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Modern pollen rain, vegetation and climate in Bolivian ecoregions

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A B S T R A C T

The aim of this study was to improve our understanding of the relationship between modern pollen rain, vegetation and climate in Bolivia, and to provide a link to interpret the fossil pollen record. Ten ecoregions were investigated: southern Puna, northern Puna, Yungas, pre-Puna, Gran Chaco, Chaco Chiquitano, Tucuman forest, inter-Andean dry forest, flooded savanna, and southwest Amazon forest. Forty soil surface samples were collected along an elevational transect from 4588 m to 160 m in 10 ecoregions and 16 sub-ecoregions. The vegetation in each sampling plot was described and the statistical analyses were performed on the pollen data set. Each ecoregion was distinguished by its pollen content and indicators. Statistical analysis performed on 26 selected pollen taxa enabled us to identify seven groups of pollen assemblages. Taxa transported out of their source ecoregion were also identified. The two Punas were grouped in one group and all the dry forests were grouped together. Statistical regressions between pollen indicators and elevation, precipitation, and temperature were computed. These data revealed clearly separated Asteraceae (high elevation, low precipitation and low temperature) from Arecaceae (low elevation, high precipitation and high temperature). Multivariate analyses of the whole pollen data set (including all the taxa) attest to the distribution of the 10 ecoregions as a function of climate. This good predictability is promising for future fossil analysis and vegetation mapping.

1. Introduction

The aim of vegetation models is to understand climate-vegetation interactions and to predict how plants will respond to future climate changes (e.g. Ni et al., 2000). The robustness of predictions by vegetation-climate models can be assessed by comparing them with known modern and past vegetation and climate data. To reconstruct past vegetation, fossil pollen records have to be examined to identify the types of ecosystems that past pollen spectra are likely to represent. Modern pollen-vegetation data are required to inform the interpretation of the fossil pollen record. In South America, different methods are used, and depending on the author and the study area, modern pollen data sets can be obtained from pollen traps (e.g. Gosling et al., 2005), moss polsters (e.g. Moscol Oliveira et al., 2009), mud water interfaces (e.g. Markgraf et al., 2002) or soil samples (e.g. Schäbitz, 1994). However, the lack of modern South American pollen samples prevents assessment of vegetation types at a continental scale and at different time scales (Marchant et al., 2009). Only modern pollen samples from Colombia (Marchant et al., 2001) and northern Argentina (Paez et al., 2001) are sufficiently consistent to enable large-scale reconstruction maps of past situations to be drawn using the biomization method (Prentice et al., 1992). Other attempts were limited to altitudinal transects in the Central Andes (e.g. Moscol Oliveira et al., 2009), changes in the upper forest limit, and climate reconstructions either by transfer function (e.g. Rull, 2006) or by multivariate analyses (e.g. Weng et al., 2004). In tropical ecosystems where regional climatic patterns are highly contrasted, pollen spectra representing the local vegetation are often lacking. Yet the natural resources of tropical countries – the most densely populated areas in the world – are already being seriously affected by the effects of climate change (e.g. floods in Ecuador, fires in Brazil) (IPCC, 2007). Thus there is an urgent need for large-scale observations of the causes and effects of both natural and human-induced environmental changes in tropical biomes.

In recent decades, Bolivia has faced major environmental changes driven by climate warming at low latitudes, mainly in the form of glaciers shrinking ten times faster than in previous decades (Francou et al., 2003; Rabatel et al., 2008). Moreover, intensification of agriculture and deforestation of the eastern slopes of the rainforests in the Yungas, as well as increased mining of some of the world's largest gas and lithium deposits are expected to lead to irreversible

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changes (IPCC, 2007). Bolivia is still almost a virgin country where no heavy industry modified the landscapes during the last century, where the three main roads were built in the 1930s, and where humid and dry forest ecosystems are still intact.

As far as biological species are concerned, Bolivia is a megadiverse country. It is located in the center of South America in a transition zone between humid tropical and dry subtropical climates including lowlands at less than 300 m above sea level (asl) as well as high mountains reaching an altitude of almost 7000 m asl. This geographical diversity is responsible for the great biodiversity, and Bolivia contains virtually all tropical vegetation formations. The country is estimated to contain approximately 20,000 species of plants (Ibisch et al., 2003), 45% of all South American bird species (Herzog, 2003), 356 species of mammals (Salazar and Emmons, 2003), and more than 200 species of amphibians (Reichle, 2003). Bolivia's National System of Protected Areas (NSPA) covers 167,415 km^2, i.e. approximately 15% of the territory. This biodiversity richness has already been challenged several times by climatic changes in the past (Abbott et al., 2003; Mourguiart and Ledru, 2003). However, little is known about paleoenvironmental changes mainly due to the scarcity of data, either because of aridity or seasonal floods or because the steep slopes of the Cordillera prevent continuous sediment deposits. Consequently, modern pollen samples are concentrated in areas where paleorecords are available. These are mainly in the Lake Titicaca area (Paduano et al., 2003), the Nevado Sajama (Reese and Liu, 2005) and in the Noel Kempf National Park (NKNP) in the Amazon lowlands (Gosling et al., 2005, 2009).

To improve our knowledge of the vegetation units in Bolivia and to address research questions related to spatial aspects that cannot be answered by the analysis of site-specific data, we collected an extended dataset of surface samples (Fig. 1) in ten Bolivian ecoregions, we analysed their pollen content in relation with associated botanical relevés and climate datasets and characterised relationships between vegetation, climate and pollen data.

2. Ecoregions, vegetation and climate in Bolivia

In the inter-tropical band in Bolivia, i.e. between latitude 9°32′ and 22°53′ S and between longitude 69°35′ and 57°27′ W (Fig. 1), ecosystems are distributed between three geographical areas: the highlands and Altiplano, the eastern Andes and dry inter-Andean valleys, and the lowlands (Ibisch et al., 2003). Our study area includes

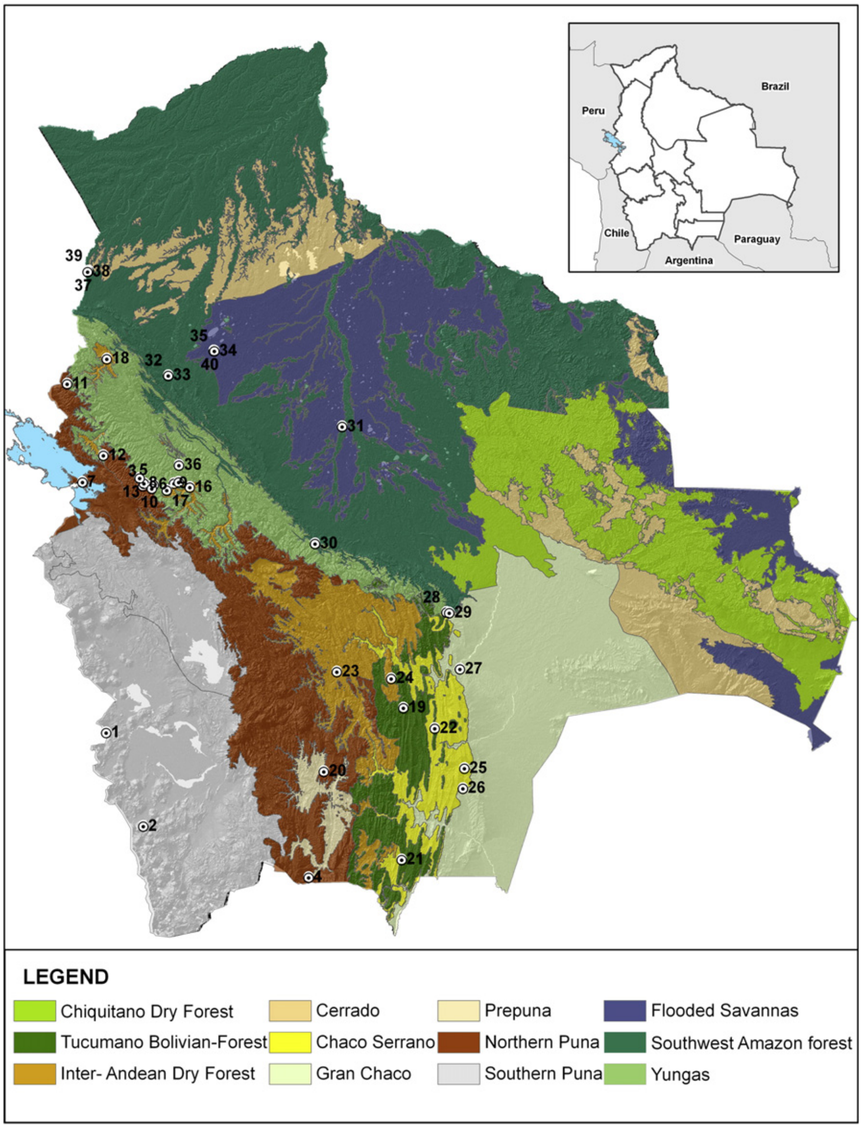

Fig. 1. Map of Bolivia showing the 12 main ecoregions and the location of the 40 surface samples of modern pollen rain analysed.

10 ecoregions according to Ibisch et al. (2003) (Fig. 1): southern Puna, northern Puna, pre-Puna, inter-Andean dry forest, forest Yungas, Tucuman Bolivian forest, Gran Chaco, Chiquitano dry forest, flooded savannas, and southwest Amazon forest. The Cerrado and southwestern Amazon forest could not be sampled for logistic reasons, but these areas have already been studied by Gosling et al. (2009). In the 10 ecoregions, 16 sub-ecoregions were sampled and analysed (Tables 1 and 2a–2i): Desert Puna, pronival desert, Altoandean steppe, marsh and bogs, *Polylepis* forest, Páramo, Ceja de Monte, Yungas forest, montane forest, Tucuman forest, inter-Andean dry forest, pre-Puna, Gran Chaco, Chiquitano dry forest, pre-Andean Amazon forest, and flooded savannas.

First we describe the composition of the vegetation and associated climate for these ecosystems based on Ibisch et al. (2003) and our relevés.

2.1. Highlands characterised by the Cordilleras and the Altiplano

Bolivia hosts the highest mountain ranges of the Andean Cordilleras, between 3500 and 5000 m asl. The open ecosystems of this region are adapted to a dry climate and high insolation.

Two ecoregions can be distinguished within this area (Tables 1, 2a, 2b):

1– The southern Puna (Table 2a) is a desert vegetation belt located between 3800 and 5000 m asl in the southern part of the Andean Cordillera, near the Atacama desert. The vegetation cover is scarce due to low precipitation and low temperatures.

2– The northern Puna (Table 2a) is located between 3200 and 5000 m asl and is composed of five sub-ecoregions:
  2a– the Pronival desert located at the margin of the glaciers on high elevation moraines characterised by low mean annual temperatures between 0 °C and 3 °C;
  2b– The Altoandean steppe located at 4700 m asl, with a mean annual temperature of 4.7 °C;
  2c– The azonal ecosystem is composed of bogs (or marshes) formed on slopes where underground water, melt water from the glaciers and precipitation accumulates. These ecosystems are unique and fragile because of their dependence on water and their sensitivity to climate change (Ruthsatz, 1993, 2000);
  2d– The semi-humid Puna located between 3200 and 4200 m asl in the mid and southern Andes;
  2e– Another azonal ecosystem is formed by the *Polylepis* forest which grows between 3000 and 4000 m asl throughout the Andes. The *Polylepis tarapacana* is the only tree adapted to this high environment.

2.2. The eastern Cordillera and the Andean valleys

Within this vegetation domain located at the foot of the eastern Cordillera, between 2000 and 4200 m asl, four ecoregions can be

Table 1

Ecoregions. Sub-ecoregions and corresponding soil surface samples analysed in this study with their climatic features (from Ibisch et al., 2003; BIOCLIM).

Ecoregion	Sub-ecoregion	Sample	Latitude (DMS)	Longitude (DMS)	Elevation (m)	Precipitation (mm)	Temperature (°C)
Southern Puna	Southern Puna	1	−19.87	−68.56	3670	49	6.2
		2	−21.25	−68.01	4173	49	6.2
Northern Puna	Semi-humid Puna	4	−22.01	−65.58	3447	324	10.9
	Pronival desert	3	−16.23	−68.03	4700	650	4.7
	Alto-andean steppe	5	−16.21	−67.86	4588	599	8.2
		6	−16.21	−67.86	4588	599	8.2
		8	−16.19	−68.01	4140	759	10
	Azonal ecosystems: – marshes – Polylepis woodland	7	−16.17	−68.92	4700	731	9.2
		10	−16.27	−67.89	3384	808	14.1
		11	−14.72	−69.14	4305	696	20
Yungas	Paramo	9	−16.19	−67.56	3500	1185	16.2
		13	−16.11	−68.07	3754	975	17.5
	Ceja de Monte	15	−16.17	−67.50	3080	1159	16.6
	Montane forest	14	−16.43	−67.87	2060	1512	19.9
		18	−14.35	−68.56	2020	1888	22.7
	Moist forest	16	−16.25	−67.33	2350	1161	18.6
		17	−16.29	−67.67	2200	1182	19.9
Tucuman forest	Tucuman forest	21	−21.74	−64.2	1250	859	10.9
		22	−19.8	−63.71	1396	915	20.3
		19	−19.5	−64.17	2010	844	19.3
Inter-Andean forest	Inter-Andean forest	12	−15.78	−68.61	2600	674	10.2
		23	−18.97	−65.16	2222	535	19
		24	−19.07	−64.35	2200	668	16.6
Pre-Puna	Pre-Puna	20	−20.44	−65.35	3074	396	11.6
Southwest Amazon forest	Pre-andean amazon forest	30	−17.08	−65.48	583	3242	23.9
		31	−15.35	−65.08	176	2293	25.4
		32	−14.6	−67.65	280	1917	24.9
		33	−14.6	−67.65	280	1917	24.9
		34	−14.24	−66.97	165	1639	26
		35	−14.23	−66.98	160	1636	26
		36	−15.92	−67.49	200	1632	23.7
		37	−13.06	−68.84	200	2263	25.4
Flooded savanna	Flooded savanna	38	−13.06	−68.84	200	2263	25.4
		39	−13.05	−68.82	200	2263	25.4
		40	−14.24	−66.97	165	1639	26
Dry forest “Gran Chaco”	Dry forest “Gran Chaco”	25	−20.39	−63.27	914	702	22.6
		26	−20.69	−63.29	756	687	23.4
		27	−18.93	−63.34	433	640	23.2
Dry forest “Chiquitano”	Dry forest “Chiquitano”	28	−18.1	−63.5	1858	1111	23.1
		29	−18.09	−63.54	1828	1043	22.2

Table 2a
Description of the vegetation types and associated pollen surface samples in the northern Puna.

Domaine	Ecoregion	Sub-ecoregions	Vegetation dominant taxa	Surface samples: characteristic pollen taxa
Cordilleras and Altiplano	Northern Puna	Pronival desert	Asteraceae *Wermeria ciliolate, Senecio rufescens*, Poaceae *Deyeuxia nitidula, D. minima, D. curta, D. densiflora* and Malvaceae *Nototriche flagelata* with a low vegetation cover.	Sample 3 *Nototriche*, Asteraceae tubuliflorae and Poaceae.
		Altoandean steppe	Poaceae *Deyeuxia minima, Poa* ssp. Brassicaceae *Pycnophyllum molle*.	Samples 5, 8 Poaceae, Juncaceae, *Plantago, Azorella*.
		Azonal ecosystem	Juncaceae *Oxychloe andina, Distichia muscoides, D. filamentosa* Plantaginaceae, *Plantago tubulosa* and Gentianaceae *Gentiana sedifolia*.	Samples 6, 7 Poaceae, Asteraceae tubuliflorae, Juncaceae, *Plantago*, *Gentiana, Ranunculus, Solanaceae, Nototriche* and Cactaceae.
			Polylepis forest *Polylepis pepei Gynoxis.*	Samples 10 and 11 The *Polylepis* forest — *Polylepis/Acaena*, Poaceae, Asteraceae tubuliflorae, *Polypodium*, Solanaceae, *Adesmia, Gomphrena.*
		Semi-humid Puna	Semi open grasslands Poaceae: *Stipa ichu, Nassella rupestris, N. asplundi, Chondrosum simplex, Aristida asplundii, Festuca* ssp. Asteraceae: *Parasthephia lepidophylla, Baccharis incarum, Gamochaeta* ssp., *Gnaphalium*. Plantaginaceae: *Plantago sericea, P. myosorus*. Oxalidaceae: *Oxalis bisfracta*.	Sample 4 Poaceae, Asteraceae tubuliflorae, Juncaceae, Solanaceae, Cactaceae and *Gomphrena*.

distinguished: Yungas, Tucuman forest, dry inter-Andean forest and pre-Puna (Tables 1 and 2c, 2d, 2e, 2f). Mean annual precipitation and temperature vary over the year depending on the geographical location (Killeen et al., 2007). These factors play an important role in the biological processes that drive endemism and speciation.

1– The humid forest or "Yungas" (Table 2b) is a cloud forest located between 1000 m and 3800 m asl where permanent moisture is supplied by cloud drizzle and rainfall brought from the Amazon basin by the easterlies. The beta diversity of this ecosystem is the highest in Bolivia. The "Yungas" ecoregion is subdivided into four sub-ecoregions:
   1a– The Paramo, located between 3700 and 4200 m asl, is a high elevation grassland. *Polylepis pepei* forest is commonly found here along with its associated treelet the Asteraceae *Gynoxis*. The presence of these forests favours the installation of a local humid microclimate and allows for the presence of many endemic animal species (Kuentz et al., 2007). Bogs are also found in this altitudinal belt;
   1b– The Ceja de Monte is located between 2800 and 3600 m asl on steep slopes and in deep valleys. The physiognomy is characterised by treelets of between 1.5 and 5 m in height;
   1c– The montane forest, located between 1000 and 3000 m asl on steep slopes, consists in an evergreen dense moist forest with trees more than 15 m tall, treelets covered with lichens, mushrooms, pteridophytes and epiphytes of the Bromeliaceae, Araceae and Orchidaceae families;
   1d– The moist "Yungas" forest grows between 2200 m and 2800 m asl on steep mountain and canyon slopes. Its vegetation is luxuriant with trees up to 10–12 m tall and treelets up to 2.5 m tall.
2– The second ecoregion, the Tucuman moist forest (Table 2c) is located between 300 and 3500 m asl in southern Bolivia and includes a band in northern Argentina. The differences between these two moist forest formations, Yungas and Tucuman, are mainly climatic: the minimum annual temperature range is lower in the Tucuman forest because of the influence of cold southerly winds, called "surazos". The vegetation cover is dense including trees more than 15 m tall.
3– The third ecoregion in this geographical area, dry inter-Andean forest (Table 2d), is located in central and southern Bolivia between 500 and 3300 m asl and includes patches of dry forest intercalated with Yungas forest and deep inaccessible valleys (Killeen et al., 2007). Due to its topographical specificity, this ecosystem is highly endemic with many endemic species including *Cardenasiodendron brachypterum* (Anacardiaceae), *Tecoma beckii* (Bignoniaceae), *Puya glabrecens* (Bromeliaceae), *Cereus comarapanus, Echinopsis pentlandii* (Cactaceae).
4– The fourth ecoregion in this geographical area, named pre-Puna (Table 2e), is a semi desert located between 2300 and 3400 m asl characterised by scant summer rainfall. The dominant plant formations are "columnar cacti" and some creeping herbs, usually *Portulacca perennis*, *Ipomoea* sp. This ecosystem is highly endemic, especially the Cactaceae family. Treelets and trees are no more than 3 m tall. Two different formations can be distinguished according to their altitude: between 2300 and 2900 m asl the dominant species are *Cercidium andicola,* and *Acacia feddeana* (Mimosaceae), while between 2900 and 3200 m asl the dominant Mimosaceae species is *Prosopis ferox*. All three species are associated with *Tricocereus* spp. (Cactaceae).

2.3. Lowland ecosystems

Located in the southern and eastern Andes below 1000 m asl, the composition and the physiognomy of the vegetation in this geographical area differ depending on seasonality, water resources, and elevation. Four ecoregions can be distinguished within the Amazon and southern lowlands (Tables 1 and 2g, 2h, 2i).

Table 2b
Description of the vegetation types and associated pollen surface samples in the southern Puna.

Domaine	Ecoregion	Sub-ecoregion	Vegetation dominant taxa	Surface samples: characteristic pollen taxa
Cordilleras and Altiplano	southern Puna		*Polylepis tarapacana. P. tomentella* (Rosaceae). Bushes of *Baccharis boliviensis* and *Parastrephia lepidophylla* (Asteraceae). *Fabiana* ssp. (Solanaceae). Halophytic species such as *Nototriche turitella* (Malvaceae), *Distichia muscoides* (Poaceae), *Sarcocornia pulvinata* (Chenopodiaceae), *Gomphrena umbellata* (Amaranthaceae).	Samples 1, 2 Poaceae. Asteraceae tubuliflorae, *Adesmia*, *Fabiana* (Solanaceae), Chenopodiaceae/ Amaranthaceae, *Prosopis* (Mimosaceae) and Cactaceae.

Table 2c
Description of the vegetation types and associated pollen surface samples in the yungas.

Domaine	Ecoregion	Sub-ecoregions	Vegetation dominant taxa	Surface samples: characteristic pollen taxa
Eastern cordillera and Andean valleys	Yungas	Paramo	High elevation grassland with *Deyuxia nitula, D. intermedia, Agrostis tolucensis* (Poaceae), *Scirpus rigidus, Cyperus andinus* (Cyperaceae), herbs such as *Rumex acetosella* (Polygonaceae), *Acaena cylindristachya* (Rosaceae), *Baccharis trimera, B. latifolia, Werneria* ssp. (Asteraceae), *Buddleja montana* (Buddlejaceae), *Escallonia* ssp. (Escalloniaceae).	Samples 9, 13 Poaceae Asteraceae tubuliflorae, *Polypodium, Plantago, Polylepis/Acaena* Cactaceae Buddlejaceae, *Escallonia, Azorella*.
		Ceja de Monte	*Gaultheria glomerata* (Ericaeae), *Brachytum microdon* (Melastomataceae), *Hesperomeles lanuginosa* (Rosaceae). Rocky walls host saxicols, bryophytes, lichens and epiphytes of the Bromeliaceae and Orchidaceae, ferns: *Hymenophyllum* sp. (Hymenophyllaceae), *Elaphoglossum* ssp. (Lomariopsidaceae), *Blechnum* sp (Blechnaceae).	Sample 15 Poaceae Asteraceae tubuliflorae, *Polypodium, Hedyosmum, Weinmannia, Escallonia, Clethra, Buddleja,* Melastomataceae/Combretaceae.
		Montane forest	*Podocarpus partolei* (Podocarpaceae), *Alnus acuminata* (Betulaceae*), Ilex aggregata, I. goudotii* (Aquifoliaceae), *Miconia brittonii, M. punctata* (Melastomataceae), *Weinmannia pinnata* (Cunoniaceae), *Hedyosmum racemosum* (Chloranthaceae), *Clusia multiflora* (Clusiaceae). Ferns: *Elaphoglossum* ssp. (Lomariopsidaceae), *Cyathea caracasana (*Cyatheaceae), *Polypodium* ssp. (Polypodiaceae).	Samples 14, 18 Poaceae Asteraceae tubuliflorae, Solanaceae, Cactaceae, *Hedyosmum, Escallonia,* Spores of *Polypodium, Cyathea, Adiantum, Pteris.*
		moist forest "Yungas"	*Clusia ducnoides* (Clusiaceae), *Hedyosmum racemosum* (Chloranthaceae), *Clethra revoluta* (Chlethraceae), *Weinmannia pinnata* (Cunoniaceae), *Gunnera* ssp. (Gunneraceae). Ferns: *Cyathea dintelmanii* (Cyatheaceae*), Polypodium* sp. (Polypodiaceae).	Samples 16, 17 Poaceae, Asteraceae tubuliflorae, Solanaceae *Hedyosmum, Weinmannia, Clethra, Cedrela*, Moraceae. Spores of *Adiantum, Polypodium, Cyathea.*

1– The southwestern Amazon forest
  1a– Lowland southwestern Amazonia**,** located between 150 and 500 m asl, is composed of all the Amazonian forest types. The species richness is the same as that in the moist Yungas forest. Trees are more than 45 m tall. In flooded areas, the palm *Mauritia flexuosa* is dominant. This region suffered from strong human pressure. This ecoregion is not included in Table 1 because no samples were collected there. Samples of modern pollen rain from this region have already been analysed by Gosling et al. (2005);
  1b– The pre-Andean Amazonian forest (Table 2f) is located at the foot of the Andes in the eastern part of Bolivia between 150 and 500 m asl. Vegetation physiognomy is mainly characterised by large trees.
2– The flooded savanna (Table 2g), located between 100 and 200 m asl, is in fact a seasonally flooded savanna due to the numerous rivers from the Andes that flow through the Amazon lowlands.
3– The dry forest or "Gran Chaco" (Table 2h) is located in an area that covers southern Bolivia, Paraguay and Argentina between 200 and 600 m asl. It is the ecoregion with the lowest mean annual precipitation (795 mm), a mean annual temperature of 21.7 °C and a maximum of 48 °C. These forests are among the largest and best preserved dry forests in the world.
4– The dry "Chiquitano" forest (Table 2h) is located in a transition zone between the moist Amazonian rain forest and the "Gran Chaco" dry forest at an altitude of between 100 and 1400 m asl.

3. Methods and data sets

Our sampling strategy was based on the fact that depositional environments receive pollen from both local and regional sources. The image of the vegetation cover given by the pollen rain is related to the taphonomy of the pollen grains which varies with the climate and the local soil (Jacobson and Bradshaw, 1981). Consequently we consider that this "palynological image" of the vegetation, climate and soil is significant and representative of the ecosystem source. We are also aware that deep lakes and wetlands are ideal catchment surfaces to maximize the regional component of modern pollen data sets and to link modern pollen rain with paleorecords (Markgraf et al., 2002). However it was not possible to find a sufficient number of swamps that had not undergone strong human pressure in the ecoregions concerned. Setting up pollen traps implies returning regularly to collect the filters, and they are often subject to damage or are stolen and were therefore not appropriate in our case. Moss polsters do not grow in all our ecoregions and for this reason they were also disregarded. In addition, in order to correlate our large-scale data set with published vegetation surveys, surface samples were mainly collected on sites previously analysed by botanists. Forty soil samples were collected most between March and April 2007. The aim was to analyse modern pollen rain along a latitudinal transect

Table 2d
Description of the vegetation types and associated pollen surface samples in the Tucuman moist forest.

Domaine	Ecoregion	Sub-ecoregion	Vegetation dominant taxa	Surface samples: characteristic pollen taxa
Eastern cordillera and Andean valleys	Tucuman moist forest		*Podocarpus partolei* (Podocarpaceae), *Tipuana spp* (Fabaceae), *Alnus acuminata* (Betulaceae), *Juglans australis* (Juglandaceae), *Cupania vernalis* (Lauraceae), *Celtis iguanea* (Ulmaceae), *Tabebuia lapacho* (Bignoniaceae).	3 samples collected in 3 different sub-types of moist forest: Sample 21 *Podocarpus, Polypodium, Juglans*, Anacardiaceae, Asteraceae tubuliflorae, *Weinmannia, Cedrela.* Sample 22 Poaceae, Asteraceae tubuliflorae, Solanaceae, *Polypodium, Cedrela, Gomphrena, Tipuana*, Bombacaceae, *Adenanthera*, Anacardiaceae. Sample 19 *Juglans australis* and *Miconia calvencens*. Tucuman forest Melastomataceae, *Juglans*, Poaceae, Asteraceae tubuliflorae, *Polypodium*, Cactaceae, *Adiantum, Gomphrena.*

Table 2e
Description of the vegetation types and associated pollen surface samples in the inter-Andean forest.

Domaine	Ecoregion	Sub-ecoregion	Vegetation dominant taxa	Surface samples: characteristic pollen taxa
Eastern cordillera and Andean valleys	Inter-Andean forest		Abundant: columnar Cactaceae *Neoraimondia herzogiana* until 5 m high. Dominant families: Anacardiaceae, Asteraceae, Cactaceae, Fabaceae, Caesalpiniaceae, Mimosaceae, Verbenaceae, Dominant trees: *Acacia* spp., *Astronium urundeuva*, *Cardenasiodendron brachypterum*, *Erythrina falcata*, *Kageneckia lanceolata*, *Polylepis neglecta*, *Prosopis* spp., *Schinus molle*, *Schinopsis haenkeana*, *Tipuana tipu*. Richest genus: *Acacia, Capparis, Ceiba*, *Prosopis*.	Sample 12 Poaceae, Asteraceae tubuliflorae, Scrophulariaceae, Buddlejaceae, *Hedyosmum*. Samples 23, 24 Poaceae, Asteraceae tubuliflorae, Solanaceae, Polypodiaceae, *Aspidosperma* Anacardiaceae, *Adenanthera, Tecoma, Prosopis*.

between 13°06′ and 21°74′ S, 68°84′ and 64°20′ W and 167 m and 4700 m asl in order to sample 10 ecoregions and 16 sub-ecoregions among those described above (Fig. 1 and Table 1).

One co-author of Ibisch et al. (2003) is also co-author of this paper. Vegetation relevés are based on his research and additional information was collected in the field during the sampling campaign. A brief description of the vegetation was made at each sampling site consisting of a general inventory of species or a survey of the main vegetation, following the method used by Gentry (1982). In addition, when possible, our surface samples were taken in areas where vegetation surveys had already been performed and published (Navarro, 2002; Bach, 2004; Quintana, 2005; Rios and Pacheco, 2006; Zenteno, 2007; Schawe et al., 2008; Gonzales et al., 2010).

Climatic data were obtained from the “BIOCLIM” data set at the Australian National University.

Soil samples were collected over an area of approximately 1 ha by taking multiple pinches of soil from the area concerned. The samples were sealed in plastic bags and mixed. Pollen grains were extracted from the sediment following the standard protocol developed by Fægri and Iversen (1989) and mounted on microscope slides in silicon oil. Concentrations were calculated according to the method of Cour (1974), which is based on measurement of volumes. Pollen counts were performed using a microscope with 600 magnifications. Pollen grains were identified by comparing them with our reference pollen collection obtained from floristic materials at the herbarium of La Paz, and with pollen atlases (Heusser, 1971; Markgraf and d'Antoni, 1978; Tryon and Tryon, 1982; Hooghiemstra, 1984; Graf, 1985; Roubik and Moreno, 1991; Colinvaux et al., 1999). The total of 300 pollen grains included Arboreal Pollen, Non Arboreal Pollen and Varia, which made up the total pollen sum. The pollen percentages in Fig. 2 were calculated using the total pollen sum excluding ferns and bryophytes.

4. Results

4.1. Vegetation — pollen indicators

To define ecoregions and sub-ecoregions, for each sub-ecoregion, out of a total of 178 taxa in 40 samples (Annex), we selected the 26 most widely represented taxa with a relative abundance of 1% or more and which were also well represented in the vegetation. Our selection was representative of the biodiversity of the Bolivian ecoregions compared to 122 taxa identified in the Amazon forest (Berrio et al., 2003), and between 73 and 82 taxa identified in different altitudinal transects of the Central Andes (Weng et al., 2004; Rull, 2006; Moscol Oliveira et al., 2009). The selected taxa are presented as a pollen diagram clustered using multivariate analysis (Fig. 2). All the results concerning vegetation, distribution and pollen analysis are shown in Table 2.

4.1.1. Calibration vegetation — elevation

The vegetation relevés enabled us to establish a clear distribution of taxa along an altitudinal gradient (Table 3). Three main groups of altitudinal distribution were distinguished. 1) The high altitude taxa were *Nototriche* (4600–4700 m), Juncaceae (4400–4600 m asl), *Plantago* (4200–4900), *Polylepis* (3100–4700 m), *Fabiana* (Solanaceae) (3400–3700 m asl) and *Escallonia* (2800–3900 m asl). 2) The mid-altitudinal taxa (2600 and 1800 m asl), were *Clusia, Clethra, Weinmannia, Hedyosmum.* All these taxa were associated with high frequencies of *Polypodium* in the montane forest. Anacardiaceae, *Aspidosperma* with *Tipuana* (Fabaceae) were identified in either Gran Chaco or Tucuman forest while *Prosopis* or Mimosaceae, *Gomphrena* and Cactaceae were identified in inter-Andean forest or pre-Puna. 3) In the lowlands, located between 0 and 1000 m asl, *Capparis*, Moraceae, Arecaceae, *Hirtella* and *Swartzia* were clearly delimited even though this altitudinal range includes a wide range of moisture and temperature conditions.

Taxa found in the highest altitudinal range, which were not regionally restricted and could therefore be identified in several ecoregions, were Poaceae, Asteraceae, Cactaceae and Polypodiaceae.

4.1.2. Data clustering: ecoregions and groups of taxa

To identify clusters of samples based on their pollen content and hence to define specific ecoregions, we used multivariate analysis. But before using any clustering technique, we needed to define a measure for distances between samples so that similar samples were located at a short distance from each other and dissimilar ones far from each other. The pollen percentages of 26 significant taxa were used to compute a matrix of Euclidean distances. Hierarchical cluster analysis was then performed using the matrix of the Euclidian distances and Ward's minimum variance method (Ward, 1963). The hierarchical relationships between clusters are illustrated by the dendrogram in Fig. 2. By applying a threshold that subdivides the dendrogram, we defined seven groups of distribution (Fig. 2) which express first elevation and second moisture rates (mainly precipitation). It should be stressed that there is no theoretical way to determine the number of clusters from results of hierarchical clustering.

Group 1 – Samples 1 to 8 – represents high elevation dry open vegetation characterised by *Fabiana* (Solanaceae), *Adesmia* (Fabaceae),

Table 2f
Description of the vegetation types and associated pollen surface samples in the pre-Puna.

Domaine	Ecoregion	Sub-ecoregion	Vegetation dominant taxa	Surface samples: characteristic pollen taxa
Eastern cordillera and Andean valleys	pre-Puna		*Cereus, Tricocereus* spp. (Cactaceae), creeping herbs as *Portulacca perennis*, *Ipomoea* sp. 2300 to 2900 m asl:*Cercidium andicola, Acacia feddeana* (Mimosaceae). 2900 to 3200 m asl: *Prosopis ferox* (Mimosaceae).	Sample 20 *Prosopis, Gomphrena,* Poaceae, Asteraceae tubuliflorae, Solanaceae, *Ipomoea*.

Table 2g
Description of the vegetation types and associated pollen surface samples in the pre andean amazon forest.

Domaine	Ecoregion	Sub-ecoregions	Vegetation dominant taxa	Surface samples: characteristic pollen taxa
Lowlands	Southwest Amazon forest	Lowland southwest Amazon forest	Cf Gosling 2005 2008	No samples
		Pre-andean Amazon forest	*Attalea phalerata* (Arecaeae), *Astrocaryum murumuru* (Araceae), *Swartzia jorori* (Fabaceae), *Ficus gomellia*, *F. coerulescens*, *Pseudolmedia* (Moraceae), *Ocotea oblonga* (Lauraceae), *Cecropia concolor* (Cecropiaceae), *Hirtella* ssp (Chrysobalanaceae). Numerous epiphytes, vines and climbing plants. Cultivated: *Teobroma*, Arecaceae *Attalea*.	Samples 30 to 37 Arecaceae, *Teobroma*, Arecaceae, Mimosaceae, Melastomataceae/Combretaceae, Poaceae, Asteraceae tubuliflorae, *Hedyosmum, Weinmannia*, Moraceae, *Adiantum*, Anacardiaceae, *Aspidosperma, Polypodium, Adiantum.*

Table 2h
Description of the vegetation types and associated pollen surface samples in the flooded savanna.

Domaine	Ecoregion	Sub-ecoregion	Vegetation dominant taxa	Surface samples: characteristic pollen taxa
Lowlands	Flooded savanna		Poaceae, Cyperaceae, *Tabebuia heptaphylla* (Bignoniaceae). Two types of forest are distinguished: the forest island with big trees above 25 m height, palms, climbing species, vines, epiphytes and *Copernicia alba, Attalea phalerata* (Arecaceae), *Coccoloba paraguensis* (Polygonaceae), *Celtis ehrenbergina* (Ulmaceae), *Cecropia concolor, C. membranacea* (Moraceae), *Tabebuia* ssp (Bignoniaceae); the gallery forest observed on the banks of the rivers with *Bauhinia corniculata* (Caesalpiniaceae), *Machaerium aristulatum* (Fabaceae) and *Casearia aculeata* (Flacourtiaceae).	Samples 38, 39, 40 Poaceae, Melastomataceae/Combretaceae, Mimosaceae, *Hirtella*, Arecaceae, *Tabebuia.*

Malvaceae, Cactaceae. Juncaceae and *Plantago* were well represented in the bogs. This group includes the northern and southern Puna ecoregions.

Nototriche (Malvaceae) were not found in the southern Puna and *Prosopis* (or Mimosaceae in Fig. 2) and *Fabiana* (Solanaceae) were not found in the northern Puna.

Group 2 – Samples 9 to 11 – High elevation moist vegetation characterised by *Polylepis* woodlands and *Polylepis* pollen grains.

Group 3 – Samples 12 to 18 – Mid-elevation moist forest characterised by the association of *Polypodium, Hedyosmum, Weinmannia, Escallonia, Clusia* and *Clethra*. This group includes all the Yungas except the Tucuman forest and one sample of dry inter-Andean forest.

Group 4 – Samples 19 to 24 – Mid-elevation dry forest with the following association: Cactaceae, *Capparis, Tipuana, Aspidosperma* and the fern spore *Polypodium*. This group characterises the Tucuman forest, the pre-Puna and the dry inter-Andean forest.

Group 5 – Samples 25 to 29 – Low elevation dry forest and transition forest with Anacardiaceae, Cactaceae, *Prosopis* (Mimosaceae), *Tipuana* (Fabaceae), *Aspidosperma*. This group characterises both dry “Chiquitano” forest and “Gran Chaco”.

Group 6 – Samples 30 to 36 – Pre-Andean Amazonian forest with Moraceae, *Aspidosperma*, Arecaceae, *Hirtella* and the fern spores *Polypodium* and *Adiantum*. This group characterises the pre-Andean Amazonian forest, except for one sample which was clustered with group 7.

Group 7 – Samples 37 to 40 – Amazonian flooded savanna with Poaceae, Arecaceae, *Swartzia* and Cactaceae. Group 7 characterises the lowland savanna.

From the 10 ecoregions, our pollen data set enabled us to identify seven groups of pollen assemblages. The two Punas were grouped in one group, the dry “Chiquitano” and “Gran Chaco” forests were also grouped in one group, which is in agreement with the review of the definition of Neotropical dry seasonal forests by Pennington et al. (2000). The pre-Puna was associated with the moist Tucuman forest, and a new group was created for the *Polylepis* woodlands.

4.2. Climate indicators

We compiled mean annual precipitation, mean annual temperature and elevation for the 26 selected taxa (Table 1). A restricted pattern of distribution related to precipitation was observed for the selected taxa. A simple regression between the 26 taxa, two climate variables and elevation was performed to characterise relationships between taxa and climate (Fig. 3). In this way we were able to separate taxa with high annual moisture requirements such as Arecaceae and the fern *Polypodium* or high temperature requirements such as Arecaceae and *Hirtella,* and taxa which require a rather dry and/or cold environment at high altitudes such as Asteraceae and *Plantago,* which are at the opposite end of the scale from Arecaceae and *Hirtella*. Marked homogeneity was observed within results between the three parameters. The same taxa were opposed:

Table 2i
Description of the vegetation types and associated pollen surface samples in the dry forests.

Domaine	Ecoregions	Sub-ecoregions	Vegetation dominant taxa	Surface samples: characteristic pollen taxa
Lowlands	Dry forest “Gran Chaco”		Deciduous forest *Chorisia insignis* (Bombacaceae), *Capparis speciosa* (Capparidaceae), *Cereus validus* (Cactaceae).	Samples 25, 26, 27 Anacardiaceae, *Capparis*, Cactaceae, *Gomphrena*, Mimosaceae, *Aspidosperma*, Poaceae, Asteraceae tubuliflorae.
	Dry forest “Chiquitano”		Deciduous forest *Machaerium scleroxylon* (Fabaceae), *Caesalpinia pluviosa* (Caesalpiniaceae), *Centrolobium microchaeta, Astronium urundeuva, Schinopsis brasiliensis* (Anacardiaceae), *Cereus dayami* (Cactaceae), *Ocotea* ssp (Lauraceae).	Samples 28, 29 Poaceae, Asteraceae tubuliflorae, Solanaceae, *Dodonea*, Melastomataceae/Combretaceae, *Zanthoxylum.*

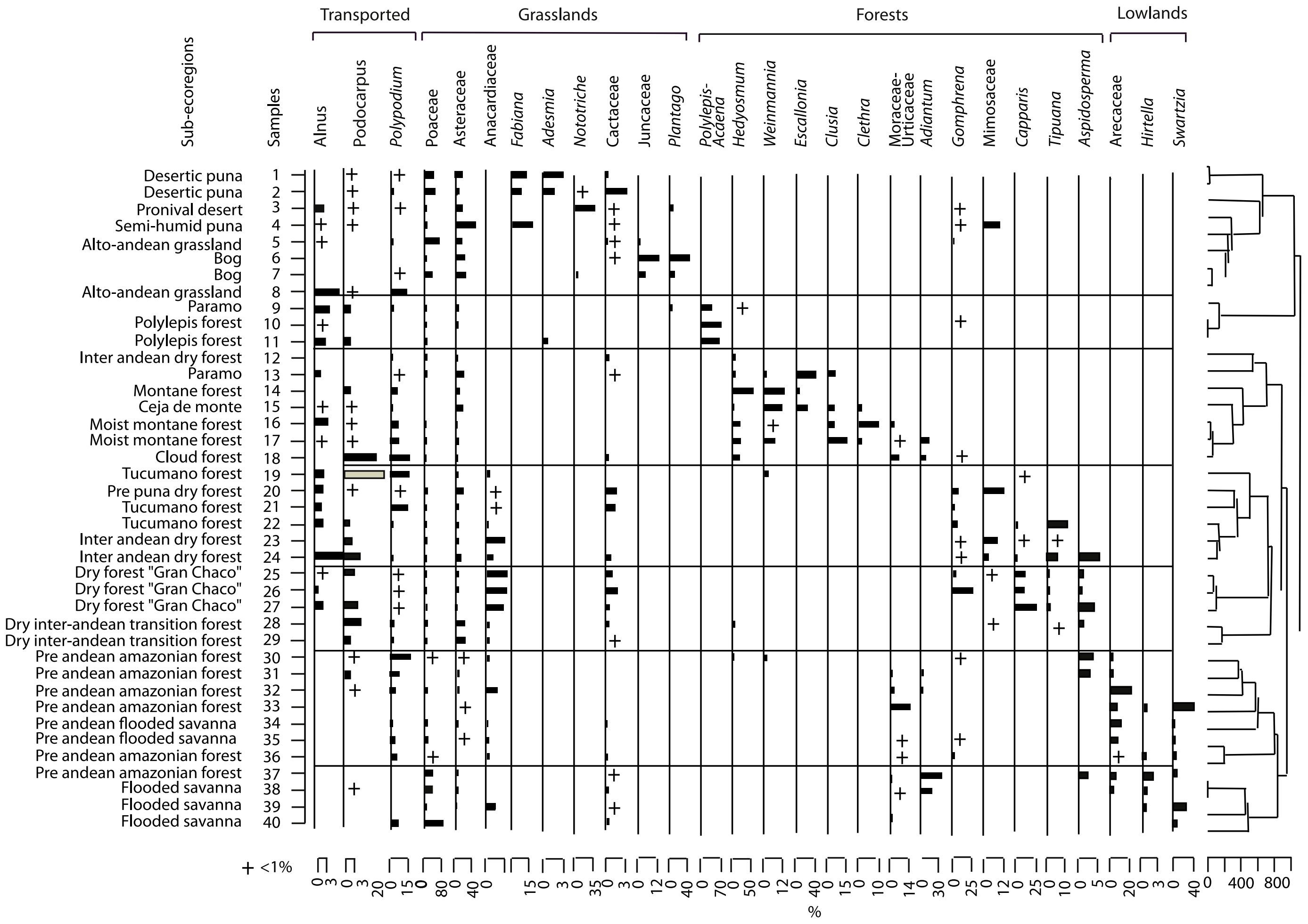

Fig. 2. Pollen percentage diagram and cluster diagram based on 26 selected taxa of the 40 soil surface samples collected in 10 ecoregions along an altitudinal gradient between 4600 m and 160 m asl. Pollen percentages are expressed as a function of the total pollen sum, ferns and aquatics excluded, the numbers 1 to 40 refer to the sample codes listed in Table 1. Pollen zones are defined according to the cluster diagram (see text for explanations). The grey bar is divided by 4.

Asteraceae, *Plantago* and *Fabiana* (Solanaceae) were opposite Arecaceae, *Hirtella, Swartzia* and *Polypodium.*

4.3. Multivariate analyses

Multivariate analyses were performed to explore to what the extent pollen assemblages were signatures of ecoregions and climate, represented by mean annual temperature and mean annual precipitation. First, to test the separability of the ecoregions from pollen assemblages, we ran a between-group correspondence analysis (BGCA) on the "sample x pollen" matrix, with samples grouped in 10 ecoregions. The "sample x pollen" matrix was composed of the frequency of each pollen taxon in each sample. The BGCA (Dodélec and Chessel, 1987; Baty et al., 2006) performed correspondence analysis (CA) of the per-group centres of gravity and the samples were then projected onto this CA as an additional row. This method provided an ordination of the groups of samples by maximizing between-group variance. The three first principal axes of the between-group correspondence analysis on "sample x pollen" matrix represented almost 50% of the total inertia. Fig. 4 shows the projection of the samples in planes 1–2 and 2–3, grouped by ecoregion. Axis 1 contrasts lowland ecoregions (Amazon forest and savannas) with higher altitude ones, which are separated in planes 2–3. Among characteristic taxa for each ecotype, we found: SW Amazon Forest: *Hirtella, Swartzia*; Flooded savanna: Myrtaceae, *Siparuma*; Amazon savannas: Melastomataceae/Combretaceae, *Casearia,* Malpighiaceae; Northern Puna : *Plantago, Polylepis, Fabiana*, Juncaceae; Southern Puna: *Fabiana, Adesmia, Lippia*, Verbenaceae; Pre-Puna: Cactaceae, Amaranthaceae/Chenopodiaceae; Dry Forest: *Capparis*, Mimosaceae, *Aspidosperma*; Inter Andean Forest: *Podocarpus, Celtis, Tecoma;* Tucuman: Acanthaceae, *Tipuana*; Yungas: *Hedyosmum, Weinmannia, Escallonia, Clusia*, *Clethra*, Moraceae–Urticaceae, *Adiantum*. Results showed that ecotypes could also be well separated from pollen

Table 3
Distribution of vegetation and pollen indicators according to their altitudinal ranges, Asteraceae and Poaceae excluded.

	High altitude	Mid altitude	Lowlands
Vegetation	*Nototriche* (Malvaceae)	*Clusia*	*Capparis*
	Juncaceae	*Clethra*	Moraceae/Urticaceae
	Plantago	*Weinmannia*	Arecaceae
	Polylepis	*Hedyosmum*	*Hirtella*
	Fabiana (Solanaceae)	*Polypodium*	*Swartzia*
	Escallonia	+ local differences	
Pollen	*Fabiana* (Solanaceae)	*Hedyosmum*	Anacradiaceae
	Adesmia (Fabaceae)	*Weinmannia*	Cactaceae
	Malvaceae	*Escallonia*	*Prosopis* (Mimosaceae)
	Cactaceae	*Clusia*	*Tipuana* (Fabaceae)
	Juncaceae	*Clethra*	*Aspidosperma*
	Plantago	*Capparis*	Moraceae/Urticaceae
	Polylepis	*Tipuana* (Fabaceae)	*Hirtella*
		Polypodium	Arecaceae
			Swartzia
			Adiantum

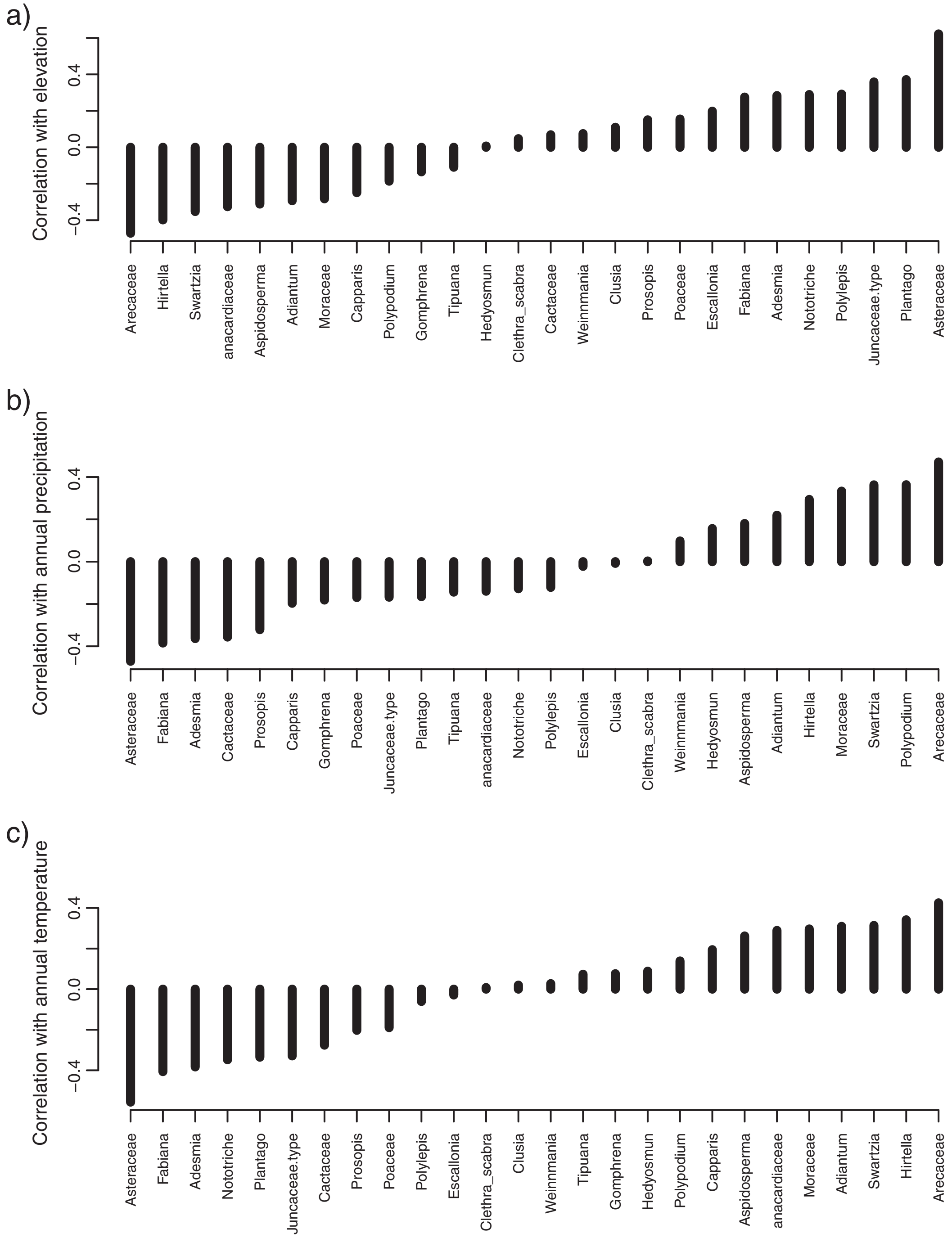

Fig. 3. Correlation coefficients of the 26 selected taxa with (a) elevation, (b) annual precipitation and (c) annual temperature (see text for explanations).

assemblages when all the taxa were taken into consideration. However some differences appeared between the two types of analysis i.e. with selected taxa only (Figs. 2 and 3) and with all the taxa (Fig. 4). When all the taxa were analysed, we observed that a taxon that enabled differentiation of one ecotype could not systematically be considered as characteristic of that ecotype, since some taxa were of limited abundance, while others are common, with tiny differences in abundance between ecotypes. Comparing the results of the two types of analyses enabled a better definition of the ecoregion concerned.

Next, we ran a co-inertia analysis (COIA) between the CA on the “sample x pollen” matrix and the principal component analysis (PCA) on the “sample x climate” matrix to reveal pollen/climate relationships. The climate matrix was composed of mean annual temperature and the logarithm of mean annual precipitation (BIOCLIM). Co-inertia is a measure of co-structure between pollen and climatic spaces: it has high values when they vary simultaneously and low values when they vary independently (see Dodélec and Chessel, 1994; Dray et al., 2003 for mathematical formulation). COIA identified vectors in the pollen space and in the climatic space with maximum co-inertia. The position of the pollen samples in the COIA space was then projected along the axes with maximum correlation with temperature. A linear fit was performed between the sample positions along this axis and actual temperatures (resp. logarithm of precipitation), which is considered as a pollen-based model of temperature (resp. logarithm of precipitation). COIA between pollen and climatic matrices showed

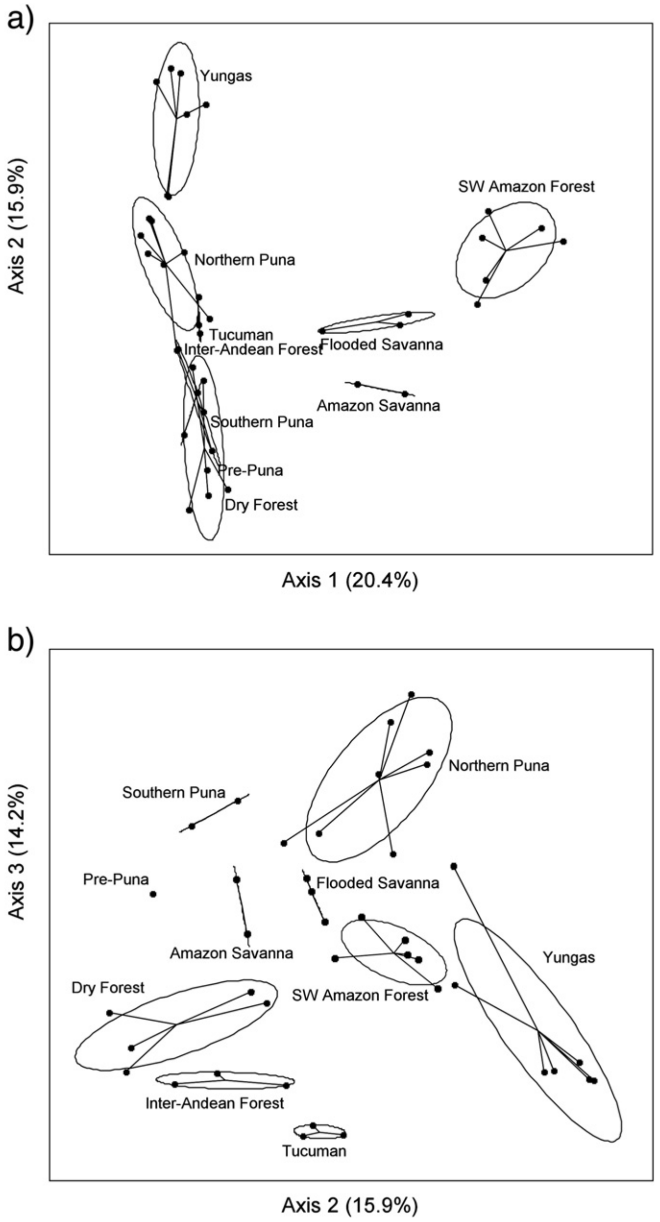

Fig. 4. Ordination diagram of the between-group correspondence analysis of the 40 surface samples grouped by ecoregion. The diagram shows the position of the 10 ecoregions and corresponding samples in (a) plane 1–2 and (b) plane 2–3. The percentage of total inertia explained by each axis is indicated.

that Bolivian pollen assemblages were closely linked to climate. The correlation between the first two axes of the CA on pollen matrix and the COIA plane was high (77% and 74%), indicating that the main variations in pollen spectra among samples were connected to climate variations. Fig. 5a shows the positions of the pollen taxa in the COIA plane, with the directions mostly correlated with temperature and precipitation. Fig. 5a provides an ordination of taxa as regards their thermophility and hygrophility. Fig. 5b and c show respectively actual temperature and precipitation vs. their values predicted from pollen assemblages. High values of coefficients of determination of the linear regressions (83% and 90%) confirmed the good predictability of climate from pollen samples. This predictability validates our data set and is important to take into consideration when reconstructing past climates or mapping vegetation on the basis of pollen spectra.

In summary, according to our observations based on both the vegetation relevés and their associated pollen rain, it was possible to divide each ecoregion into several sub-ecoregions according to their altitude and hydrological conditions (e.g. limit of cloud condensation in the montane forest), which sub-divided the Yungas into four different groups of indicators. Other taxa appeared to be easily transported along the slopes of the mountains. For instance, spores of Polypodiaceae were found in the highest altitudinal ranges, which do not correspond to their source region. In the *Polylepis* forest, *Cyathea* and *Podocarpus* were transported from another sub-ecoregion of the Puna. In the Yungas, *Hedyosmum* was transported to the Paramo from the lowest sub-ecoregions. In the dry inter Andean forest, the pre Puna, the dry forest “Gran Chaco”, *Podocarpus* is also allochtonous (Fig. 2). Wind transport and the convective activity favour pollen transport from the forest to open highland landscapes along the slope of the eastern Cordillera. Areas subject to frequent convective moisture and cloud drizzle with mean annual precipitation values equal to or above 1000 mm, but for which we were unable to differentiate the origin of moisture, were included in group 3 of the cluster analysis, i.e. the mid-elevation moist forest group.

Statistical analysis of a selection of 26 pollen indicators led to reorganisation of the ecoregions according to the types of vegetation, such as dry open high vegetation, moist high elevation vegetation, but did not distinguish between the ecoregions. On the other hand, multivariate analysis of all the taxa using both pollen and climate data sets was able to distinguish between the 10 ecoregions with good climate predictability based on the pollen samples.

5. Discussion

Comparing other studies made in the same geographical areas of the central Andes, tropical high, mid and low elevation ecosystems, is hazardous mainly because of their restricted spatial scale, e.g. along a slope or in a single valley. However some major features are common to all these ecosystems and it is thus possible to reconstruct the main indicator taxa for the different vegetation types that grow in the tropical band between the Pacific Ocean and the Amazonian rainforest. In the central Andes, Reese and Liu (2005) undertook systematic analysis of the modern pollen rain between 13° and 22°S encompassing Bolivian Peruvian and Chilean central Andean regions and showed that in the Yungas, high percentages of Moraceae–Urticaceae and fern spores are the dominant taxa with trace amounts of Piperaceae, Bignoniaceae and Malpighiaceae. In the present study we distinguished four types of Yungas, all dominated by a Poaceae–Asteraceae tubuliflorae assemblage, differentiated by the presence of specific indicator taxa as a function of elevation and/or moisture rates, e.g. the increasing frequency of spores in the lowest Yungas, or of Plantago and Juncaceae in the bogs (Fig. 2). In the Puna, the dominance of Poaceae with moderate frequencies of Asteraceae generally characterises this ecoregion although some differences enabled us to distinguish four types of Puna based on the presence of *Nototriche*, the assemblage of *Prosopis-Fabiana, Polylepis,* and Juncaceae. In high elevation open ecosystems near the Nevado Sajama in Bolivia, Reese and Liu (2005) defined a Poaceae/Asteraceae index to characterise a precipitation gradient across the Altiplano. This index shows that the percentage of grasses tends to increase with an increase in precipitation. The method was successfully applied in a paleoanalysis performed on ice core samples (Liu et al., 2005) and on sediment samples in southern Peru (Kuentz et al., in revision). However attempts to use this index at a broader scale, like the one used in the present study, failed, probably because of differences in pollen deposition under closed vegetation covers at lower elevations.

Using light microscopy, pollen analysts are unable to distinguish *Acaena* from *Polylepis*. *Acaena* is currently present in warm humid valleys and could be confused with *Polylepis*. In our data set, the pollen grains of *Polylepis/Acaena* were found only near the *Polylepis* forests, which considerably reduces the possibility of the presence of *Acaena*

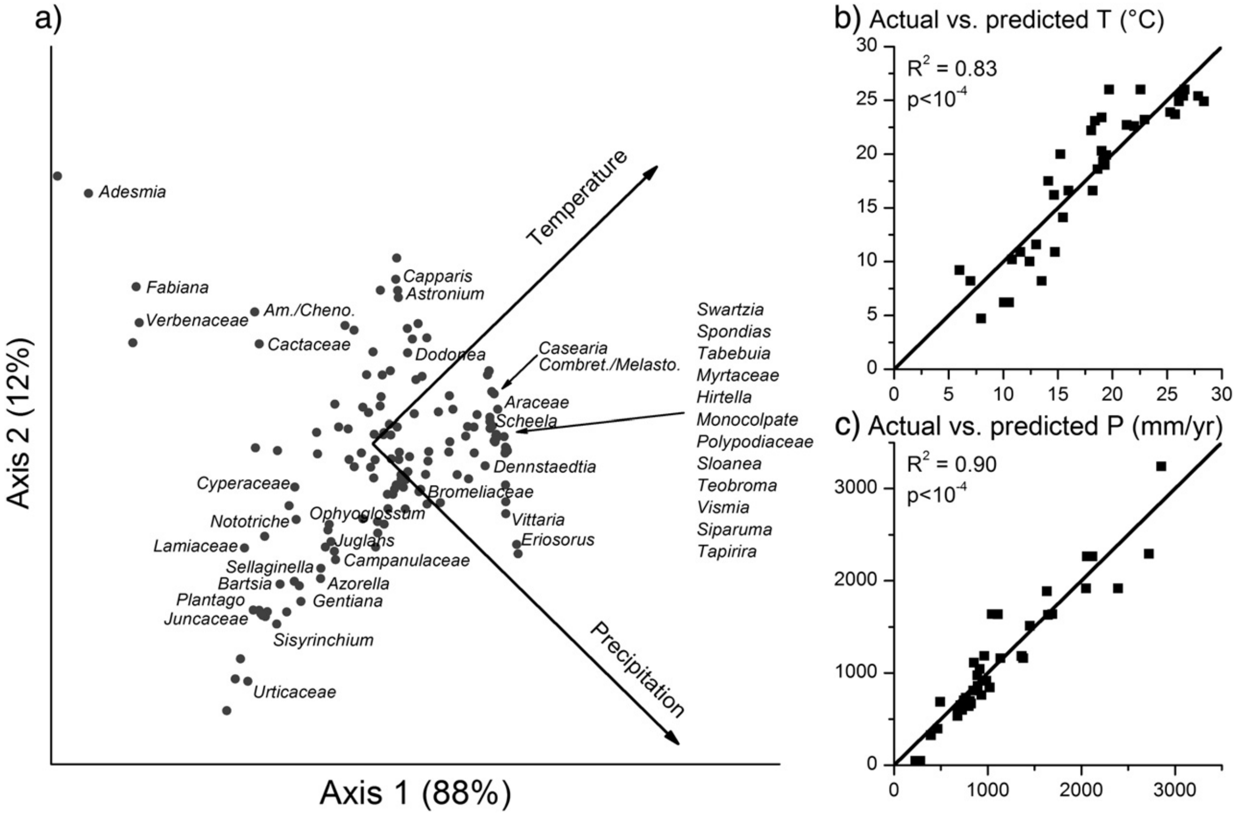

Fig. 5. (a) Ordination diagram of co-inertia analysis (COIA) between pollen CA and climate PCA. The diagram shows the position of pollen taxa in the COIA plane (89% and 11% of inertia supported by axes 1 and 2) and the directions of the original climatic axes (temperature and logarithm of rainfall). Only the names of the most abundant taxa in pollen samples and that contribute most to the COIA axes are included. This provides an ordination of pollen taxa according to their temperature and precipitation affinity. (b–c) actual mean annual temperature (precipitation) vs. mean annual temperature (precipitation) modelled from pollen assemblage based on COIA results. The models were derived from linear regressions of actual climatic parameters and the projection of pollen samples along the temperature and precipitation axes. R^2 and p-values of these linear regressions are indicated.

and reinforces the determination of *Polylepis* in our samples and in fossil samples.

Along an altitudinal gradient in northern Ecuador, pollen spectra of paramos are clearly separated from forest spectra. Statistical analysis revealed that high percentages of pollen from *Puya*, Apiaceae, Poaceae and Cyperaceae indicated the presence of paramo vegetation, while high percentages of *Clusia, Ilex, Weinmannia* indicated the presence of forest (Moscol Oliveira et al., 2009). Along another altitudinal transect from lowland Amazonian swamps up to Puna vegetation in southern Peru (Weng et al., 2004), Asteraceae, Poaceae, *Myrica* and *Myrsine* were most abundant at high elevations, while *Hedyosmum* was most abundant at mid- to high-elevations. In Bolivia, *Myrica*, *Myrsine* were rarely represented at high and mid-elevations, and *Hedyosmum* show the same pattern as in other central Andean *regions.* Differences in pollen/plant representation between the Peruvian and the Bolivian eastern Cordillera were also observed concerning *Alchornea, Acalypha* and Rubiaceae. These taxa showed maximum abundances in pre montane elevations (but not in lowlands) in Peru but were not represented in Bolivia.

In the eastern lowlands of Peru, pollen assemblages were characterised by abundant *Mauritia, Ficus,* Arecaceae, *Iriartea* and *Sloanea* pollen types (Weng et al., 2004), and the three first species were also observed in Bolivian flooded savannas. According to Gosling et al. (2009) Moraceae/Urticaceae were over-represented in the three ecosystems studied: moist forest, semi-deciduous forest and wooded savanna. In the moist forest, high percentages of Moraceae/Urticaceae were observed, together with *Cecropia, Hyeronima, Celtis*. In the semi-deciduous forest, pollen taxa of *Anadenanthera* (Mimosaceae), *Apuleia, Ferdinandusa*, Asteraceae, Bromeliaceae, *Piper* and fern spores were dominant; in the wooded savanna or cerradão, Poaceae (although not dominant), Myrtaceae, *Borreria, Solanum* (Solanaceae), Asteraceae, fern spores are considered to be an indicator assemblage for this ecosystem (Gosling et al., 2009). Moraceae/Urticaceae were rarely identified in samples collected in moist forest montane (Hansen and Rodbell, 1995), which is in agreement with our results.

Alnus is always over-represented in high altitude ecosystems due to transport along the slope by strong winds (Weng et al., 2004; Moscol Oliveira et al., 2009). In some cases, *Alnus* even appears to be the dominant taxon, although it does not occur within our study area (Niemann et al., 2010). In northern Peru, *Hedyosmum* is well represented in wet montane forest where it grows as a tree and has been successfully transported to the paramo (Hansen and Rodbell, 1995). The same pattern is observed in Bolivia (the present study) and in northern Ecuador, where the associated vegetation relevé attests to the over-representation of this taxon in the pollen rain of the paramo (Moscol Oliveira et al., 2009). In the present study, *Alnus* and *Podocarpus* pollen grains and *Polypodium* spores were found, sometimes at high frequencies, in four ecoregions where they are not observed as a plant, Puna, pre-Puna, dry inter-Andean and Gran Chaco (Fig. 2). This attests to wind transportation from their source for these taxa (*Alnus, Podocarpus*, *Hedyosmum* and *Polypodium*) in the central Andes from Ecuador to Bolivia, which could lead to discrepancies between reconstructed forest limits and pollen data in the paleo records.

Differences in past hydrological cycles in the central Andes (Abbott et al., 2003) and in modern moisture transport and convection activities between northern and southern Andes (Ecuador–Peru–Bolivia) (Vuille and Keimig, 2004) could explain the variations in the expression and frequency of the taxa reported by different authors depending on the geographical locations of their sites. Differences between sites are due to geographical changes in hydrological conditions, and to the regional history of plant migration and climate with – for instance – more frequent Asteraceae in the southern Andes (Kuentz et al., 2007) and *Clusia* or *Alchornea* in the northern Andes

(Moscol Oliveira et al., 2009). In this study, we also observed a geographical limit between the Punas, with no *Nototriche* (a high elevation herb of the Malvaceae family) in the southern Puna while *Prosopis* (Mimosaceae) and *Fabiana* (Solanaceae) were not observed in the northern Puna and vice versa.

6. Conclusion

We showed that it is possible to distinguish several sub-ecoregions from their source ecoregion based on their pollen content. Main indicator taxa were defined for each sub-ecoregion. These distinctions are due to specific edaphic conditions such as the presence of bogs (bofedales) in the Puna or local climatic features such as convective activity in the Yungas. Although a strong correlation was demonstrated between the floristic composition of the ecoregions and their associated pollen content, comparison with botanical relevés allowed us to clearly distinguish certain taxa such as *Alnus, Hedyosmum,* Arecaceae and *Podocarpus* and ferns, including *Cyathea* and *Polypodium,* which had often been transported long distances from their source to other ecoregions.

Statistical analyses of the selected pollen taxa split the 10 ecoregions into seven groups of pollen assemblages: 1 — high elevation grassland or Puna, 2 — *Polylepis* woodlands, 3 — Andean forest or Yungas, 4 — pre-Andean forest, 5 — dry inter-Andean forest, 6 — savanna and 7 — dry lowland forest. An assemblage of five taxa was assigned to each of these groups with specific associated climate parameters. A clear contrast was observed between Asteraceae and Arecaceae, which is surprising at the family level because Asteraceae is a widely distributed plant family. However in the Bolivian ecoregions, high frequencies of Asteraceae are closely associated with high elevation, dry climate and high insolation. Ferns also appeared to be a significant indicator. It is important to take ferns into consideration when interpreting pollen results from paleorecords. Multivariate analyses of the total pollen taxa showed a good correlation between pollen assemblages and climate. This is an important result for future climate or vegetation reconstruction. Indeed, the relationship between modern pollen and vegetation defined from surface sediment samples will allow a better reconstruction of the vegetation changes from fossil pollen data and validation of global vegetation simulations at a broad scale, although more data from Bolivia and surrounding regions are still needed to improve this first broad-scale attempt.

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Annex 1. List of identified pollen and spore taxa in the surface soil samples of the Bolivian ecoregions

Arboreal Pollen
Adesmia (Fabaceae)
Albizia (Caesalpiniaceae)
Alchornea (Euphorbiaceae)
Alnus (Betulaceae)
Annonaceae
Arecaceae monocolpate

Annex 1 (*continued*)

Arboreal Pollen
Arrabidea (Bignoniaceae)
Aspidosperma (Apocynaceae)
Astrocaryum (Arecaceae)
Astronium (Anacardiaceae)
Bauhinia (Caesalpiniaceae)
Berberis (Berberidaceae)
Bignoniaceae
Bombacaceae
Buddleja (Buddlejaceae)
Caesalpinea (Caesalpiniaceae)
Capparis (Capparidaceae)
Cardenasiodendron (Anacardiaceae)
Carica (Caricaceae)
Casearia (Flacourtiaceae)
Cedrela (Meliaceae)
Ceiba (Bombacaceae)
Celtis (Ulmaceae)
Cercidium (Caesalpiniaceae)
Cestrum (Solanaceae)
Cissus (Vitaceae)
Clethra (Clethraceae)
Clusia (Clusiaceae)
Coccoloba (Polygonaceae)
Dendropanax (Araliaceae)
Dodonea (Sapindaceae)
Ephedra (Ephedraceae)
Ericaceae
Escallonia (Escalloniaceae)
Fabiana (Solanaceae)
Ficus (Moraceae)
Guarea (Meliaceae)
Hedyosmum (Chloranthaceae)
Hirtella (Chrysobalanaceae)
Ilex (Aquifoliaceae)
Jacaranda (Bignoniaceae)
Juglans (Juglandaceae)
Ladenvergia (Rubiaceae)
Lauraceae
Lippia (Verbenaceae)
Lithraea (Anacardiaceae)
Machaerium (Fabaceae)
Maytenus (Celastraceae)
Melastomataceae/Combretaceae
Mimosaceae
Moraceae
Myrica (Myricaceae)
Myrsinaceae
Myrsine (Myrsinaceae)
Myrtaceae
Neea (Nyctaginaceae)
Oreopanax (Araliaceae)
Palicourea (Rubiaceae)
Parkinsonia (Fabaceae)
Podocarpus (Podocarpaceae)
Polygala (Polygalaceae)
Polylepis (Rosaceae)
Pouteria (Sapotaceae)
Protium (Burseraceae)
Pseudobombax (Bombacaceae)
Psychotria (Rubiaceae)
Rubiaceae
Sapindaceae
Scheelea (Arecaceae)
Schinopsis (Anacardiaceae)
Schinus (Anacardiaceae)
Serjania (Sapindaceae)
Siparuma (Monimiaceae)
Sloanea (Eleocarpaceae)
Spondias (Anacardiaceae)
Swartzia (Caesalpiniaceae)
Symplocos (Symplocaceae)
Tabebuia (Bignoniaceae)
Tapirira (Anacardiaceae)
Tecoma (Bignoniaceae)
Teobroma (Sterculiaceae)
Terminalia (Combretaceae)
Tipuana (Fabaceae)

Annex 1 (*continued*)

Arboreal Pollen
Trichilia (Meliaceae)
Triplaris (Polygonaceae)
Vallea (Elaeocarpaceae)
Vernonia type (Asteraceae)
Virola (Myristicaceae)
Vismia (Clusiaceae)
Weinmannia (Cunoniaceae)
Zygophyllaceae

Non Arboreal Pollen
Acanthaceae
Agalinis (Scrophulariaceae)
Agavaceae
Apiaceae
Araceae
Asteraceae
Astragalus (Fabaceae)
Azorella (Apiaceae)
Bartsia (Scrophulariaceae)
Brassicaceae
Bromeliaceae
Cactaceae
Campanulaceae
Centrosema (Fabaceae)
Chenopodiaceae/Amaranthaceae
Colobanthus (Caryophyllaceae)
Croton (Euphorbiaceae)
Cucurbitaceae
Desmodium (Fabaceae)
Drymaria (Caryophyllaceae)
Fabaceae
Gentiana (Gentianaceae)
Geranium (Geraniaceae)
Gunnera (Gunneraceae)
Heliotropium (Boraginaceae)
Hoffmannseggia (Caesalpiniaceae)
Ipomoea (Convolvulaceae)
Jatropha (Euphorbiaceae)
Lamiaceae
Lupinus (Fabaceae)
Malpighiaceae
Malvaceae
Opuntia (Cactaceae)
Oxalis (Oxalidaceae)
Passifloraceae
Peperonia (Piperaceae)
Phytolacaceae
Piper (Piperaceae)
Piperaceae
Plantago (Plantaginaceae)
Poaceae
Polemoniaceae
Polygonaceae
Puya (Bromeliaceae)
Pycnophyllum type (Caryophyllaceae)
Randia (Rubiaceae)
Ranunculus (Ranunculaceae)
Rosaceae
Solanaceae
Spermacoce (Rubiaceae)
Tillandsia (Bromeliaceae)
Urticales
Valerianaceae
Verbenaceae
Zanthoxylum (Rutaceae)

Aquatics / related to water level
Cyperaceae
Sisyrinchium (Iridaceae)
Juncaceae
Salviniaceae

FERNS
Adiantum (Pteridaceae)
Anemia (Schizaeaceae)
Asplenium (Aspleniaceae)
Cheilanthes (Polypodiaceae)

Annex 1 (*continued*)

FERNS
Cnemidaria (Cyatheaceae)
Cyathea (Cyatheaeceae)
Cyatheaceae
Cyptopteris (Polypodiaceae)
Dennstaedtia (Dennstaedtiaceae)
Dryopteris (Dryopteridaceae)
Elaphoglossum (Lomariopsidaceae)
Eriosorus (Pteridaceae)
Grammitis (Grammitidaceae)
Hymenophyllum (Hymenophyllaceae)
Hystiopteris (Polypodiaceae)
Lophosoria (Lophosoriaceae)
Lycopodium 1 (Lycopodiaceae)
Lycopodium 2 (Lycopodiaceae)
Ophyoglossum (Ophyoglossaceae)
Palmera (Polypodiaceae)
Pellaea (Polypodiaceae)
Pityrogramma (Pteridaceae)
Polypodiaceae
Polypodium (Polypodiaceae)
Pteridium (Pteridaceae)
Pteris (Pteridaceae)
Selaginella (Selaginellaceae)
Sticherus (Gleicheniaceae)
Thelypteris (Thelypteridaceae)
Vittaria (Vittariaceae)

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