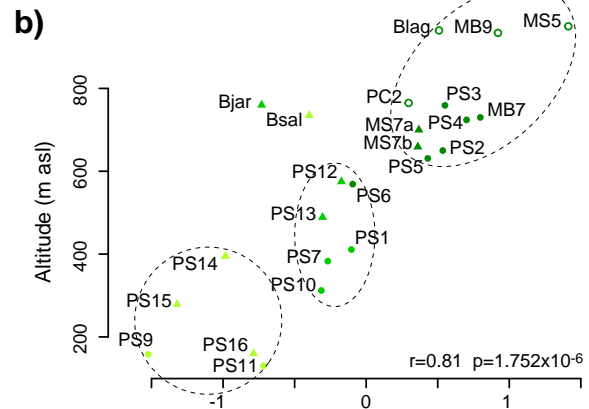
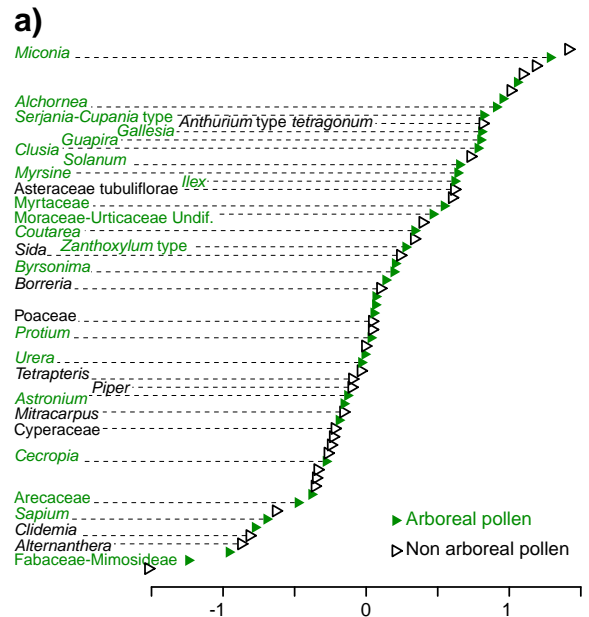


Fig. 5. (a) The distribution of main pollen taxa percentages discussed in the text, (b) the altitude values of surface soil samples and (c) the mean annual precipitation of surface soil samples according to axis 1 values of the correspondence analysis.

The dense ombrophilous forest (sub-montane): in this forest type, Myrtaceae remains among the most frequent tree pollen taxa associated with high percentages of *Miconia* (Melastomataceae), *Guapira* (Nyctaginaceae), *Ilex* (Aquifoliaceae), Moraceae-Urticaceae undif. or *Byrsonima* (Malpighiaceae). The dominance of these pollen taxa is generally observed from the upper limit of the semi-deciduous montane forest

Table 2

Main pollen taxa ordered by their respective percentage values for each surface soil samples. Arboreal pollen taxa are represented in bold. Surface soil samples are ordered according to axis 1 values of the correspondence analysis (CA) except for the five underlined samples removed from the CA. Color scale of surface samples from black to light gray represents the three main vegetation types, from the ombrophilous, semi-deciduous to deciduous forest (samples with “*” indicate ombrophilous forest located close to the crest).

Names	Main pollen taxa
MS5*	Miconia 50, Guapira 15, Serjania-Cupania type 4, Myrsine 4, Myrtaceae 3, Alchornea 2
MS4*	Alchornea 63, Miconia 11, Piper 5, Poaceae 3, Mitracarpus 2
MB9*	Moraceae-Urticaceae undif. 21, Miconia 13, Asteraceae tubuliflorae 8, Myrtaceae 5, Guapira 4, Alchornea 4, Solanum 3
MB7	Myrtaceae 26, Guapira 19, Miconia 7, Mitracarpus 5, Borreria 5, Tetrapteris 4, Ilex 3, Moraceae-Urticaceae undif. 2
PS4	Myrtaceae 40, Guapira 24, Mitracarpus 4, Cyperaceae 3, Poaceae 3
PS3	Guapira 29, Mitracarpus 12, Myrtaceae 9, Protium 7, Piper 4, Clusia 4, Moraceae-Urticaceae undif. 4, Miconia 3
PS2	Guapira 16, Zanthoxylum type 14, Anthurium type tetragonum 14, Mitracarpus 7, Cyperaceae 6, Myrtaceae 4, Arecaceae 4, Miconia 3
Blag*	Guapira 17, Mitracarpus 16, Zanthoxylum type 7, Myrsine 6, Myrtaceae 6, Clusia 5, Ilex 5
PS5	Ilex 40, Mitracarpus 12, Myrtaceae 9, Arecaceae 5, Cyperaceae 4, Moraceae-Urticaceae undif. 3
MS7a	Myrtaceae 16, Ilex 9, Fabaceae-Mimosideae 7, Mitracarpus 6, Piper 5, Miconia 4, Cyperaceae 4, Galesia 4, Byrsonima 4
MS7b	Myrtaceae 22, Mitracarpus 13, Guapira 9, Zanthoxylum type 6, Tetrapteris 5, Moraceae-Urticaceae undif. 4, Fabaceae-Mimosideae 3, Piper 3
PC2*	Mitracarpus 35, Ilex 10, Guapira 9, Myrtaceae 7, Zanthoxylum type 3, Asteraceae tubuliflorae 3, Clusia 3
PS6	Arecaceae 19, Mitracarpus 16, Borreria 6, Protium 6, Piper 4, Myrtaceae 4, Coutarea 4, Guapira 4
Barv	Byrsonima 81, Mitracarpus 6, Myrtaceae 3, Miconia 2
Bsin	Byrsonima 53, Mitracarpus 8, Miconia 7, Myrtaceae 3
Btav	Byrsonima 23, Miconia 21, Mitracarpus 14, Poaceae 10, Sida 2, Moraceae-Urticaceae undif. 2
PS1	Mitracarpus 14, Borreria 10, Arecaceae 8, Piper 7, Tetrapteris 6, Cecropia 4, Moraceae-Urticaceae undif. 4, Guapira 4, Fabaceae-Mimosideae 4
PS12	Cecropia 31, Arecaceae 9, Piper 8, Mitracarpus 8, Moraceae-Urticaceae undif. 6, Myrtaceae 5, Astronium 4, Fabaceae-Mimosideae 4, Miconia 3
PS7	Arecaceae 29, Cecropia 20, Piper 7, Miconia 7, Fabaceae-Mimosideae 4, Zanthoxylum type 3
PS13	Arecaceae 28, Protium 12, Tetrapteris 11, Piper 6, Cecropia 4, Zanthoxylum type 4, Mitracarpus 4, Fabaceae-Mimosideae 3
PS8	Ureia 43, Arecaceae 17, Cecropia 7, Mitracarpus 5, Myrtaceae 4, Fabaceae-Mimosideae 3, Poaceae 2
PS10	Arecaceae 31, Myrtaceae 14, Fabaceae-Mimosideae 8, Mitracarpus 5, Zanthoxylum type 5, Moraceae-Urticaceae undif. 4
Bsal	Mitracarpus 34, Piper 14, Alternanthera 12, Fabaceae-Mimosideae 7, Moraceae-Urticaceae undif. 5, Arecaceae 4, Myrtaceae 3, Cecropia 2
PS11	Fabaceae-Mimosideae 25, Mitracarpus 20, Cyperaceae 17, Alternanthera 11, Myrtaceae 8, Arecaceae 4, Poaceae 3
Bjar	Mitracarpus 32, Alternanthera 24, Fabaceae-Mimosideae 8, Arecaceae 8, Sapium 4, Myrtaceae 3
PS16	Clidemia 22, Mitracarpus 20, Alternanthera 13, Fabaceae-Mimosideae 12, Cecropia 6, Arecaceae 5, Cyperaceae 3
PS14	Fabaceae-Mimosideae 36, Arecaceae 24, Senna 5, Cecropia 4, Piper 3, Moraceae-Urticaceae undif. 3
PS15	Fabaceae-Mimosideae 50, Alternanthera 12, Mitracarpus 9, Arecaceae 8, Cecropia 4
PS9	Fabaceae-Mimosideae 68, Arecaceae 8, Cyperaceae 7, Mitracarpus 3, Poaceae 2

upwards. However, pollen assemblages of ombrophilous forests located close to the crest or to the mountain top reveal some differences. Indeed, in these samples we recorded a percentage increase of *Miconia*, *Alchornea* (Euphorbiaceae) or *Mitracarpus* (Rubiaceae) and a slight increase of *Clusia* (Clusiaceae). The altitude in which such assemblages are observed, changes according to the maximum elevation of mountainous massifs, ~900 m asl at Baturité and Maranguape and ~700 m asl at Pacatuba.

The seasonal semi-deciduous montane forest: in this forest type, Arecaceae, the most frequent tree pollen taxon, is associated with Fabaceae-Mimosideae, Myrtaceae, *Piper* (Piperaceae), *Cecropia* (Urticaceae), *Ureia* (Urticaceae) and *Mitracarpus*. These assemblages are

recorded up to ~500 m asl on the windward side and up to ~600 m asl on the leeward side.

The seasonal deciduous forest: the tree pollen signature is mainly characterized by Fabaceae-Mimosideae and Arecaceae and the percentages of herbaceous pollen taxa, such as *Alternanthera* (Amaranthaceae), Cyperaceae and *Mitracarpus*, increase. This pollen assemblage is observed from the base up to ~200 m asl on the windward side and up to ~400 m asl on the leeward side. In Baturité Massif, located more inland than massifs of Pacatuba and Maranguape, this pollen assemblage is observed up to ~700 m asl on the leeward side.

3.2. Representativeness of pollen taxa in the ombrophilous forest

Within the botanical plots of the ombrophilous forest studied in the Maranguape Massif, in which surface soil samples have been collected (MB9, MB7, MS7a, MS7b), between thirteen and seventeen woody taxa are present in both the vegetation and pollen rain (see Appendix A). Principal among them is Myrtaceae, which is the most common taxon (~20% stems) in all the plots. In order to compare the relative representativeness of the pollen rain to the vegetation, we selected the p/v values for the twelve taxa that are most significant in the vegetation and pollen rain (Fig. 3). Although the p/v values can vary between plots for a same taxon, we recognized three main groups of important taxa. The taxa of the first group, characterized by Moraceae-Urticaceae undif. (mean p/v = 5.1), *Miconia* (3.9), *Alchornea* (2.3) and Arecaceae (2), are highly overrepresented in the pollen rain relative to their abundance in the vegetation. Except for Arecaceae, the p/v values for all the plots are higher than 2. The second group, that is also overrepresented, is characterized by taxa with mean p/v values between 1 and 2: *Guapira* (mean p/v = 1.6), Myrtaceae (1.3) and *Byrsonima* (1.2). The taxa Rubiaceae undif. (mean p/v = 0.9), *Clusia* (0.8), Fabaceae-Mimosideae (0.8), *Zanthoxylum* (Rutaceae) type (0.7) and *Serjania-Cupania* type (0.2) that correspond to the third group, are generally underrepresented in the pollen rain relative to their abundance in the vegetation. Several taxa, Bignoniaceae, Lauraceae, Monimiaceae and Phyllanthaceae, including significant woody species such as, *Handroanthus serratifolius*, *Nectandra cuspidate*, *Cinnamomum triplinerve*, *Mollinedia ovata*, *Margaritaria nobilis*, are completely absent in the pollen rain.

3.3. Multivariate data analysis

Among the 91 different pollen taxa identified, 64 pollen taxa occurring with a frequency higher than 1% have been used to perform the CA. A first CA analysis clearly separates a group that includes all samples except five outlier samples (see Appendix B). These samples characterize the ombrophilous forest of the Baturité Massif with high frequencies of *Byrsonima* (Btav, Bsin and Barv) or highly disturbed vegetation (PS8 and MS4). In order to improve ordination results and provide a better understanding of the relationships between pollen assemblages and natural vegetation distribution, the outlier samples were removed and a new CA was performed (Fig. 4). Eigenvalues for the first and second axes represent respectively 17.8% and 11.7% of the total variation. The distribution of samples in the CA diagram (Fig. 4a) displays a continuous pattern along axis 1 which reflects the vegetation variation from the seasonal deciduous forest, the seasonal semi-deciduous montane forest to the dense ombrophilous forest (sub-montane). Along this gradient we observe a clear distinction between these three main vegetation types. Ombrophilous forests located close to the crest or to the mountain top are not well defined by the CA except for two samples from the Maranguape Massif (MS5 and MB9). Several passive environmental parameters (Altitude, MAP1, MAP2, Slope and Distance to the crest) have been projected in the axes 1–2 bi-plot of the CA. As shown in Fig. 4b and by the correlation coefficient (Table 3), the environmental parameters are mainly correlated with axis 1. The closest environmental parameters related to axis 1 are MAP2 (0.87), altitude (0.81), MAP1

(0.67) and distance to the crest (−0.66). The main correlation concerning axis 2 is with the Slope (0.19).

Ordination of the pollen taxa according to axis 1 values reveals a distribution pattern similar to the pollen taxa distribution observed in our synthetic pollen diagram according to the altitudinal gradient (Fig. 5a). Altitude and precipitation values of surface samples plotted according to axis 1 values reflect the general structure of the three main vegetation types (Fig. 5b and c). We observe that the samples of the seasonal deciduous forest remain below 400 m asl with an annual precipitation lower than 1400 mm and the samples of the seasonal semi-deciduous montane forest remain below 600 m asl with an annual precipitation of 1400–1600 mm. Two samples of the Baturité Massif (Bjar and Bsal) differ from this general pattern showing altitude values higher for their respective forest type than at the Pacatuba Massif. For the ombrophilous forest, all samples (except PS6), are located above 600 m asl with an annual precipitation higher than 1600 mm.

4. Discussion

4.1. Pollen-vegetation relationship and characteristic pollen taxa

One of the most typical features of the dense ombrophilous forests (sub-montane) of the mountainous massifs from north-eastern Brazil, is the dominance of Myrtaceae which represents the most diversified tree family (Lima et al., 2009; Siqueira et al., 2001). A dominance of Myrtaceae is evident in the massifs of Baturité and Maranguape, for instance, only in Baturité more than forty species of Myrtaceae have been identified (Araújo et al., 2007). In the pollen rain, although Myrtaceae is not always the most abundant pollen taxon, it remains among the main arboreal pollen percentages in the ombrophilous forest in all mountainous massifs (Fig. 2 and Table 2). However, in both the vegetation and pollen rain, the association of Myrtaceae with other dominant taxa allows to characterize different communities within the ombrophilous forests. In the Baturité Massif, among the most dominant trees, species of Myrtaceae such as *Myrcia splendens* are frequently associated with *Byrsonima sericea*, *Clusia nemorosa*, *Miconia cecidophora* or *Ilex sapotifolia* (Araújo et al., 2007; Cavalcante et al., 2000). Pollen contents of this vegetation type (Barv, Bsin and Btav) from surface soil samples collected in Baturité are characterized by a high amount of *Byrsonima* in the pollen rain associated with *Miconia* and Myrtaceae (Fig. 2).

In the Pacatuba and Maranguape massifs, *Byrsonima* is no longer among the main pollen taxa and Myrtaceae is frequently associated with *Guapira*, *Miconia* and Moraceae-Urticaceae undif. in surface soil samples from the ombrophilous forest (Fig. 2 and Table 2). This difference in pollen contents observed between the Baturité and Pacatuba/Maranguape massifs is also supported by botanical data. Indeed, at Maranguape, while species of Myrtaceae remain the most abundant and diversified tree family (see Appendix A), the most common trees identified are *M. splendens*, *Guapira nitida* and *Cupania impressinervia*. On the leeward side (MS7a and MS7b), the forest composition changes slightly and the latter trees are frequently associated with *Pilocarpus spicatus*, *H. serratifolius* and several species of Fabaceae-Mimosideae such as *Senegalia polyphylla*. These forest composition changes are also partly observed in the corresponding pollen assemblages of the leeward side with a slight increase of Fabaceae-Mimosideae and *Zanthoxylum* type (including *Pilocarpus*) (Fig. 2).

Table 3

Pearson correlation test (r) of passive ecological variables with axes 1 and 2 of correspondence analysis.

Ecological variables	Axis 1	Axis 2
Altitude	0.81	−0.04
MAP 1	0.67	−0.14
MAP 2	0.87	−0.09
Slope	−0.11	0.19
Distance to the crest	−0.66	−0.08

The forests located closer to the crest or on the mountain top differ partly in their structure and composition from the ombrophilous forest located just below. This forest type is generally characterized by a lower canopy and a high proportion of epiphytic plants. Among the trees, an increase of *Alchornea glandulosa*, *Miconia mirabilis*, *C. nemorosa* and *Clusia melchiorii* is observed in the Baturité and Maranguape massifs (Araújo et al., 2007 and Appendix A). In the tropical rainforest, these species are considered as pioneer and heliophilous trees (Pessoa et al., 2012; Souza et al., 2006). In addition, several species of *Clusia* (e.g., *C. nemorosa*) can facultatively apply crassulacean acid metabolism (CAM) or C3 metabolism according to water availability (Lüttge, 2006; Vaasen et al., 2006). Species characterized by this a useful adaptation have the ability to adjust to dry conditions by switching to the CAM mode, but also back to the C3 mode under humid conditions. The pollen rain from surface soil samples located close to the crest also reveals these changes in composition of trees with high frequencies of *Alchornea*, *Miconia* (MS5, MS4) or a slight percentage increase of *Clusia* (Blag). Representativeness increase of such taxa in both the pollen rain and vegetation, probably highlights specific environmental conditions prevailing on the mountain tops or areas located close to the crest.

The forest composition of seasonal semi-deciduous and deciduous montane forests was studied in two plots on the leeward side of the Baturité Massif (Bjar and Bsal, Araújo et al., 2007). In this zone, the Myrtaceae, which is no longer the structural family, is replaced in abundance and diversity by the Euphorbiaceae (i.e. *Sebastiania macrocarpa*, *Manihot carthaginensis*, *Croton blanchetianus*, *Croton argyrophyloides*, *Sapium obovatum*), Fabaceae-Mimosideae (i.e. *Mimosa caesalpiniiifolia*, *Mimosa arenosa*) and Fabaceae-Caesalpinioideae (i.e. *Bauhinia cheilantha*). Species of Fabaceae-Mimosideae and Euphorbiaceae are frequent components of the Caatinga growing generally under low humidity conditions prevailing in the lowlands of north-eastern Brazil (Ferraz et al., 1998). Their associated pollen assemblages are characterized by a decrease of Myrtaceae at the expense of Fabaceae-Mimosideae and by high frequencies of herbaceous pollen taxa (*Mitracarpus* or *Alternanthera*). This change in pollen signature highlights an opening of the forest canopy, as shown in other semi-arid regions in north-eastern Brazil (dos Santos et al., 2015; Gomes et al., 2014). Most of the surface soil samples of the semi-deciduous montane forest were collected at Pacatuba. They differ from the deciduous forest samples by an increase in Arecaceae pollen frequencies (Fig. 2). Moreover, the pollen rain of the semi-deciduous forests shows a significant increase of *Cecropia*, a pioneer tree taxon (Santo-Silva et al., 2013), and *Piper* indicating secondary successional shrubs (Pearson et al., 2002). Recurrent droughts could favor the development of these two taxa in comparison with the ombrophilous forest where higher altitude and moisture could limit drought impact on vegetation. In addition, more frequent human disturbance through this altitudinal range (e.g., banana crop) could also explain the development of these taxa characteristic of forest fragmentation and regeneration.

4.2. Over- and underrepresented pollen taxa in the ombrophilous forest

In order to compare directly the botanical with pollen data for the dense ombrophilous forest, four surface soils samples have been collected in the same locations as the botanical plots (MB7, MB9, MS7a and MS7b). In particular, calculating of p/v values allowed us to obtain a rough assessment of the over- and underrepresentation of each pollen taxon relative to their floristic abundance (Fig. 3 and see Appendix A). Among the most significant tree taxa represented in the vegetation and pollen rain, anemophilous taxa such as Moraceae-Urticaceae undif. and *Alchornea* are highly overrepresented in all the plots. Characterized by a high pollen productivity and dispersion, such anemophilous taxa are frequently among the most overrepresented in the pollen rain (Burn and Mayle, 2008; Bush and Rivera, 2001; Gosling et al., 2005). *Miconia* and Arecaceae which are not typical anemophilous taxa are also overrepresented in all the plots. Generally pollinated by bees (Ishara and Maimoni-Rodella,

2011), species of *Miconia* as *M. mirabilis* frequently identified in the Maranguape Massif are characterized by flowers with a large number of well exposed anthers. This could favor the pollen representation increase and can be attributed to a ‘messy pollination’ (Bush and Rivera, 2001; Horn and B, 1990). Well represented in pollen spectra, *Guapira*, Myrtaceae and *Byrsonima* indicate mean p/v values > 1 showing probably messy pollination syndromes. Although taxa such as Myrtaceae have already been reported as overrepresented (Gosling et al., 2009; Grabandt, 1980), the p/v values for these taxa are also variable and can reach values < 1 in several plots. The floristic composition changes between each plot, which could partly explain the observed variability of p/v values. Other significant tree taxa represented in the vegetation, Rubiaceae undif., *Clusia*, Fabaceae-Mimosidae, the *Zanthoxylum* type and the *Serjania-Cupania* type, are rather underrepresented; Bignoniaceae, Lauraceae, Monimiaceae and Phyllanthaceae are completely absent in the pollen rain. Several of these taxa have already been reported as underrepresented or silent taxa, e.g., *Clusia* (Grabandt, 1980), Rubiaceae, Bignoniaceae, and the *Serjania-Cupania* type (Gosling et al., 2009). Otherwise, our p/v values are also not always consistent with previous trends observed in other regions. Among the most striking, the *Zanthoxylum* type has been reported as overrepresented, while *Miconia*, generally included in Melastomataceae, has been reported as underrepresented (Bush and Rivera, 2001; Gosling et al., 2009). Apart from the fact that species included in pollen taxa are not necessarily the same between the different regions, which certainly generates differences in terms of pollen representation, our study focused on surface soil samples which also could generate differences in terms of pollen preservation and representation in comparison with studies focused on pollen traps. Although this approach based on p/v values, including different biases, is not perfect, values for some taxa are in accordance with predictions associated with their pollination strategy (e.g., Moraceae-Urticaceae undif. and *Alchornea*) as it has been shown in different tropical regions (Bush, 1995; Bush and Rivera, 2001; Gosling et al., 2005).

4.3. Impact of environmental factors on forest distribution

Modern pollen samples from the Maranguape, Pacatuba and Baturité massifs closely reflect the different vegetation types along the altitudinal gradient. On the windward side of Maranguape and Pacatuba, close to the coast, the lowland seasonal deciduous forest is replaced by a seasonal semi-deciduous montane forest at 200 m asl, which in turn is replaced by a dense ombrophilous forest (sub-montane) at 500 m asl. The same pattern is observed on the leeward side although each ecotone is located between 100 and 200 m higher than on the windward side.

The spatial distribution of the vegetation in mountainous areas is commonly related to precipitation and temperature changes induced by the altitudinal gradient. The studied massifs from north-eastern Brazil are not high enough to result in temperatures that could be considered as a direct limiting factor on the vegetation, as was already described from other tropical areas (Duarte et al., 2005; Sarthou et al., 2009). Consequently, precipitation (MAP2) highly correlated with the distribution of modern pollen samples on axis 1 of the CA represents the main factor controlling the distribution of the different forest types (Table 3 and Fig. 4). Such a pattern of precipitation changes is controlled by the elevation of air masses on the windward side generating orographic precipitation. On the leeward side, the altitude decrease, warms up and dries the air masses, which dissipate fogs, decrease rainfalls and increase evaporation. This mechanism, the “foehn effect”, is frequently observed in tropical mountainous islands like Hawaii (Giambelluca et al., 2012) and Cape Verde (Duarte et al., 2005). A high correlation coefficient ($r = 0.82$) between altitude and precipitation (MAP2) changes of surface soil samples shows the influence of the altitude gradient on precipitation increase and vegetation distribution.

While altitude increase represents one of the main factors influencing precipitation, the distance from the coast is also an important factor for explaining changes in precipitation rates. In particular, rainfall decrease is observed when the distance from the coast increases. For example, at

Baturité (80 km inland) the deciduous forest grows up to 700 m asl on the leeward side (Bsal), while it remains below 400 m asl on the same side at Pacatuba Massif (30 km from the coast). Slope angle could also influence vegetation distribution. However, the slope angle has been generally shown as a relevant factor at values > 40° (Fernández-Palacios and de Nicolás, 1995). None of our surface samples reaches such values, which could explain that no correlation is observed between the slope angle values and the vegetation distribution revealed by the CA axes (Table 3). Distance to the crest is inversely correlated with axis 1 of the CA, because when this distance increases, altitude generally decreases, thus reflecting the decreasing precipitation.

In areas located close to the crest or on the mountain top, pollen assemblages from surface soil samples reflect a different community of the ombrophilous forest, with abundant heliophilous and pioneer tree taxa such as, *Alchornea*, *Clusia* or *Miconia*. Different edaphic conditions related to the rocky soil of the summit reduce the water-holding capacities. Such local conditions could explain the development of plant communities that are more dependent on atmospheric moisture and thus more strongly correlate with changes therein. This is particularly well illustrated by a greater abundance of epiphytic plants near the crest. In addition, associated with strong winds, the drying effect and falling trees are more important in these areas. The strong development of pioneer trees in these forests confirms strong dynamics and probably a high resilience related to frequent natural disturbances. Consequently, this different forest community is more disturbed and affected by the frequent droughts of this region than the dense ombrophilous forest (Hastenrath and Heller, 1977). Moreover, although rainfalls would reach their maxima close to the mountain tops, local environmental conditions induce drier moisture conditions than in the dense ombrophilous forest, only located a few tens of meters below. At this point, additional and exhaustive botanical surveys would be essential to better describe such a forest community, preferably focusing on epiphytic plant or liana diversity, which seems to be important structural plant components at higher elevation.

5. Conclusions

Our complementary approach between pollen analysis of surface soil samples and present-day vegetation in mountainous massifs in north-eastern Brazil shows that the pollen rain accurately reflects the different vegetation types. Based on the different pollen assemblages, the following tropical forest types can be recognized: i) a dense ombrophilous forest (or tropical moist broadleaf forest) characterized by Myrtaceae associated with high percentages of *Miconia*, *Guapira*, *Ilex*, Moraceae-Urticaceae undif. or *Byrsonima*, ii) a seasonal semi-deciduous montane forest characterized by an increase of *Arecaceae* associated with Fabaceae-Mimosidae, Myrtaceae, *Piper*, *Cecropia*, *Urera* and *Mitracarpus*, and iii) a seasonal deciduous forest dominated by Fabaceae-Mimosidae and *Arecaceae* tree taxa associated with *Alternanthera*, *Cyperaceae* and *Mitracarpus*. In areas located close to the crest, a different ombrophilous forest community has been identified by the increase of *Alchornea*, *Miconia* or *Clusia*. Being typical heliophilous and pioneer trees, these taxa indicate drier moisture conditions, related to local environmental factors than in the dense ombrophilous forest just located a few tens of meters below. Concerning the dense ombrophilous forest, pollen rain has also been directly compared with data from several botanical plots. Although we observed some differences with previous studies performed in tropical regions, pollen representativeness for several taxa are conform to the predictions inferred from their pollination strategies. In particular, anemophilous pollen taxa are always overrepresented relative to their floristic abundance.

In addition to characterize each vegetation type, our ordination of pollen data, based on surface soil samples distributed at different altitudes and mountain sides, allows the reconstruction of the spatial distribution of different vegetation types. Unlike previous studies, this approach combining vegetation and pollen data also allows studying the influence of environmental factors on vegetation distribution. In particular, we

characterize the high importance of precipitation changes (associated with increasing altitude) that represents the main environmental factor controlling vegetation distribution, except for the forest located close to the crest in which changes of edaphic conditions also seem to be important. Our study provides a better understanding of the ecosystem functioning in mountainous massifs in north-eastern Brazil. As these areas can be considered as “islands” of tropical rainforest, this knowledge will be useful for conservation or restoration purposes. Furthermore, development of this type of comparison between pollen and vegetation data will be helpful, to improve our understanding of fossil pollen records for reconstructing past vegetation dynamics, climate changes and diversity processes of tropical rainforest in a semi-arid environment.

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Appendix A. List of pollen taxa present in both the pollen rain and vegetation of the botanical plots from Maranguape Massif including botanical and pollen data. Taxa in gray represent plant families absent in the pollen rain. pbh: perimeter at breast height

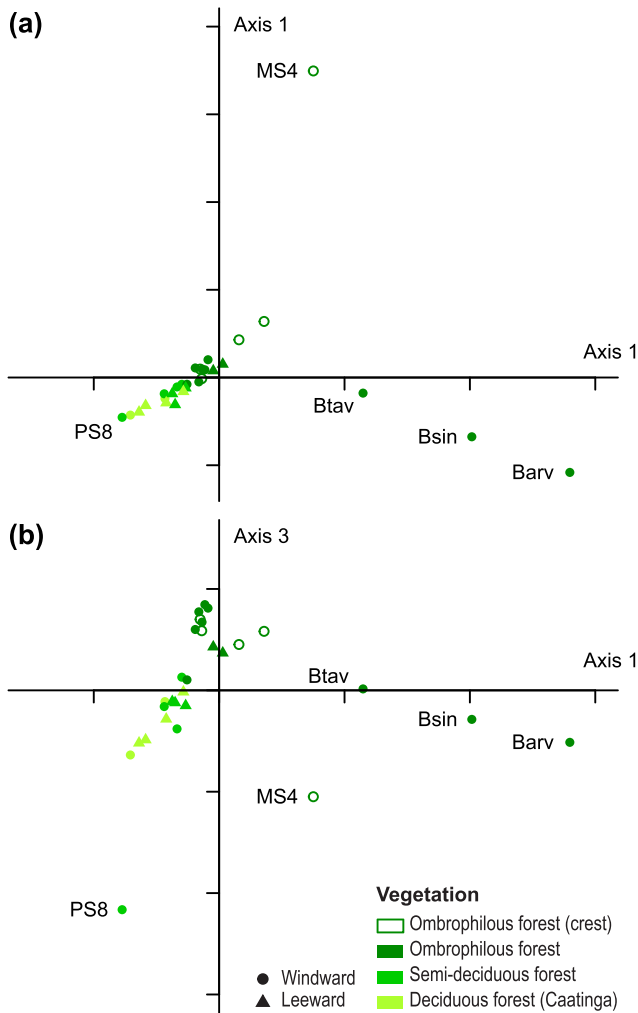
MB9					
Pollen taxa	Vegetation data		Pollen data		p/v
	No. of stems ≥ 15 cm pbh	% of total stems (v)	No. of pollen	% of pollen (p)	
Myrtaceae	114	23.8	15	6.5	0.3
<i>Guapira</i>	62	12.9	13	5.7	0.4
<i>Serjania-Cupania</i> type	54	11.3	8	3.5	0.3
<i>Miconia</i>	28	5.8	39	17.0	2.9
Rubiaceae undif.	15	3.1	10	4.3	1.4
<i>Clusia</i>	13	2.7	3	1.3	0.5
Moraceae-Urticaceae undif.	13	2.7	64	27.8	10.3
<i>Roupala</i>	12	2.5	8	3.5	1.4
<i>Alchornea</i>	10	2.1	11	4.8	2.3
<i>Ficus</i>	6	1.3	2	0.9	0.7
<i>Byrsonima</i>	5	1.0	2	0.9	0.8
<i>Solanum</i>	3	0.6	9	3.9	6.2
<i>Symplocos</i>	3	0.6	4	1.7	2.8
<i>Ilex</i>	2	0.4	1	0.4	1.0
<i>Senna</i>	1	0.2	3	1.3	6.2
<i>Pouteria</i>	1	0.2	1	0.4	2.1
<i>Acalypha</i>	1	0.2	1	0.4	2.1
Total	343	71.6	194	84.3	
Lauraceae	44	9.2			
Monimiaceae	38	7.9			
Fabaceae-Mimosideae	28	5.8			
Bignoniaceae	2	0.4			
Total	112	23.4			

MB7					
Pollen taxa	Vegetation data		Pollen data		p/v
	No. of stems ≥ 15 cm pbh	% of total stems (v)	No. of pollen	% of pollen (p)	
Myrtaceae	100	18.7	86	37.9	2.0
Rubiaceae undif.	60	11.2	8	3.5	0.3
<i>Guapira</i>	46	8.6	62	27.3	3.2
<i>Serjania-Cupania</i> type	37	6.9	2	0.9	0.1
Fabaceae-Mimosideae	28	5.2	2	0.9	0.2
<i>Zanthoxylum</i> type	24	4.5	7	3.1	0.7
<i>Miconia</i>	20	3.7	24	10.6	2.8
<i>Ficus</i>	14	2.6	1	0.4	0.2
Moraceae-Urticaceae undif.	8	1.5	8	3.5	2.4
<i>Ilex</i>	7	1.3	10	4.4	3.4
<i>Solanum</i>	5	0.9	1	0.4	0.5
Arecaceae	4	0.7	3	1.3	1.8
<i>Clusia</i>	4	0.7	2	0.9	1.2
<i>Sapium</i>	4	0.7	1	0.4	0.6
<i>Myrsine</i>	3	0.6	2	0.9	1.6
<i>Alchornea</i>	2	0.4	2	0.9	2.4
<i>Gallesia</i>	1	0.2	2	0.9	4.7
Total	367	68.6	223	98.2	
Bignoniaceae	21	3.9			
Lauraceae	30	5.6			
Phyllanthaceae	20	3.7			
Monimiaceae	2	0.4			
Total	73	13.6			

MS7a					
Pollen taxa	Vegetation data		Pollen data		p/v
	No. of stems ≥ 15 cm pbh	% of total stems (v)	No. of pollen	% of pollen (p)	
Myrtaceae	76	21.2	48	23.1	1.1
Fabaceae-Mimosideae	25	7.0	22	10.6	1.5
<i>Zanthoxylum</i> type	24	6.7	10	4.8	0.7
<i>Guapira</i>	22	6.1	8	3.8	0.6
<i>Serjania-Cupania</i> type	13	3.6	3	1.4	0.4
Rubiaceae undif.	12	3.3	7	3.4	1.0
<i>Byrsonima</i>	9	2.5	12	5.8	2.3
Arecaceae	8	2.2	5	2.4	1.1
<i>Astronium</i>	5	1.4	4	1.9	1.4
<i>Aspidosperma</i>	5	1.4	1	0.5	0.3
Moraceae-Urticaceae undif.	4	1.1	6	2.9	2.6
<i>Miconia</i>	3	0.8	12	5.8	6.9
<i>Myrsine</i>	1	0.3	3	1.4	5.2
<i>Senna</i>	1	0.3	2	1.0	3.5
Total	208	57.9	143	68.8	
Bignoniaceae	21	5.8			
Lauraceae	8	2.2			
Phyllanthaceae	8	2.2			
Total	37	10.3			

MS7b					
Pollen taxa	Vegetation data		Pollen data		p/v
	No. of stems ≥ 15 cm pbh	% of total stems (v)	No. of pollen	% of pollen (p)	
Myrtaceae	33	20.2	68	33.0	1.6
<i>Zanthoxylum</i> type	19	11.7	17	8.3	0.7
<i>Serjania-Cupania</i> type	17	10.4	1	0.5	0.0
<i>Byrsonima</i>	11	6.7	8	3.9	0.6
<i>Guapira</i>	10	6.1	28	13.6	2.2
Fabaceae-Mimosideae	10	6.1	8	3.9	0.6
Rubiaceae undif.	9	5.5	10	4.9	0.9
<i>Roupala</i>	4	2.5	7	3.4	1.4
<i>Astronium</i>	4	2.5	2	1.0	0.4
<i>Senna</i>	3	1.8	1	0.5	0.3
Arecaceae	2	1.2	8	3.9	3.2
<i>Ficus</i>	2	1.2	1	0.5	0.4
<i>Miconia</i>	1	0.6	4	1.9	3.2
Total	125	76.7	163	79.1	
Bignoniaceae	12	7.4			
Phyllanthaceae	6	3.7			
Lauraceae	4	2.5			
Total	22	13.5			

Appendix B. Bi-plot of correspondence analysis with all modern pollen samples for axes 1 and 2 (a) and for axes 1 and 3 (b). Only the names of outlier samples have been indicated



References

Andrade, L.A., Oliveira, F.X., Nascimento, I.S., Fabricante, J.R., Sampaio, E.V.S.B., Barbosa, M.R.V., 2006. Análise florística e estrutural de matas ciliares ocorrentes em brejo de altitude no município de Areia. Paraíba. Rev. Bras. Ciênc. Agrár. 1, 31–40. <http://dx.doi.org/10.5039/agraria.v1i1.9>.

Andrade-Lima, D., 1982. Present-day forest refuges in northeastern Brazil. In: Prance, G.T. (Ed.), *Biological Diversification in the Tropics*. Columbia University Press, New York, pp. 245–251.

Araújo, F.S., Gomes, V.S., Silveira, A.P., Figueiredo, M.A., Oliveira, R.F., Bruno, M.M.A., Lima-Verde, L.W., Silva, E.F., Otutumi, A.T., Ribeiro, K.A., 2007. Efeito da variação topoclimática e estrutura da vegetação da serra de Baturité, Ceará. In: Oliveira, T.S., Araújo, F.S. (Eds.), *Diversidade E Conservação Da Biota Da Serra de Baturité*. Ceará. UFC/COELCE, Fortaleza, pp. 73–136.

Ashton, P.S., 2003. Floristic zonation of tree communities on wet tropical mountains revisited. *Perspect. Plant Ecol. Evol. Syst.* 6, 87–104. <http://dx.doi.org/10.1078/1433-8319-00044>.

Barthlott, W., Mutke, J., Rafiqpoor, D., Kier, G., Krefl, H., 2005. Global centers of vascular plant diversity. *Nova Acta Leopold. NF* 92 (342), 61–83.

Bennett, K.D., 1994. "psimpoll" version 2.23: a C program for analysing pollen data and plotting pollen diagrams. INQUA Comm. Study Holocene Work. Group Data-Handl. *Methods Newlett.* 11, 4–6.

Burn, M.J., Mayle, F.E., 2008. Palynological differentiation between genera of the Moraceae family and implications for Amazonian palaeoecology. *Rev. Palaeobot. Palynol.* 149, 187–201. <http://dx.doi.org/10.1016/j.revpalbo.2007.12.003>.

Burn, M.J., Mayle, F.E., Killeen, T.J., 2010. Pollen-based differentiation of Amazonian rainforest communities and implications for lowland palaeoecology in tropical South America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 295, 1–18. <http://dx.doi.org/10.1016/j.palaeo.2010.05.009>.

Bush, M.B., 1995. Neotropical plant reproductive strategies and fossil pollen representation. *Am. Nat.* 145, 594–609. <http://dx.doi.org/10.1086/285757>.

Bush, M.B., Rivera, R., 2001. Reproductive ecology and pollen representation among neotropical trees. *Glob. Ecol. Biogeogr.* 10, 359–367. <http://dx.doi.org/10.1046/j.1466-822X.2001.00247.x>.

Cárdenas, M.L., Gosling, W.D., Pennington, R.T., Poole, I., Sherlock, S.C., Mothes, P., 2014. Forests of the tropical eastern Andean flank during the middle Pleistocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 393, 76–89. <http://dx.doi.org/10.1016/j.palaeo.2013.10.009>.

Cavalcante, A., Soares, J.J., Figueiredo, M.A., 2000. Comparative phytosociology of tree sinusiae between contiguous forests in different stages of succession. *Rev. Brasileira Biol.* 60, 551–562.

Colinvaux, P., De Oliveira, P.E., Patiño, J.E.M., 1999. *Amazon Pollen Manual and Atlas*. Harwood Academic Publisher, Amsterdam.

Costa-Junior, R.F., Ferreira, R.L.C., Rodal, M.J.N., Feliciano, A.L.P., Marangon, L.C., Silva, W.C., 2008. Estrutura fitossociológica do componente arbóreo de um fragmento de Floresta Ombrófila Densa na mata sul de Pernambuco, nordeste do Brasil. *Ciênc. Forest.* 18, 173–183. <http://dx.doi.org/10.5902/19805098455>.

Cottam, G., Curtis, J.T., 1956. The use of distance measures in phytosociological sampling. *Ecology* 37, 451–460. <http://dx.doi.org/10.2307/1930167>.

Duarte, M.C., Rego, F., Moreira, I., 2005. Distribution patterns of plant communities on Santiago Island, Cape Verde. *J. Veg. Sci.* 16, 283–292. <http://dx.doi.org/10.1111/j.1654-1103.2005.tb02366.x>.

Fægri, K., Iversen, J., 1975. *Textbook of Pollen Analysis*. John Wiley & Sons, London.

Fernández-Palacios, J.M., de Nicolás, J.P., 1995. Altitudinal pattern of vegetation variation on Tenerife. *J. Veg. Sci.* 6, 183–190. <http://dx.doi.org/10.2307/3236213>.

Ferraz, E.M.N., Rodal, M.J.N., Sampaio, E.V.S.B., Pereira, R.d.C.A., 1998. Composição florística em trechos de vegetação de caatinga e brejo de altitude na região do Vale do Pajeú. Pernambuco. *Braz. J. Bot.* 21, 7–15. <http://dx.doi.org/10.1590/S0100-84041998000100002>.

Ferraz, E.M.N., Araújo, E.L., Silva, S.I., 2004. Floristic similarities between lowland and montane areas of Atlantic Coastal Forest in Northeastern Brazil. *Plant Ecol.* 174, 59–70. <http://dx.doi.org/10.1023/B:VEGE.0000046062.77560.f5>.

Giambelluca, T.W., Chen, Q., Frazier, A.G., Price, J.P., Chen, Y.-L., Chu, P.-S., Eischeid, J.K., Delparte, D.M., 2012. Online rainfall atlas of Hawai'i. *Bull. Am. Meteorol. Soc.* 94, 313–316. <http://dx.doi.org/10.1175/BAMS-D-11-00228.1>.

Gomes, J.M.d.S., Lima e Lima, L.C., Santos, F.d.A.R., Silva, F.H.M.e., 2014. First records of pollen rain in bromeliad tanks in an area of Caatinga in northeastern Brazil. *Acta Bot. Bras.* 28, 176–183. <http://dx.doi.org/10.1590/S0102-33062014000200004>.

Gosling, W., Mayle, F.E., Tate, N.J., Killeen, T.J., 2005. Modern pollen-rain characteristics of tall terra firme moist evergreen forest, Southern Amazonia. *Quat. Res.* 64, 284–297.

Gosling, W.D., Mayle, F.E., Tate, N.J., Killeen, T.J., 2009. Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. *Rev. Palaeobot. Palynol.* 153, 70–85. <http://dx.doi.org/10.1016/j.revpalbo.2008.06.007>.

Grabandt, R.A.J., 1980. Pollen rain in relation to arboreal vegetation in the Colombian cordillera oriental. *Rev. Palaeobot. Palynol.* 29, 65–147. [http://dx.doi.org/10.1016/0034-6667\(80\)90043-3](http://dx.doi.org/10.1016/0034-6667(80)90043-3).

Hastenrath, S., Heller, L., 1977. Dynamics of climatic hazards in northeast Brazil. *Q. J. R. Meteorol. Soc.* 103, 77–92. <http://dx.doi.org/10.1002/qj.49710343505>.

Hemp, A., 2005. Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. *Plant Ecol.* 184, 27–42. <http://dx.doi.org/10.1007/s11258-005-9049-4>.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978. <http://dx.doi.org/10.1002/joc.1276>.

Horn, S.P., B, W.R., 1990. On the occurrence of *Ficus* pollen in neotropical Quaternary sediments. *Palynology* 14, 3–6.

Ishara, K.L., Maiimoni-Rodella, R.d.C.S., 2011. Pollination and dispersal systems in a Cerrado remnant (Brazilian Savanna) in Southeastern Brazil. *Braz. Arch. Biol. Technol.* 54, 629–642. <http://dx.doi.org/10.1590/S1516-89132011000300025>.

Jones, H.T., Mayle, F.E., Pennington, R.T., Killeen, T.J., 2011. Characterisation of Bolivian savanna ecosystems by their modern pollen rain and implications for fossil pollen records. *Rev. Palaeobot. Palynol.* 164, 223–237. <http://dx.doi.org/10.1016/j.revpalbo.2011.01.001>.

Leal, A., Berrío, J.C., Raimúndez, E., Bilbao, B., 2011. A pollen atlas of premontane woody and herbaceous communities from the upland savannas of Guayana, Venezuela. *Palynology* 35, 226–266. <http://dx.doi.org/10.1080/gspalynol.35.2.226>.

Lima, J.R., Sampaio, E.V.S.B., Rodal, M.J.N., Araújo, F.S., 2009. Composição florística da floresta estacional decídua montana de Serra das Almas, CE. Brasil. *Acta Bot. Bras.* 23, 756–763.

Lüttge, U., 2006. Photosynthetic flexibility and ecophysiological plasticity: questions and lessons from Clusia, the only CAM tree, in the neotropics. *New Phytol.* 171, 7–25. <http://dx.doi.org/10.1111/j.1469-8137.2006.01755.x>.

Martin, P.H., Sherman, R.E., Fahey, T.J., 2007. Tropical montane forest ecotones: climate gradients, natural disturbance, and vegetation zonation in the Cordillera Central, Dominican Republic. *J. Biogeogr.* 34, 1792–1806. <http://dx.doi.org/10.1111/j.1365-2699.2007.01726.x>.

Pearson, T.R.H., Burslem, D.F.R.P., Mullins, C.E., Dalling, J.W., 2002. Germination ecology of neotropical pioneers: interacting effects of environmental conditions and seed size. *Ecology* 83, 2798–2807. [http://dx.doi.org/10.1890/0012-9658\(2002\)083\[2798:GEONPI\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2002)083[2798:GEONPI]2.0.CO;2).

Pessoa, M.d.S., Vleeschouwer, K.M.D., Talora, D.C., Rocha, L., Amorim, A.M.A., 2012. Reproductive phenology of *Miconia mirabilis* (Melastomataceae) within three distinct physiognomies of Atlantic Forest, Bahia, Brazil. *Biota Neotrop.* 12, 49–56. <http://dx.doi.org/10.1590/S1676-06032012000200006>.

Peulvast, J.-P., de Claudino Sales, V., 2004. Stepped surfaces and palaeolandforms in the northern Brazilian "Nordeste": constraints on models of morphotectonic evolution. *Geomorphology* 62, 89–122. <http://dx.doi.org/10.1016/j.geomorph.2004.02.006>.

- QGIS Development Team, 2015. QGIS Geographic Information System Developers Manual. Open Source Geospatial Foundation Project.
- Richter, M., 2008. Tropical mountain forests – distribution and general features. In: Gradstein, S., Homeier, J., Gansert, D. (Eds.), *The Tropical Mountain Forest – Patterns and Processes in a Biodiversity Hotspot* Biodiversity and Ecology Series. Göttingen Centre for Biodiversity and Ecology, pp. 7–24.
- Rizzini, C.T., 1963. Nota prévia sobre a divisão fitogeográfica do Brasil. *Rev. Bras. Geogr.* 1, 1–64.
- Roubick, D.W., Moreno, J.E., 1991. Pollen and Spores of Barro Colorado Island. Missouri Botanical Garden, Saint Louis, MO.
- Rull, V., 2003. An illustrated key for the identification of pollen from Pantepui and the Gran Sabana (eastern Venezuelan Guayana). *Palynology* 27, 99–133. <http://dx.doi.org/10.2113/27.1.99>.
- Santo-Silva, E.E., Almeida, W.R., Melo, F.P.L., Zickel, C.S., Tabarelli, M., 2013. The nature of seedling assemblages in a fragmented tropical landscape: implications for forest regeneration. *Biotropica* 45, 386–394. <http://dx.doi.org/10.1111/btp.12013>.
- Santos, D.A.d., Lima e Lima, L.C., Santos, F.d.A.R., Silva, F.H.M.e., 2015. First report of modern pollen deposition in moss polsters in a semiarid area of Bahia Brazil. *Acta Bot. Bras.* 29, 534–544.
- Sarthou, C., Kounda-Kiki, C., Vaçulik, A., Mora, P., Ponge, J.-F., 2009. Successional patterns on tropical inselbergs: a case study on the Nouragues inselberg (French Guiana). *Flora - Morphol. Distrib. Funct. Ecol. Plants* 204, 396–407. <http://dx.doi.org/10.1016/j.flora.2008.05.004>.
- Schüler, L., Hemp, A., Behling, H., 2014. Relationship between vegetation and modern pollen-rain along an elevational gradient on Kilimanjaro, Tanzania. *The Holocene* 24, 702–713. <http://dx.doi.org/10.1177/0959683614526939>.
- Shoo, L.P., Storlie, C., Vanderwal, J., Little, J., Williams, S.E., 2011. Targeted protection and restoration to conserve tropical biodiversity in a warming world. *Glob. Change Biol.* 17, 186–193. <http://dx.doi.org/10.1111/j.1365-2486.2010.02218.x>.
- Siqueira, D.R., Rodal, M.J.N., Lins-e-Silva, A.C.B., Melo, A.L., 2001. Physiognomy, structure and floristic in an area of Atlantic Forest in northeast Brazil. In: Gottsberger, G., Liede, S. (Eds.), *Life Forms and Dynamics in Tropical Forest*. Gebr. Borntraeger, Berlin, pp. 11–27.
- Souza, J.P., Araújo, G.M., Schiavini, I., Duarte, P.C., 2006. Comparison between canopy trees and arboreal lower strata of urban semideciduous seasonal forest in Araguari - MG. *Braz. Arch. Biol. Technol.* 49, 775–783. <http://dx.doi.org/10.1590/S1516-89132006000600012>.
- Stockmarr, J., 1972. Tablets with spores used in absolute pollen analysis. *Pollen Spores* 13, 615–621.
- Urrego, D.H., Silman, M.R., Correa-Metrio, A., Bush, M.B., 2011. Pollen-vegetation relationships along steep climatic gradients in western Amazonia. *J. Veg. Sci.* 22, 795–806. <http://dx.doi.org/10.1111/j.1654-1103.2011.01289.x>.
- Vaasen, A., Begerow, D., Hampp, R., 2006. Phosphoenolpyruvate carboxylase genes in C3, crassulacean acid metabolism (CAM) and C3/CAM intermediate species of the genus *Clusia*: rapid reversible C3/CAM switches are based on the C3 housekeeping gene. *Plant Cell Environ.* 29, 2113–2123. <http://dx.doi.org/10.1111/j.1365-3040.2006.01583.x>.
- Veloso, H.P., 2012. *Manual técnico da vegetação brasileira*, IBGE. ed. 2th ed. IBGE, Rio de Janeiro.
- Weng, C., Bush, M.B., Silman, M.R., 2004. An analysis of modern pollen rain on an elevational gradient in southern Peru. *J. Trop. Ecol.* 20, 113–124. <http://dx.doi.org/10.1017/S0266467403001068>.
- Williams, S.E., Bolitho, E.E., Fox, S., 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proc. R. Soc. Lond. B Biol. Sci.* 270, 1887–1892. <http://dx.doi.org/10.1098/rspb.2003.2464>.