Research paper

Trapping pollen in the tropics — Comparing modern pollen rain spectra of different pollen traps and surface samples across Andean vegetation zones

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ABSTRACT

The analysis of modern pollen rain is an important prerequisite for detailed and comprehensive studies on fossil pollen assemblages, as it is necessary for obtaining valuable information about present pollen spectra in a more quantitative way. At present, several sampling media are used for modern pollen rain collection in tropical environments, without knowing a lot about their trapping properties. We compared modern pollen rain spectra of different pollen rain sampling media along an altitudinal gradient from ca. 1000 to ca. 3300 m a.s.l. in southern Ecuador. The vegetation types covered are premontane forest, lower montane forest, upper montane forest and páramo. Pollen assemblage composition, representation, diversity and palynological abundance in the modern pollen spectra of Behling traps, modified Oldfield traps, reference traps and soil samples were assessed in comparison to the vegetation. All sampling media showed distinguishable pollen spectra for each vegetation type. For the páramo, the most characterising taxa are Poaceae and Melastomataceae, accompanied by other, less frequent taxa such as Arcytophyllum, Valeriana and Ericaceae. The pollen spectrum of the upper montane forest is dominated by Melastomataceae, Hedyosmum and Weinmannia. The lower montane and premontane forests both have similar spectra, with high proportions of Moraceae/Urticaceae, Melastomataceae, Alchornea and Cecropia. Soil samples had a bias towards an over-representation of pollen and spore taxa with a thick exine, such as Poaceae, whereas taxa with fragile pollen grains, as Moraceae/Urticaceae, were represented to a lesser extent than in the pollen traps. Behling traps and modified Oldfield traps show similar patterns in taxa composition, pollen accumulation rates and pollen taxa proportions, as well as in representation of pollen spectra in comparison with the vegetation. However, especially in the páramo samples, modified Oldfield traps were disintegrated after one year in the field, due to temporarily dry and windy conditions, as well as strong radiation. We therefore recommend the use of Behling traps for the collection of modern pollen rain in areas with open vegetation, which are subjected to drought periods and strong radiation. In forested areas, modified Oldfield and Behling traps show similar results.

1. Introduction

The understanding of the modern pollen rain–vegetation relationship is crucial for a comprehensive analysis of processes and patterns of past ecosystem and climate dynamics using pollen data. The study of modern pollen rain–vegetation relationships has had a long and diverse history which started off in Europe in the 19th century (Giesecke et al., 2010). The establishment of the European pollen monitoring programme resulted in the development of increasingly advanced and more comprehensive studies on modern pollen rain (Hicks et al., 1996). In Europe, Tauber traps (Tauber, 1974) are the most commonly used pollen rain collectors and serve in their modified

way as a standardised model in the European pollen monitoring programme (http://www.pollentrapping.net, e.g. Hicks et al., 2001). In the Neotropics, investigations into modern pollen–vegetation relationships started off in the 1970s (Flenley, 1973; Salgado-Labouriau, 1979). However, in the tropics, the quantity of heavy rainfall in some regions meant that Tauber traps were inappropriate for trapping due to flooding, and the incapability to cope with large quantities of water (Flenley, 1973).

Therefore, Tauber traps were rejected as a standard pollen trap model in very humid areas, where the Oldield trap (Flenley, 1973) and later the Behling trap (Behling, et al., 2001) became frequently used trap types.

In 1973, Flenley first published data on modern pollen rain from the tropics which was collected in a trap designed by Oldfield. It consisted of a plastic funnel with a Whatman GF/B glass filter attached to it. The filter was covered by de-oiled acetate yarn and a mosquito net was placed over it to prevent bigger particles to fall in. The trap was put

onto a conical flask which was filled by distilled water to assure a good moisture-balance. This model of the Oldfield trap has been modified by Bush (1992) who used viscose rayon staple instead of de-oiled acetate yarn, as it is more easily purchased and is dissolved during standard lab procedures and replaced the conical flask by a bottle with drain holes near the top (Fig. 1b). Gosling et al. (2003) further simplified the design by replacing the bottle by a stake. The modified Oldfield pollen trap is the most widespread pollen trap that has been used for assessing modern pollen rain of tropical rainforests in Panama and Costa Rica (Bush and Rivera, 1998, 2001; Bush, 2000), as well as mountain rainforest and páramo vegetation in northern Ecuador (Olivera et al., 2009), rainforest, savannah, and dry forest ecosystems in Amazonia (Bush et al., 2001; Gosling et al., 2005, 2009; Burn et al., 2010; Jones et al., 2011), and pollen diversity of habitats on the Galapagos islands (Collins and Bush, 2010).

A second model of a pollen trap used for the study of pollen rain in tropical environments was developed by Behling and first published in 2001 (Behling et al., 2001). It consists of a plastic tube which is filled with synthetic cotton and liquid glycerol and covered by a mosquito net (Fig. 1a). It has served for the analysis of modern pollen rain in the tropical mountain rainforest of South Ecuador (Niemann et al., 2010, Jantz et al., submitted for publication), Panama, Colombia, and Brazil (Behling, unpublished).

Modern pollen rain analyses from the temperate zone demonstrated that different sampling media may affect taxonomic composition of pollen spectra and their proportions on a noteworthy level, especially when looking at the differences between moss or soil samples and pollen traps. Studies from the temperate regions have mostly assessed the differences in pollen recording of moss samples and Tauber traps (Cundill, 1991; Fall, 1992; Pardoe et al., 2010; Lisitsyna et al., 2011). Cundill (1991) observed that moss records the modern pollen rain in a different way than do the Tauber traps. He concluded that the lack in precision of sampling and variability in moss growth and sedimentation rates are responsible factors. Fall (1992) discovered that moss polsters and Tauber traps both record the local vegetation more accurately than do lake surface sediments. He further detected that moss polsters collect higher amounts of Pinaceae pollen, whereas in the Tauber traps, pollen of insect pollinated plants is increased, possibly due to the introduction of insects into the traps. Similar findings were reported by Lisitsyna et al. (2011). They found a bias towards higher percentages of shrubs, herbs and Cyperaceae and lower values of tree pollen in the Tauber traps. Pardoe et al. (2010) discovered that moss samples correspond best to pollen deposition of two or more years in the pollen traps. They stated that pronounced regional differences occur.

However, because of other environmental conditions, floristic differences and different pollen production patterns in tropical taxa, these studies can only be very indirectly compared to tropical modern pollen rain collection.

Also, many times, soil samples are analysed instead of moss polsters, due to the lack of terrestrial mosses in some ecosystems (Wilmshurst and McGlone, 2005; Ortuño et al., 2011).

Studies comparing the pollen collection characteristics of different trapping media in the tropics are scarce and different trap types have never been compared to each other. Olivera et al. (2009) compared modified Oldfield traps to moss samples in the páramo of northern Ecuador. However, their approach was different, as for one moss sample at least 10 subsamples were mixed to obtain a broader picture of the surrounding vegetation.

In this study, we provide the first assessment of modified Oldfield traps and Behling traps, which are the two pollen trap models most frequently used for the analysis of modern pollen rain spectra in tropical humid environments. Furthermore, we include an assessment of soil samples and reference traps to give a comprehensive overview of the similarities and differences of diverse sampling media for modern pollen rain composition and its proportional distribution in the Andean mountain vegetation of South Ecuador. We selected sites along an altitudinal gradient from ca. 1000 m a.s.l. to ca. 3300 m a.s.l. to cover the wide range of vegetation types, including premontane forest, lower montane forest, upper montane forest and páramo. All of these vegetation types are of substantial importance for palaeoecological studies that deal with the long-term forest dynamics of the northern to central Andes region. We especially focused on the páramo, as this region has received comparably little attention in terms of annual pollen rain collection, but is at the same time of major importance for the recording of past environmental changes of the high Andes region (e.g. Hansen et al., 2003; Brunschön and Behling, 2009; Jantz and Behling, 2011).
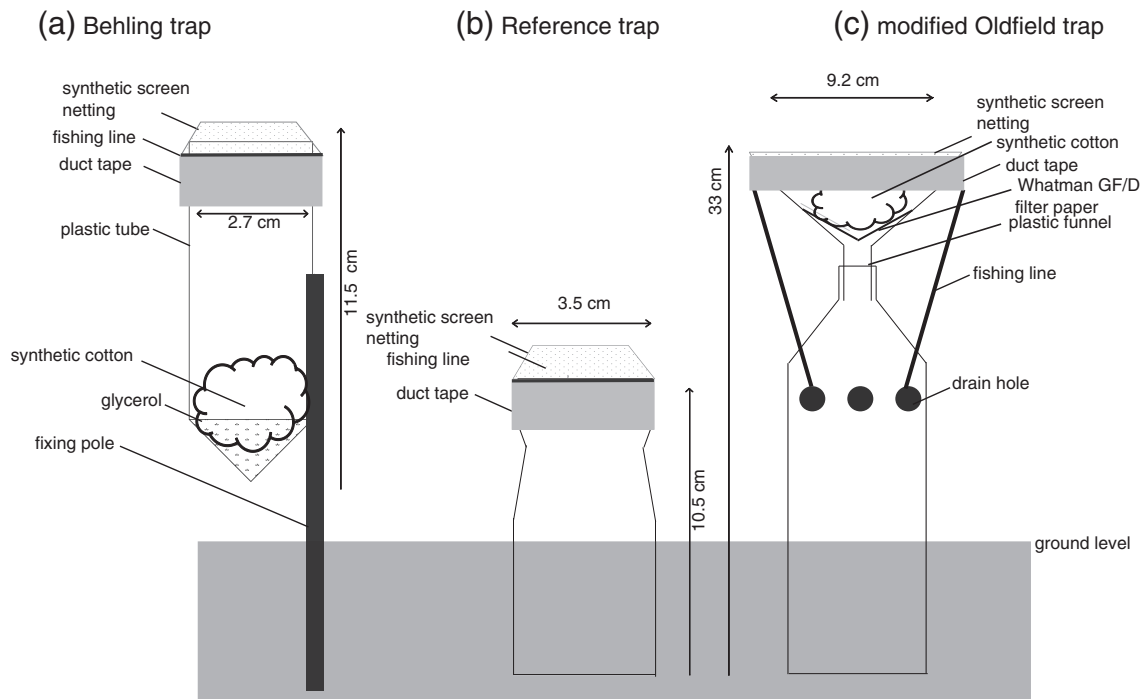

Fig. 1. Cross-sectional views of the three pollen traps used in this study. (a) Behling trap, (b) reference trap, (c) modified Oldfield trap (modified after Bush, 1992).

In this study, we focus on answering the following research questions:

1. To what extent do different pollen trap types and soil samples collect pollen rain in a different way and how is this reflected in the data?
2. Which pollen trap is most suitable for which tropical vegetation type?

2. Study sites

2.1. Climate

All sites are located in the area of the Podocarpus National Park and the San Francisco biological reserve in the provinces of Loja and Zamora–Chinchipe in the Eastern Andean Cordillera del Consuelo in South Ecuador (Fig. 2a). The study sites are located along an altitudinal gradient of ca. 2500 m. The altitudinal gradient translates to a climate range of 0.61 °C per 100 m elevation (Bendix et al., 2008), and ca. 2000 to up to more than 6000 mm pa precipitation (Bendix et al., 2006). The climate of the research area is in general tropical humid with a wet season occurring from April to July and a slightly drier season from September to December (Bendix et al., 2006; Emck, 2007). The wind system is dominated by the tropical trade winds with strong easterlies throughout the year (Beck et al., 2008). However, local climatic conditions may differ due to microclimatic influence caused by topography.

2.2. Vegetation

There are four vegetation types encompassed by the transect: 1) Páramo, 2) Upper montane forest, 3) Lower montane forest and 4) Premontane forest.

2.2.1. Premontane forest (PMF)

The lowermost site, Bombuscaro, is situated at 900–1100 m a.s.l. It is covered by premontane forest (PMF), with tall trees reaching heights of up to 40 m. The most common tree families are Fabaceae, Melastomataceae, Moraceae, Myristicaceae, Rubiaceae and Sapotaceae (Homeier et al., 2008).

2.2.2. Lower montane forest (LMF)

The lower montane forest (LMF) at 1900–2100 m a.s.l. (San Francisco) is covered by trees of up to 22 m height. Here, tree species of the families

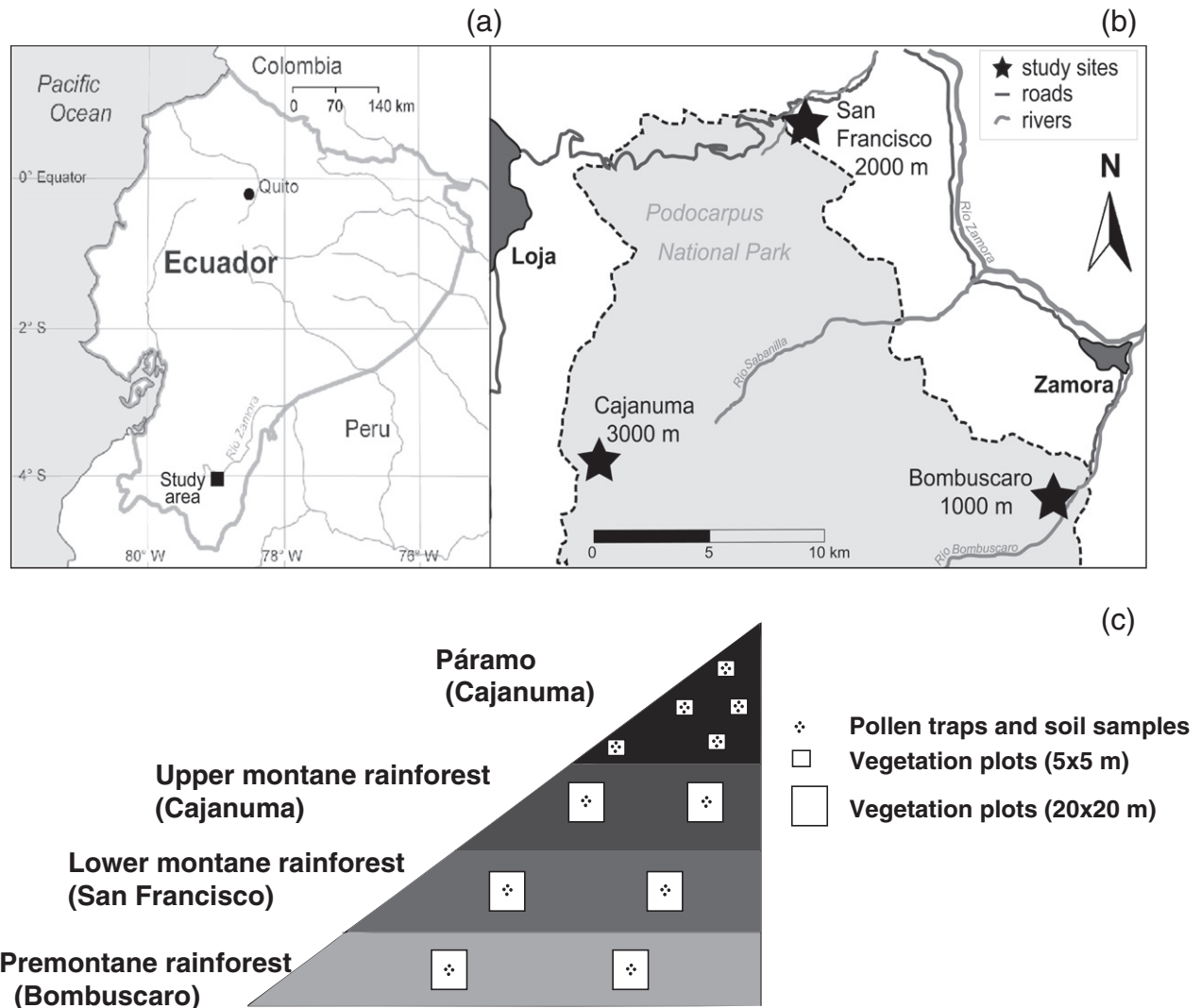**Fig. 2.** (a) Ecuador and the location of the study area. (b) Location of the study sites in the study area. (c) Sampling design of the experiment. We established five 25 m² plots on the páramo-sites and two 400 m² plots on each of the forested sites of upper montane forest, lower montane forest and premontane forest. We distributed one trap of each type in the centre of each plot and collected soil samples close to the traps.

Euphorbiaceae, Lauraceae, Melastomataceae and Rubiaceae dominate the vegetation (Homeier et al., 2008).

2.2.3. Upper montane forest (UMF)

Characteristic arboreal families of the upper montane forest (UMF) at Cajanuma (2800–2900 m a.s.l.) are Aquifoliaceae, Clusiaceae, Cunoniaceae, Lauraceae and Melastomataceae (Homeier et al., 2008). The trees at this altitude do not grow higher than 8–10 m.

2.2.4. Páramo

The uppermost site is the páramo (PAR) at Cajanuma, which is situated above the upper forest line, which is defined as the present limit of tree occurrence. It is dominated by herbs and small shrubs up to 1 m. The most important plant families of this vegetation type are Poaceae, Asteraceae, Ericaceae, Bromeliaceae, and Rosaceae, as well as Hypericaceae and Rubiaceae. Another important feature of this vegetation type is the abundance of Bryophytes (up to 40% cover in the vegetation plots).

3. Methods

3.1. Vegetation analysis

For the forested sites at PMF, LMF and UMF plots of a size of 20 × 20 m were established. All tree species with a DBH (diameter at breast height) ≥ 5 cm were recorded. For the páramo sites, plots were smaller with a size of 5 × 5 m, as here, plant composition changes on a much smaller scale. Here, all vascular plant species were identified and their abundance (% of the total coverage) was recorded. For mosses and bare soil, total coverage was documented. For family classification, we followed (APG (= The Angiosperm Phylogeny Group) III, 2009).

3.2. Pollen trap design and sampling

We distributed three different types of pollen traps in the field for one year from October 2010 to October 2011 (see Fig. 2c and Table 1 for details). The trap models used were: 1) Modified Oldfield traps (Fig. 1c), 2) Behling traps (Fig. 1 a) and 3) reference traps (Fig. 1 b). All three pollen trap types were distributed next to one another in the middle of each plot. Additionally, for each plot a soil sample was taken close to the traps to record the pollen composition of the surface soil.

3.2.1. Modified Oldfield traps

The first pollen trap model was the modified Oldfield trap developed by Bush (1992), which has been used extensively in pollen rain studies throughout the Neotropics. It consists of a Whatman filter as a pollen collector which is glued to a plastic funnel with a diameter of 9.2 cm. For additional pollen collection, rayon fibre is placed onto the filter. The trap is attached to a bottle with holes in it to ensure the water-outflow, and covered by a screen mesh for protection against smaller animals and litter.

3.2.2. Behling traps

The second pollen trap model was developed by Behling (Behling et al., 2001, see also Niemann et al., 2010 and, more detailed, Jantz et al., submitted for publication). For this trap, rayon fibre is placed into a plastic tube with a diameter of 2.7 cm. The tube is then filled with about 5 ml of liquid glycerol. This medium has a higher density than water and thus creates a separate liquid phase at the bottom of the tube. Therefore, during heavy rainfalls, water can flow out over the top of the tube, without removing the pollen which is trapped in the glycerol and synthetic rayon fibre. For protection against smaller animals and litter the trap is covered by a screen mesh.

3.2.3. Reference traps

The third pollen trap type was a reference to record the effect of not using a specific pollen collector tool such as synthetic cotton or filters. This trap consisted of a plastic bottle with an opening diameter of 3.5 cm which was dug into the ground and covered by a screen mesh to protect it against smaller animals and litter.

3.3. Pollen analysis

Pollen was extracted from the Behling traps and from the reference traps by centrifuging and sieving the samples. Afterwards, acetolysis was carried out on the samples to dissolve cellulose material and to stain the pollen residues. For the modified Oldfield traps and the surface-samples, HF-treatment was applied to the samples before acetolysis. For the calculation of concentration values and pollen accumulation rates, three tablets of $20,848 \pm 1546$ exotic *Lycopodium clavatum* spores were added to each sample (with the exception of the Behling traps of the PMF, where only two tablets were used). Samples were counted to a minimum of 300 pollen grains. However, samples with a very high pollen concentration were counted to a minimum of 100 *Lycopodium* spores to ensure the reliability of concentration values and pollen accumulation rates (see Maher, 1981). Spores were excluded from the pollen sum. For pollen determination, we used the reference collections of Ecuador and Brazil of the Department of Palynology and Climate Dynamics, University of Göttingen. Furthermore, we used literature (Hooghiemstra, 1984; Roubik and Moreno, 1991; Colinvaux and De Oliveira, 1999) and the electronic pollen keys of Ecuador, southern Brazil (Department Palynology and Climate Dynamics, Göttingen) and the Neotropics (Bush and Weng, 2007).

3.4. Data analysis

Pollen diagrams were obtained using the programmes TILIA and TILIAGRAPH (Grimm, 1987). We calculated Euclidean distances for the species abundance in the studied vegetation types (basal area

Table 1
Geographical location, size, and dates of pollen trap distribution as well as recollection for the study sites.

Location (vegetation)	Position	Date distributed	Date recollected	UTM 17 M coord. (N)	UTM 17 M coord. (E)	m a.s.l.	Plot area (m²)
Cajanuma	Slope 1	14.10.2010	16.10.2011	9543944	704434	3224	25
(páramo)	Slope 2	14.10.2010	16.10.2011	9543993	704330	3244	25
	Valley 1	14.10.2010	16.10.2011	9543888	704335	3237	25
	Valley 2	14.10.2010	16.10.2011	9543919	704330	3238	25
	Valley 3	14.10.2010	16.10.2011	9543941	704360	3240	25
Cajanuma	Upper slope 3	10.10.2010	14.10.2011	9545640	702192	2869	400
(UMF)	Mid-slope 4	10.10.2010	14.10.2011	9545040	702595	2900	400
San Francisco	Upper slope 3	03.10.2010	20.10.2011	9560140	713666	2089	400
(LMF)	Lower slope 2	02.10.2010	20.10.2011	9560310	713655	1993	400
Bombuscaro	Upper slope 3	06.10.2010	12.10.2011	9544990	725729	1072	400
(PMF)	Lower slope 2	06.10.2010	12.10.2011	9544600	725315	1069	400

of trees for the UMF, LMF and PMF plots and percentage of total vegetation cover for the páramo samples) compared to the pollen percentage values for selected taxa, as well as the individual-based rarefaction (Krebs, 1989) for a sum of 280 counted pollen grains with the programme PAST (Hammer et al., 2001). This method is used for the comparison of taxa diversity between different sites at a specified number of individuals encountered. Furthermore, we carried out a PCA for the data of each vegetation type using CANOCO and CanoDraw (terBraak and Šmilauer, 2002). Before doing so, we first carried out a DCA to determine the length of the environmental gradient, which measures the beta diversity in community composition of our datasets (terBraak and Šmilauer, 2002). As it was lower than 2.5 for each dataset analysed, we could assume that the taxa responses correspond to a linear model and chose principal components analysis (PCA). For the PCA, we used relative pollen abundance data of all taxa which were present with least one value of 0.6% in the specific vegetation type. We did not transform or weigh the data further. We centred for species and samples. Only the species with a fit of > 50% are shown in the diagram.

3.5. Association and representation indices

For the calculation of association (A), over-representation (O) and under-representation (U) indices which compare pollen and plant presence–absence data, we used the following equations which were first described by Davis (1984):

$$A = B0/(P0 + P1 + B0)$$
$$U = P1/(P1 + B0)$$
$$O = P0/(P0 + B0).$$

With B0 being the number of samples where the pollen type is present in both the pollen sample and the associated vegetation plot, P0 as the number of samples where the taxon is present in the pollen sample but not in the associated vegetation plot and P1 as the number of samples where the taxon is only present in the vegetation plot. We calculated these indices separately for each sampling medium (Behling trap, modified Oldfield trap, Reference trap and soil sample) and each vegetation type (páramo, UMF, LMF, and PMF).

4. Results

4.1. Pollen diagrams

The percentage pollen diagram of the most abundant taxa is shown in Fig. 3. The different vegetation types of páramo, UMF, LMF and PMF are each dominated by characteristic pollen assemblage composition and palynological abundance. In the páramo, herb taxa characterise the vegetation. Herb taxa frequently found in the pollen rain of all traps as well as in the soil samples are Poaceae (10–70%), *Arcytophyllum* type, *Valeriana*, *Huperzia*, *Baccharis* type and Cyperaceae. Furthermore, shrubs that occur in the local vegetation are recorded in the pollen rain. These include *Acalypha*, *Myrica*, Melastomataceae, *Weinmannia*, and *Myrsine*. However, other taxa, which do not occur as plant in the páramo but in adjacent vegetation zones contribute to a great extent to the total pollen rain of the páramo samples, such as Moraceae/Urticaceae (up to ~40%), *Hedyosmum*, *Alnus* and Podocarpaceae. In general, all pollen trapping media show the same tendencies regarding species composition and percentage values of important pollen taxa. However, some marked differences are visible especially when comparing the soil samples to the pollen trap samples. In the pollen spectra of the soil samples, Poaceae show almost exceptionally higher percentage values than in the corresponding trap samples, whereas values of Moraceae/Urticaceae are lower in the former. For all other taxa, this is not the case. In the pollen spectra of the modified Oldfield traps, Moraceae/Urticaceae also show slightly

lower values, but instead of Poaceae Melastomataceae are increased in their percentages. The pollen accumulation rates of the pollen rain for pollen traps of the páramo (Fig. 4) are generally lower than those of the traps which were distributed in forested vegetation. Maximum values reach ca. 6500 grains cm^{-2} year^{-1}, but 12 of the 15 traps distributed collected between 1000 and 3000 grains cm^{-2} year^{-1}. Most of the grains derive from trees and shrubs, whereas herbs only contribute comparatively little to the pollen accumulation rate in the páramo. Concerning the most important taxa, values of the different trap types do not vary significantly, however some marked differences are visible when looking at the values of important taxa, such as Melastomataceae, *Hedyosmum* and Moraceae/Urticaceae. The Behling traps show higher pollen accumulation rates than the other two trap types for Moraceae/Urticaceae, whereas the modified Oldfield traps often show the highest pollen accumulation rates in general.

Characteristic taxa for the modern pollen rain of the UMF are forest taxa which are common in the local vegetation, such as Melastomataceae, *Hedyosmum*, *Weinmannia*, *Clusia* type, Podocarpaceae, *Myrica*, *Ilex*, and *Myrsine*. However, also here, non-arboreal taxa and taxa that do not occur in the local vegetation are found in the pollen spectra. These include Poaceae, *Alnus*, and Moraceae/Urticaceae. Soil samples show the same deviations in the páramo with lower percentages of Moraceae/Urticaceae but higher percentages of Poaceae than were recorded in the corresponding pollen traps. Pollen accumulation rates are considerably higher in the UMF than in the páramo, with values ranging from ca. 3500 grains cm^{-2} year^{-1} to about 11,000 grains cm^{-2} year^{-1}. The pollen accumulation rates of the most important taxa do not vary to a great extent (maximum variation found about 3300 grains cm^{-2} year^{-1} for Melastomataceae, compared to changes of up to 4500 grains cm^{-2} year^{-1} for the same taxon in the LMF) in the different trap types. However, as can be seen for the pollen accumulation rate of Poaceae in the reference trap of UMF US 3, single taxa sometimes bias the data.

In the LMF, pollen spectra mainly consist of tree taxa such as Melastomataceae, Moraceae/Urticaceae, *Hedyosmum*, *Myrsine*, Myrtaceae, Podocarpaceae, *Hieronyma*, *Alchornea* type, *Cecropia*, and Piperaceae. Fern spores of different species of *Cyathea*, as well as various taxa of monolete psilate spores reach highest values in this vegetation zone. Unlike in samples of the páramo or the UMF, pollen composition changes greatly from one sample to the next. However, within one site, all pollen sampling media record approximately the same pollen spectrum. The soil sample of LMF LS 2 is greatly biased towards a greater abundance of fern spores. The total pollen accumulation rates of the pollen traps from the LMF vary between ca. 3000 and ca. 20,000 grains cm^{-2} year^{-1}. Here, values of particular taxa are greatly increased in single samples (e.g. *Weinmannia* in the modified Oldfield trap of LMF LS 2). However, the general tendency seems to be the same for most of the taxa and traps.

The pollen spectra of the PMF samples are represented by few taxa which reach high percentages, such as Moraceae/Urticaceae with values of up to 70% and Melastomataceae (up to ca. 30%), and taxa with lower values, such as *Hedyosmum*, *Alchornea* type, *Cecropia*, Piperaceae, Rubiaceae type 1, Burseraceae, and different fern spores, such as *Cyathea* spore morphotypes verrucate and psilate, as well as by monolete psilate and verrucate fern spores <50 μm. Percentage values of different sampling media remain rather consistent within one plot. Pollen accumulation rates vary between ca. 10,000 and ca. 26,000 grains cm^{-2} year^{-1} for samples of the PMF, mostly due to a very high pollen accumulation rate of Moraceae/Urticaceae, which reach values of between 5000 and 20,000 grains cm^{-2} year^{-1}. The pollen accumulation rates of herbs are low in this vegetation type, with maximum values below 500 grains cm^{-2} year^{-1}. As in the different traps of the LMF, also here pollen accumulation rates of some taxa are increased in single traps, as for example Moraceae/Urticaceae in the reference trap of PMF-US 3.
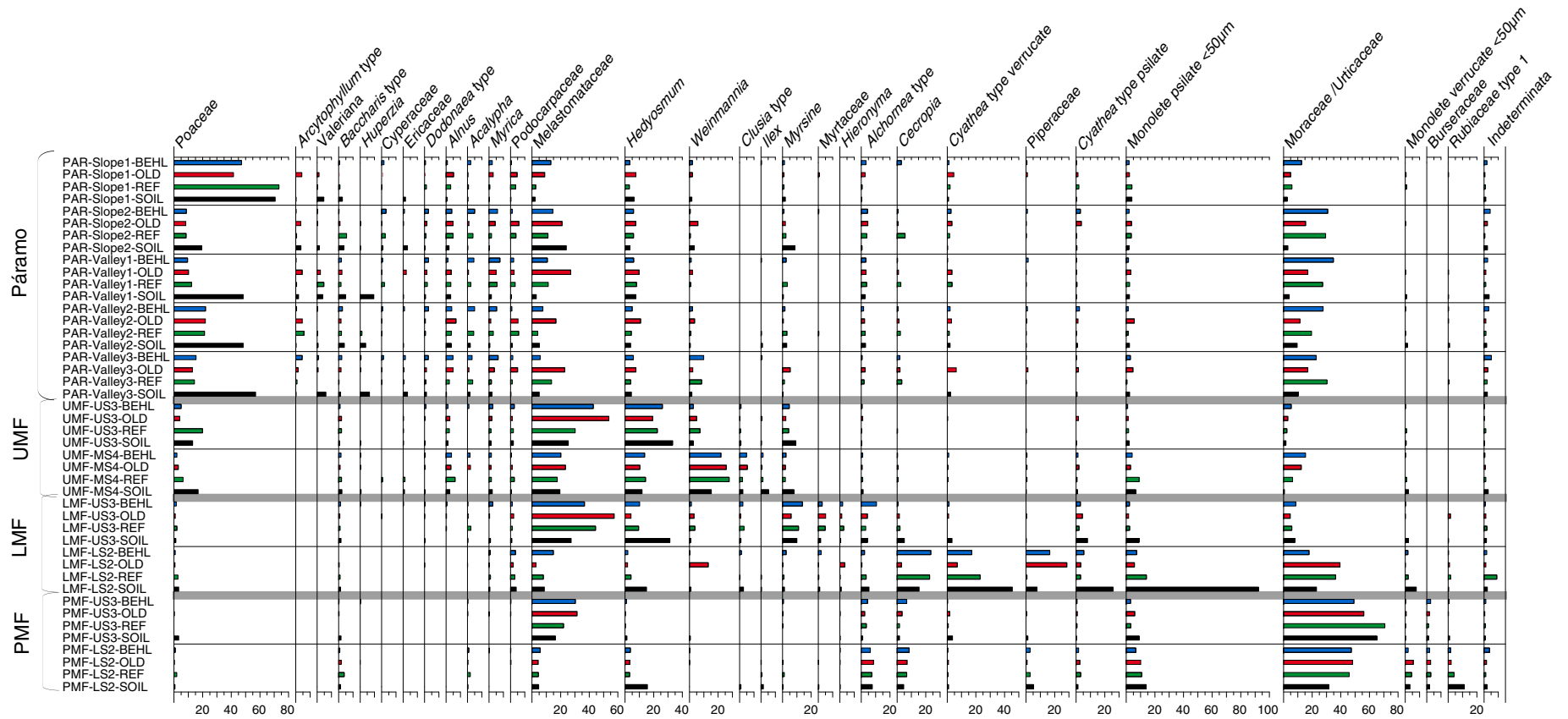
Fig. 3. Pollen percentage diagram for the most important pollen and spore taxa from the different vegetation types. PAR — páramo, UMF — upper montane forest, LMF — lower montane forest, PMF — premontane forest, BEHL — Behling trap, OLD — modified Oldfield trap, REF — reference trap, SOIL — soil sample.
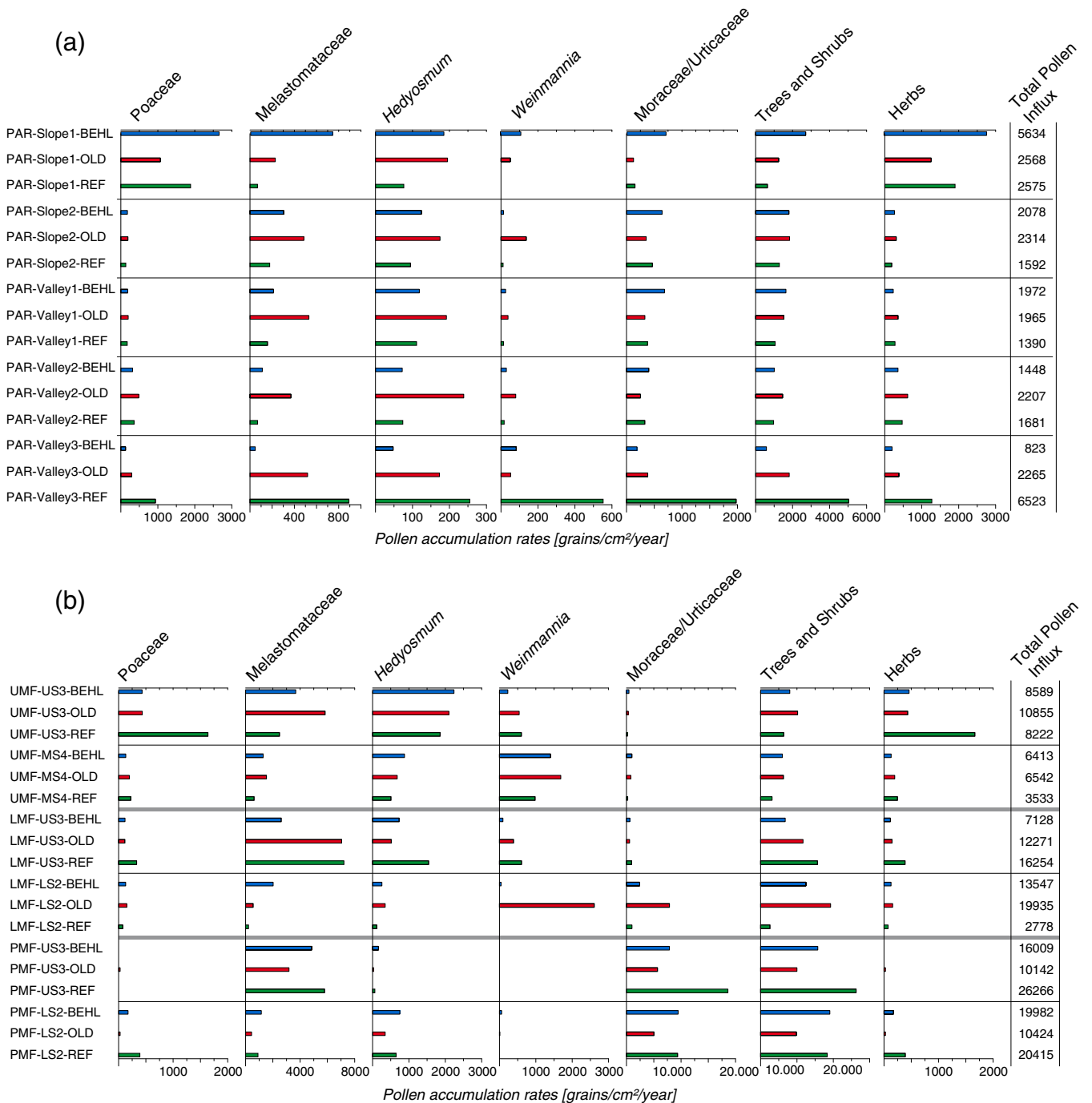
(a)

(b)

Fig. 4. Pollen accumulation rates for the 5 most important pollen taxa across all of the studied vegetation types of (a) Páramo and (b) UMF, LMF and PMF. PAR — páramo, UMF — upper montane forest, LMF — lower montane forest, PMF — premontane forest, BEHL — Behling trap, OLD — modified Oldfield trap, REF — reference trap, SOIL — soil sample. Note the different scales.

4.2. Multivariate data analyses

The PCAs of the different sampling media for every vegetation type are shown in Fig. 5. For the samples of the páramo, differences in the pollen spectra of the sampling media account for most of the gradient. Most modified Oldfield traps are located close to one another and correlate with higher values of Melastomataceae. The Behling traps and the reference samples correlate to a similar extent to one another and to Moraceae/Urticaceae, *Acalypha*, *Myrica* and *Dodonaea* type. The soil samples in general, as well as the samples of Slope 1, correlate positively with the abundance of Poaceae.

The analyses of taxa from the forested vegetation zones show a different pattern. Here, the location of the sample is more important and, the x-axis accounts for the gradient which is created by the difference in pollen composition of the specific samples within one vegetation type.

For the UMF, samples from US 3 are separated from the ones of MS 4. The former correlate well with Melastomataceae and *Hedyosmum*, whereas the latter correspond positively to the abundance of Piperaceae, *Clusia* type, *Alnus*, Cyatheaceae, Moraceae/Urticaceae and *Weinmannia*. Here, Behling trap samples and modified Oldfield trap samples correlate well with each other, whereas the distance of the former to the soil samples is bigger. These correlate well with Poaceae, *Myrsine*, and *Symplocos*.
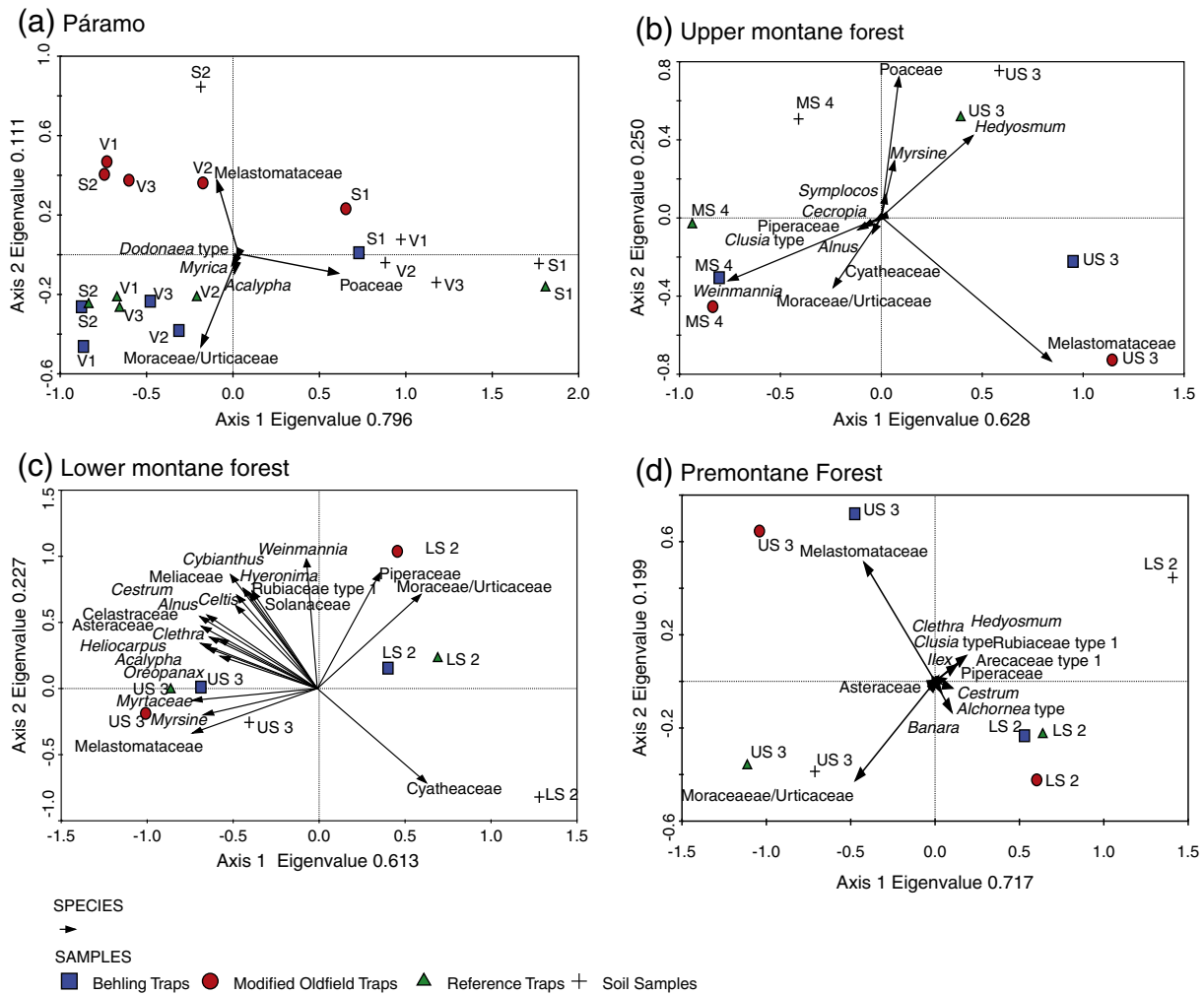
Fig. 5. PCAs of pollen and plant data for the different vegetation types. (a) Páramo; (b) upper montane forest; (c) lower montane forest; (d) premontane forest. S — slope, V — valley, LS — lower slope, MS — mid-slope, US — upper slope.

The PCA of samples from the LMF shows that samples of US 3 correlate positively with the abundance of Melastomataceae, *Myrsine*, and Myrtaceae, whereas the ones of LS 2 show a higher correlation to Piperaceae and Moraceae/Urticaceae. The soil sample of this plot shows a positive response to the abundance of Cyatheaceae.

For the PMF, samples show a different pattern. The samples of US 3 spread over a large gradient on the y-axis, which is determined by the positive correlation of both the Behling and the modified Oldfield trap with Melastomataceae on the one side and the positive correlation to Moraceae/Urticaceae of the soil and the reference sample on the other side. For the samples of LS 2, the Behling trap as well as the reference trap and the modified Oldfield trap samples correlate positively to higher abundance of *Cestrum*, *Alchornea* type, and *Banara*, whereas the soil sample responds to a higher affinity to *Hedyosmum*, Arecaceae type 1, Rubiaceae type 1, and Piperaceae.

4.3. Indices of association and representation and diversity

The comparison of indices of association and representation per collection medium for the most important taxa of each vegetation zone are seen in Table 2a–d. Only the most characteristic taxa with high scores that had values of at least 2% in the vegetation or pollen data are shown. Many times, the association indices of one taxon are the same for all sampling media. Generally, very few taxa are

strongly associated taxa which can be found to an equal extent in the vegetation as well as in the modern pollen spectra. These are often taxa which are wind-pollinated and/or abundant in the vegetation of the specific vegetation type, as for example Melastomataceae for LMF, UMF and páramo, and Moraceae/Urticaceae for PMF and LMF. Under-represented taxa in the pollen spectra are often insect-pollinated and/or not frequent, such as *Licania* or Sapotaceae in the PMF samples, Annonaceae, *Gordonia*, *Tabebuia* or *Alzatea* in the LMF samples, Celastraceae or *Symplocos* in the UMF samples or *Xyris* and *Hypericum* in the páramo samples. The same is true for generally fragile and easily destroyable pollen grains such as the ones of Lauraceae. Very abundant taxa that are over-represented in the pollen rain are often light grains which belong to wind-pollinating species, such as Piperaceae, *Cecropia*, Moraceae/Urticaceae, *Acalypha* or Poaceae. Not all of the trapping media recorded the representation indices in the same way. This is especially conspicuous in the soil samples, which frequently show differences in comparison to the other traps. Some taxa are either especially under-represented or not over-represented in the soil samples. These are Lauraceae in the PMF, *Alnus* in the LMF, *Acalypha* and *Cecropia* in the UMF, and Cyperaceae, Lauraceae as well as *Cecropia* in the páramo samples. The same is true for some taxa in the reference samples, such as Ericaceae in the páramo, *Acalypha* and Celastraceae in the UMF, and *Hieronyma* in the PMF. For the Behling and modified Oldfield traps, similar patterns of under-representation can be observed, but mostly

with taxa that are not very abundant in the corresponding pollen spectrum and/or vegetation type.

The results of the individual-based rarefaction (N = 280 counted pollen grains) of mean values for every type of vegetation and sampling medium with their standard deviation can be seen in Fig. 6.

The values do not differ to one another to a significant extent. However, for the páramo, the Behling traps and the modified Oldfield traps show a higher pollen type richness than the reference traps and the soil samples whereas in the other vegetation types, soil samples tend to have the highest diversity.

Table 2

a–d. Association and representation indices after Davis (1984) for important pollen taxa that are abundant in either pollen rain or vegetation for the different vegetation types: (a) premontane forest; (b) lower montane forest; (c) upper montane forest; (d) páramo. Data for premontane, lower montane and upper montane forests are based on two traps of each type, whereas for the páramo, we used five traps of each type for the calculations. A = association, U = under-representation and O = over-representation, Behl = Behling trap, Old = modified Oldfield trap, Ref = reference trap, Soil = soil sample. Values over 0.5 are shaded in light grey, values over 0.7 are shaded in dark grey.

(a) Premontane forest

	A				U				O			
	Behl	Old	Ref	Soil	Behl	Old	Ref	Soil	Behl	Old	Ref	Soil
Arecaceae	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Burseraceae	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hieronyma	1.0	0.5	0.0	0.5	0.0	0.0	1.0	0.0	0.0	0.5	0.0	0.5
Lauraceae	1.0	1.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0
Melastomataceae	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Moraceae/Urticaceae	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Licania	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
Sapotaceae	0.0	1.0	0.0	0.0	1.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0
Hedyosmum	0.5	0.5	0.5	0.5	0.0	0.0	0.0	0.0	0.5	0.5	0.5	0.5
Alchornea type	0.3	0.3	0.3	0.3	0.0	0.0	0.0	0.0	0.7	0.7	0.7	0.7
Asteraceae	0.3	0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.7	0.7	1.0	0.7
Ilex	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Poaceae	0.0	0.3	0.0	0.3	0.0	0.0	0.0	0.0	1.0	0.7	1.0	0.7

(b) Lower montane forest

	A				U				O			
	Behl	Old	Ref	Soil	Behl	Old	Ref	Soil	Behl	Old	Ref	Soil
Alchornea type	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Moraceae/Urticaceae	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hieronyma	1.0	0.5	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.5	0.5	0.5
Lauraceae	1.0	0.5	1.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	1.0
Piperaceae	1.0	0.5	1.0	0.5	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.5
Weinmannia	0.5	0.5	1.0	0.5	0.0	0.0	0.0	0.0	0.5	0.5	0.0	0.5
Alzatea	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
Annonaceae	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
Gordonia	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
Tabebuia	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
Acalypha	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.7
Alnus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.0
Myrica	0.3	0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.7	0.7	1.0	0.7
Myrsine	0.3	0.3	0.3	0.3	0.0	0.0	0.0	0.0	0.7	0.7	0.7	0.7
Melastomataceae	0.5	0.5	0.5	0.5	0.0	0.0	0.0	0.0	0.5	0.5	0.5	0.5
Myrtaceae	0.5	0.5	0.5	0.5	0.0	0.0	0.0	0.0	0.5	0.5	0.5	0.5
Hedyosmum	0.5	0.5	0.5	0.5	0.0	0.0	0.0	0.0	0.5	0.5	0.5	0.5

Table 2 (*continued*)

(c) Upper montane forest

	A				U				O			
	Behl	Old	Ref	Soil	Behl	Old	Ref	Soil	Behl	Old	Ref	Soil
Melastomataceae	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Myrsine	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oreopanax	1.0	1.0	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0
Podocarpaceae	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Weinmannia	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ilex	0.5	1.0	0.5	1.0	0.5	0.0	0.5	0.0	0.0	0.0	0.0	0.0
Lauraceae	0.3	1.0	0.5	0.3	0.7	00	0.5	0.7	0.0	0.0	0.0	0.0
Celastraceae	0.5	0.0	0.0	1.0	0.0	1.0	1.0	0.0	0.5	0.0	0.0	0.0
Symplocos	0.3	0.3	0.5	1.0	0.7	0.7	0.5	0.0	0.0	0.0	0.0	0.0
Hedyosmum	0.5	0.5	0.5	0.5	0.0	0.0	0.0	0.0	0.5	0.5	0.5	0.5
Clusia type	0.5	0.5	0.5	0.5	0.0	0.0	0.0	0.0	0.5	0.5	0.5	0.5
Acalypha	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.0	0.0	0.0
Clethra	0.3	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.7	1.0	0.7	0.7
Cecropia	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.7	0.0
Cybianthus	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.7
Piperaceae	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.7	1.0

(d) Páramo

|	A				U				O			
	Behl	Old	Ref	Soil	Behl	Old	Ref	Soil	Behl	Old	Ref	Soil
Asteraceae	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Melastomataceae	0.7	0.8	0.8	0.8	0.0	0.0	0.0	0.0	0.3	0.2	0.2	0.2
Cyperaceae	0.8	0.8	0.8	0.3	0.0	0.0	0.0	0.8	0.2	0.2	0.2	0.0
Valeriana	0.2	0.8	0.5	0.6	0.7	0.0	0.3	0.0	0.7	0.3	0.3	0.4
Ericaceae	0.6	0.6	0.2	1.0	0.4	0.4	0.8	0.0	0.0	0.0	0.0	0.0
Arcytophyllum type	0.4	0.6	0.4	0.6	0.3	0.0	0.3	0.0	0.5	0.4	0.5	0.4
Eriocaulaceae	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
Xyris	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
Hypericum	0.3	0.0	0.0	0.5	0.7	1.0	1.0	0.3	0.0	1.0	1.0	0.3
Acalypha	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0
Alchornea type	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0
Myrsine	0.3	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.8	0.8	0.7	1.0
Alnus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0
Cecropia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.0
Celtis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0
Dodonaea type	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0
Hedyosmum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0
Lauraceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.0
Moraceae/Urticaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0
Myrica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0
Podocarpaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0
Weinmannia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0
Theaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	1.0
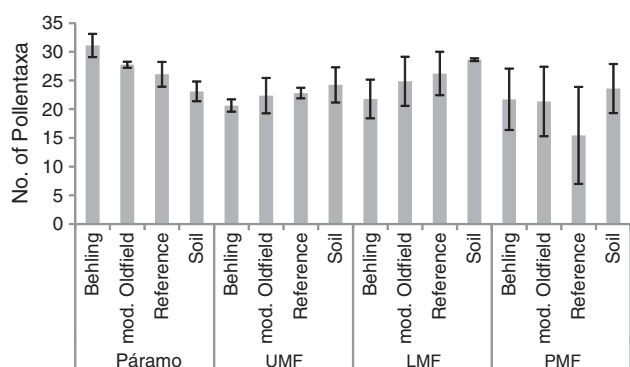
Fig. 6. Individual-based rarefaction data (Krebs, 1989) for the medium pollen and spore taxa diversity of each vegetation type and for each trapping medium. The calculation is based on N = 280 counted pollen and spore grains. The error bars are standard deviations.

5. Discussion

The different sampling media, Behling traps, modified Oldfield traps, reference traps and soil samples, all recorded similar patterns in the modern pollen rain spectra of the different vegetation types of páramo, UMF, LMF, and PMF. However, some marked differences between the results of the sampling media which were revealed by different analyses are discussed below.

5.1. To what extent do different pollen trap types and soil samples collect pollen rain in a different way and how is it reflected in the data?

All sampling media roughly represent the same pollen composition for each of the sites. However, abundances sometimes vary between the sampling media. The most striking differences can be seen between the pollen traps and the soil samples. This is due to several factors which determine pollen abundance in a sample. The first reason is that soil samples collect pollen for an unknown amount of time. Unlike in all of the traps, where pollen rain has been collected for exactly one year and thus all data refer to this year, soil samples collect pollen for several to many years, depending on the sedimentation rate. Unfortunately, the exact time a soil sample covers cannot be determined with certainty. Therefore, a soil sample may not only capture the pollen composition and abundance of the given vegetation at the time the sample was collected, but may also contain information about past vegetation and its changes. This can have an effect in areas with bigger human influence, such as deforestation, logging of single tree taxa or burning. However, to our knowledge, this is not the case in our study region. On the other hand, soil samples, in comparison to pollen traps, do neither record annual production peaks nor periods of low pollen production which hinder an average overview of the pollen spectrum of an area or vegetation type, as it can be the case when collecting too few years of modern pollen rain in pollen traps (Hicks et al., 2001). The second reason for the different pollen composition and abundance in soil samples is the fact that fragile grains with a thin exine can get destroyed in soils due to mechanical or chemical corrosion (Wilmshurst and McGlone, 2005), and are thus not recorded anymore. Therefore, taxa such as Moraceae/Urticaceae, Acalypha, Cyperaceae, Cecropia and Lauraceae are always under-represented or less over-represented in the soil samples, whereas grains with a thick and stable exine, such as Cyatheaceae, Hedyosmum and some Poaceae are generally recorded with a higher abundance than in other sampling media, as seen by the representation indices, as well as in the pollen diagrams and the PCAs.

The sampling medium which shows the most similar pollen composition to the soil samples is the reference trap. Often, the reference samples record similar proportions of important taxa as the soil samples and also here, some taxa are less over-represented or sometimes

under-represented, as Ericaceae in the páramo, Acalypha and Celastraceae in the UMF, and Hieronyma in the PMF. As the reference sample has no trapping device such as synthetic cotton or a filter, pollen is simply collected in a bottle of water and can thus easily flow out during heavy rainfalls. This may especially affect pollen grains with a low fall speed, such as Moraceae/Urticaceae (with a fall velocity of c. 0.34–0.4 cm/s, cited after Holmes, 1994), which do not sink easily. Surprisingly, some of the reference traps still have the same or even higher pollen accumulation rates than the other traps. However, the reference samples collect pollen in a more random way, which can be seen by their position in the PCAs and by their percentages, which often lie between the soil samples and the other pollen trap types. Also, especially in the páramo, soil samples and reference traps have a lower number of recorded pollen taxa per 280 counted pollen grains than Behling and modified Oldfield traps. This may be explained by the formally mentioned fact of random pollen collection which results from a lack of specific trapping devices in these sampling media. Interestingly, soil samples show highest diversity values in the analysed forest types. This is, because Moraceae/Urticaceae, which dominate the modern pollen spectra of the traps especially in LMF and PMF are less over-represented in soil samples, which thus have an increased probability for the detection of rare taxa.

5.2. Which pollen trap is most suitable for which tropical vegetation?

The modified Oldfield and Behling traps are mostly closely related to one another when regarding pollen taxonomic composition and their proportions, as well as association and representation indices. However, in the páramo, this does not seem to be the case, as here, the pollen composition of the Behling traps is more similar to the reference traps, which is especially due to their positive correlation to Moraceae/Urticaceae, Acalypha, Myrica, and Dodonaea type. A possible reason which may explain this observation is the fact that in the páramo, environmental conditions to which the pollen traps are exposed are different than in the forested regions of tropical mountains. In both regions humidity is very high. Therefore, the Oldfield trap, which can handle very wet environmental conditions, is commonly used in tropical moist regions. Bush (1992) modified the Oldfield trap design so that a bottle with a drainage system was used instead of a conical flask. However, even though humidity in tropical regions may be very high during rainy periods, radiation increases with altitude (Bendix et al., 2008) and dry periods can occur. As Gosling et al. (2003) reported, a bottle which is attached to the Oldfield trap does not prevent the trap from drying out, so that using a simple stake would lead to the same results. This could be seen in our study as well. When the traps were recollected, many of them showed signs of disintegration and all of the modified Oldfield traps were dried out completely and the filter and cotton could only be recollected in pieces. This may explain why in these traps, the abundance of fragile grains such as Moraceae/Urticaceae and Acalypha is lower than in the Behling or reference traps, which can hold more water. However, pollen accumulation rates do not seem to have decreased greatly in the modified Oldfield traps of the páramo and the diversity is also almost as high as in the Behling traps. Higher pollen accumulation rates in the modified Oldfield traps may be caused also by the larger trap opening, which could lead to higher wind turbulences within the trap and thus to more pollen influx. However, this assumption has to be proven by further studies. Another point that may have affected the different pollen spectra and proportions especially in the modified Oldfield traps of the páramo is the fact that they generally trapped pollen from at least 20 cm above ground, whereas the Behling traps was installed at about 12 cm above ground and the reference trap at almost ground level. The same is true for the traps in the forest, but here, the effect on pollen composition may not be as strong, as almost all

pollen grains are transported from the canopy-layer downwards to the pollen traps. In open, low vegetation, the traps stick out of the vegetation and the pollen grains have to be transported at least slightly upwards to be caught in the traps. This is especially true for the modified Oldfield traps. Possibly, different wind patterns carrying other pollen grains from a larger distance affect those pollen traps. However, yet further research has to be done to determine the distribution properties, vertical pollen distribution and prevailing wind patterns in different neotropical ecosystems. Nevertheless, for the reasons mentioned above, we recommend the use of Behling traps for the páramo and other types of tropical open and/or dry vegetation, whereas for forest vegetation, all trap types seem to provide equally good results.

6. Conclusions

1. All studied four vegetation types, páramo, UMF, LMF and PMF, show distinct pollen spectra of modern pollen rain which reflect local to regional vegetation conditions.
2. All of the trap types as well as the soil samples are useful pollen and spore sampling media which in general produce similar modern pollen rain spectra.
3. In the soil samples, taxa with a fragile exine, such as Moraceae/Urticaceae, *Acalypha*, Cyperaceae, *Cecropia* and Lauraceae are represented to a lesser extent (i.e. more often under-represented or less over-represented) than in the pollen traps, whereas Poaceae have a higher representation than in the traps.
4. For the collection of pollen rain from open vegetation, Behling traps are a better choice than modified Oldfield traps, as they collect pollen closer to the ground and do not dry out as easily. Thus, with Behling traps, pollen grains are less corroded and the pollen spectra and their pollen accumulation rates are more similar to the ones that arrive on the soil surface.
5. Generally, more effort should be attempted to develop pollen traps that withstand the difficult collection circumstances of tropical environments and to establish long-term pollen rain monitoring sites for different tropical ecosystems.

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