Research paper

Modern pollen assemblages of surface samples and their relationships to vegetation in the *campos* region of Uruguay

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ABSTRACT

This study documents the relationship between the modern pollen assemblages and the main vegetation types of the *campos* region of Uruguay. A total of 46 surface soil samples from grasslands, riparian forests, low mountain shrublands-forests, psammophilous forests and "Candela" coastal shrublands were studied. Cluster Analysis and Detrended Correspondence Analysis, performed on 23 selected pollen taxa, revealed five distinct pollen assemblages which correlate well with each vegetation type. Grasslands are characterized by Poaceae, Asteraceae subf. Asteroideae, Cyperaceae and Apiaceae. The limited taxonomic resolution of their main pollen grains did not make it possible to classify the grasslands in more detail. Riparian forests are characterized by exclusive hydrophilous trees, aquatic herbs and high values of Myrtaceae. Comparison of modern pollen and vegetation revealed that some important floristic elements from riparian forests were completely absent from the pollen assemblages or appeared in very low percentages. Low mountain shrublands-forests are co-dominated by herbaceous (Poaceae and Cyperaceae) and arboreal (*Lithraea/Schinus* and Myrtaceae) pollen, together with Asteraceae subf. Asteroideae. Psammophilous forests are also characterized by the co-dominance of herbaceous and arboreal pollen, but with higher values of *Ephedra tweediana* and Rhamnaceae, and minor of Asteraceae subf. Asteroideae. "Candela" coastal shrublands are characterized by maximum values of *Dodonaea viscosa*. The samples ordination in DCA on the first axis suggests a gradient related to the substrate water availability, reflecting major availability in riparian forests and minor availability in grasslands. Samples progressively separated along the second axis probably reflect the substrate-type and topography. Grasslands pollen assemblages, dominated by anemophilous pollen, represent the regional vegetation of the *campos* region. However, grasslands are masked in local forests and shrublands samples, where the zoophilous pollen of their characteristic species dominates, representing each local vegetation type. This pollen dataset completes the information available for the Río de la Plata grasslands, useful for the interpretation of the region's fossil pollen records and for similar environments in different geographical areas.

1. Introduction

Pollen analysis, the study of fossil pollen and spores, is the principal technique for long-term vegetation reconstructions (Seppä, 2007). However, pollen records do not directly reflect plant abundance due to several factors such as differences in pollen production, dispersal and preservation of taxa (Prentice, 1988), which cause that some taxa are over-represented and others under-represented in pollen samples. Species with anemophilous pollination which produce high quantities of pollen grains are frequently over-represented in pollen assemblages while the zoophilous ones, with low pollen productivity, are under-represented (Fægri and Iversen, 1989). In consequence, the interpretation of fossil pollen records to reconstruct past vegetation changes can be improved by a better understanding of modern pollen–vegetation relationships, in order to assess how pollen percentages correspond with the vegetation (Seppä, 2007).

In South America, many authors have used modern pollen spectra to assist the interpretation of fossil pollen records (e.g., Salgado-Labouriau, 1973; Markgraf et al., 1981; Heusser, 1989; Mancini, 1993; Schäbitz, 1994; Behling et al., 1997; Lupo, 1998; Behling and da Costa, 2000; Bush et al., 2001; Paez et al., 2001; Ledru, 2002; Berrío et al., 2003; Reese and Liu, 2005; Gosling et al., 2009; Olivera et al., 2009; Bamonte and Mancini, 2011; Ortuño et al., 2011; Marcos and Mancini, 2012). In Río de la Plata grasslands (RPG), the main complex of grassland ecosystems in South America (Bilenca and Miñarro, 2004), modern pollen studies have been carried out in one of the sub-regions, the *pampas* (in the eastern Argentina), at regional (Prieto, 1992; Tonello and Prieto, 2008, 2009) and local scales (Stutz and Prieto, 2003; Fontana, 2005). On the contrary, few modern pollen studies are available in the *campos* (Uruguay and southern Rio Grande do Sul, Brazil), the other sub-region of the RPG. Only two

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studies at microscales have been carried out in Rio Grande do Sul (Behling et al., 2001; Jeske-Pieruschka et al., 2010) (Fig. 1) but none in Uruguay. Recent studies on vegetation history of the *campos* region of Uruguay (Iriarte, 2006; García-Rodríguez et al., 2010) demand additional evidence of modern pollen data in relation to modern vegetation to improve the interpretation of fossil pollen records.

The principal aim of this study is to establish the relationship between modern pollen assemblages and the principal vegetation types of the *campos* region of Uruguay. This will provide information currently unavailable for this region of South America. In this study, we present the modern pollen data from the *campos* region of Uruguay statistically quantified to respond to the following questions: (1) How is modern vegetation reflected in modern pollen assemblages? (2) Is it possible to distinguish the different vegetation types of the *campos* by modern surface pollen data? (3) How does prevailing pollination (anemophilous and zoophilous) influence the representation of modern pollen assemblages? (4) What type of information can we obtain from the modern pollen data for objective interpretation of fossil pollen records?

2. Study area

2.1. Environmental setting

Río de la Plata grasslands (Soriano, 1991) extend between 28° and 38°S latitude, covering about 700,000 km² of eastern Argentina, Uruguay and southern Rio Grande do Sul (Brazil) (Fig. 1), and are characterized by the dominance of grasses and other herbs. Based on geomorphological, hydrological and edaphic features and their linkages with natural vegetation and land use, the RPG were divided by León (1991) into the *pampas* in the eastern Argentina, and the *campos* in Uruguay and southern Rio Grande do Sul (Brazil) (Fig. 1). The high species richness of the *campos*, composed of about 2500–3000 species of vascular plants (Bilenca and Miñarro, 2004), together with the relatively high amounts of woody

species and grasses with C_4 metabolism, are some of the characteristics that differentiate it from the *pampas*. The presence of these woody species gradually diminishes from north to south, one of the facts that allowed the division of this sub-region in *southern* and *northern campos* (León, 1991) (Fig. 1). Most of these shrubby and arboreal species reach in Uruguay their southern distribution range and so they are absent in the *pampas*.

The study area is located in Uruguay and extends between 30–35°S and 53.5–58.5°W (Fig. 1). The *southern campos* are a gently-rolling area extending from the Negro and Yí rivers southward to the Atlantic coast. Drainage is unimpeded and the rivers generally flow in rocky channels (León, 1991). Rock outcrops are frequent in this area and hilly relief is located southward (highest altitude of Uruguay, 514 m a.s.l.). The relief of the *northern campos* is generally flat, but in some areas it is interrupted by low mesas or rock outcrops and sand deposits. Drainage is free and the westward slope results in a rich fluvial network tributary of the Uruguay River (León, 1991).

Some authors considered that Uruguay should not be fully included in the RPG (Chebataroff, 1960; Grela, 2004). According to Grela (2004), the relatively narrow strip that occupies the eastern part of the Uruguay River should be considered a transition between the Chaco and the Paranaense phytogeographical provinces, taking into account the penetration of tropical vegetation along this river and the species from Chaco phytogeographic province that develop in the adjacent plains (Fig. 1).

After the European colonization, the *campos* have progressively become one of the most important areas of livestock and grain production in the world (Bilenca and Miñarro, 2004). Furthermore, the expansion of cropland areas, the introduction of exotic grass species and their associated weeds, and more recently the substitution of grasslands for exotic forest plantations deeply modified the original landscape. However, natural or semi-natural grasslands and woody vegetation are found in uncultivated or undisturbed areas, and many of them are protected.
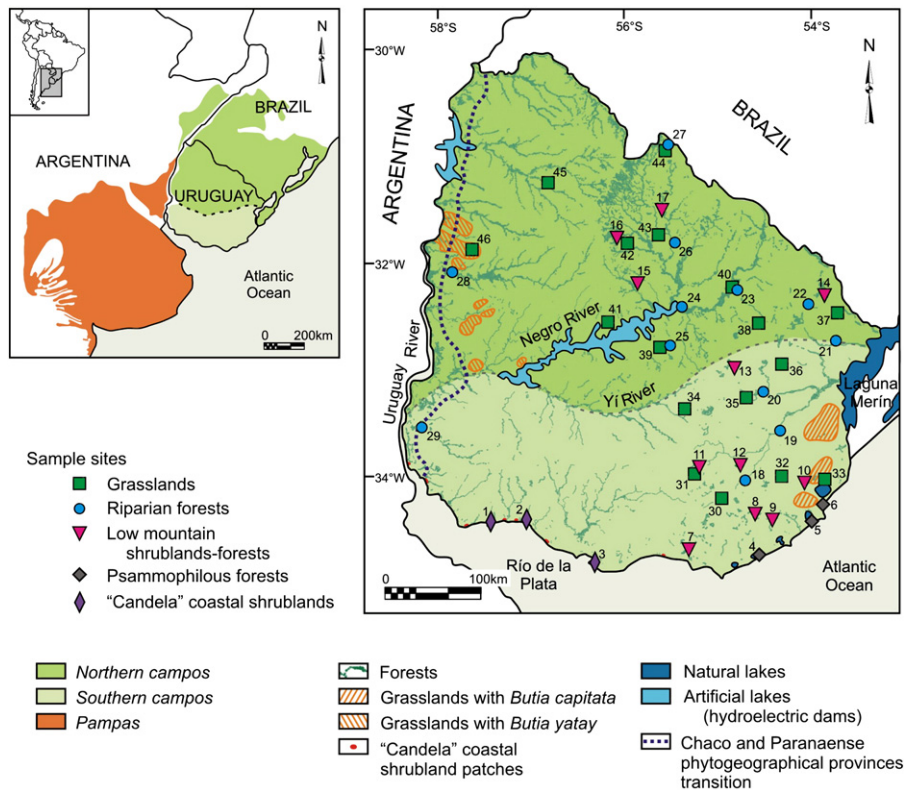

Fig. 1. Río de la Plata grasslands (RPG) and Uruguay map showing the main vegetation types and the location of the 46 modern pollen samples analyzed. RPG map modified from León (1991) and Tonello and Prieto (2008).

2.2. Climate

The climate in the study area is temperate, and the lack of major orographic features results in a gentle SW–NE precipitation gradient that ranges from 1100 mm/yr in the south-west to 1600 mm/yr in the north-east. Mean annual temperature ranges between 16° and 19 °C, with a maximum in summer (January) and a minimum in winter (July) (DNM, 2009).

2.3. Vegetation

Natural grasslands are the predominant vegetation type of the *campos* region and are extended all over Uruguay (*ca.* 77% of the territory), in flat and gently-rolling relief, hills, gentle hills and low mountains (del Puerto, 1987; Lezama et al., 2011) (Fig. 2a). Despite the fact that the climatic conditions are similar to other temperate world regions where forests predominate, woody vegetation (trees and shrubs) in the *campos* is limited to certain topographic features that provide relatively high water availability or wind protection, such as drainage systems and rocky slopes. The dominance of grasslands in this region can be explained by: (1) the brief frequent droughts, causing insufficient soil moisture to support the growth of woody species; (2) the occurrence of spring frosts; (3) the frequent winds that act as a drying agent, increasing the droughts; (4) the soil heterogeneity and water retention; and (5) the seedling inhibition and competition from grasses (del Puerto, 1969; Facelli and León, 1986).

Natural grasslands are very heterogeneous, composed of about 2000 species of vascular plants (del Puerto, 1987). This heterogeneity is also reflected in the biological and morphological plant characteristics (Brussa and Grela, 2007). The most important families, in terms of species number, are Poaceae (*ca.* 400 species) and Asteraceae (*ca.* 350 species) (del Puerto, 1969, 1987). Other important families are Cyperaceae, Fabaceae and Lamiaceae (Brussa and Grela, 2007). The most frequent taxa are shown in Table 1.

The floristic variations of the grasslands are mainly associated with macrotopographic and edaphic landscape scale differences, related to the water availability and drainage (Lezama et al., 2011).

The grasslands developed on the hills of the southeast are the most heterogeneous, due to the geomorphological and geological heterogeneity of these areas. In addition, shrubby grasslands are also common, with *Baccharis* as one of the genera most represented. Shrublands and forests are locally important. In some areas, scattered individuals of *Butia capitata* and *B. yatay* develop interspersed among grasslands (Figs. 1 and 2b) (Geymonat and Rocha, 2009).

Woody vegetation covers approximately 4.3% of the territory (Petraglia and Dell'Acqua, 2006) (Fig. 2c–f), and is composed of about 300 species of trees and shrubs (Brussa and Grela, 2007). The most widespread vegetation types are the riparian forests and low mountain shrublands-forests. Additionally, psamophilous forests and "Candela" shrublands develop along the coastal area but, due to the increasing tourism activities, urbanization and plantations, fragmentation has occurred through splitting the original distribution range into reduced isolated small patches (Alonso-Paz and Bassagoda, 1999) with no more than 100 ha.

For this work it was necessary to define the different vegetation types because there are no descriptions encompassing all vegetation types that develop in Uruguay, and they are subject to different classification systems, on which not all authors agree. Additionally, regional-scale descriptions are limited by methodological incompatibilities (Sayagués Laso et al., 2000; Lezama et al., 2011), which make it difficult to adopt a classification to study pollen–vegetation relationships. The frequent taxa of each vegetation type are shown in Table 1.

The riparian forests develop in narrow strips along the margin of rivers and water streams all over the territory (Brussa and Grela, 2007). They are dominated by tree species that are spatially arranged according to their water requirements: hydrophilous trees develop in the floodplains, while mesophilous ones develop in areas with somewhat reduced water availability. The understorey supports many ferns, herbs, small shrubs and tree seedlings. Additionally, epiphytes, climbers and parasitic plants can be very abundant. In the grassland-forest boundary, grasses and shrubby species usually grow (Brussa and Grela, 2007).

Low mountain shrublands-forests develop in rocky slopes and hills (Brussa and Grela, 2007). These low mountains normally support mesophytic or xerophytic species adapted to dry conditions. The tree-
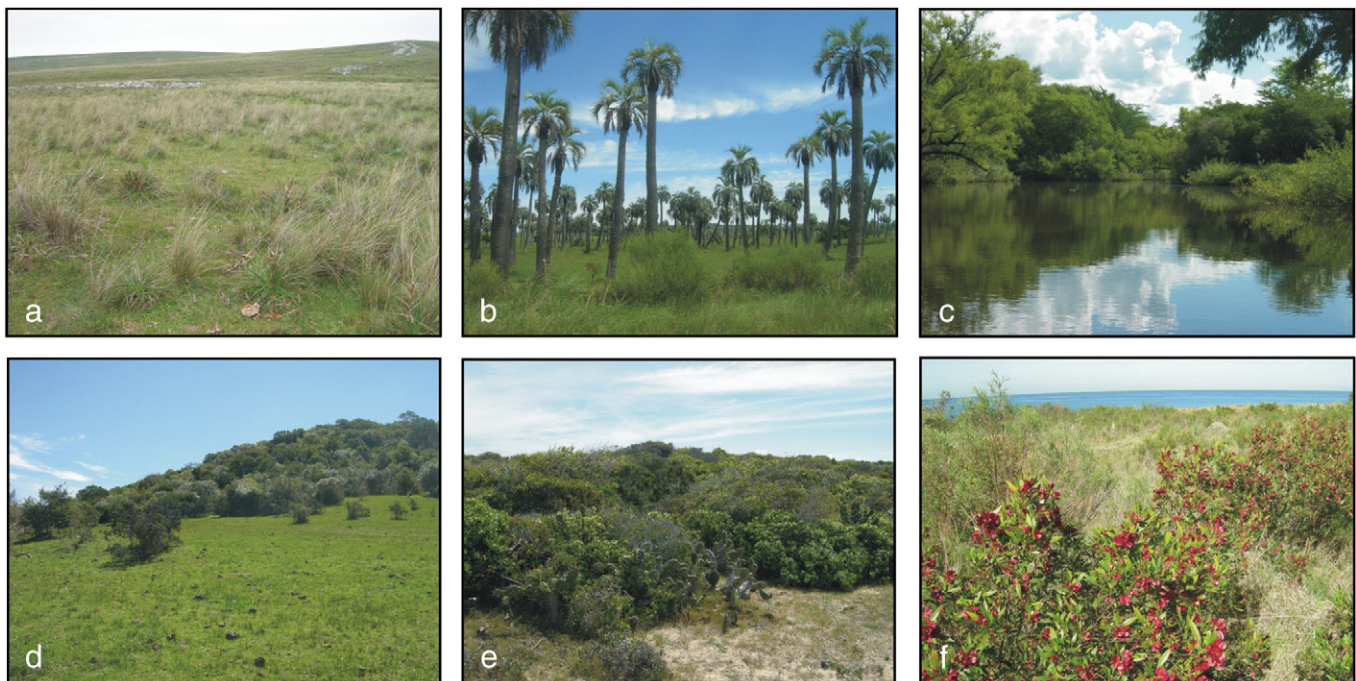
Fig. 2. Different vegetation types in the *campos* region of Uruguay: (a) grasslands; (b) grassland with *Butia capitata* individuals; (c) riparian forests; (d) low mountain shrublands-forests; (e) psammophilous forests; and (f) "Candela" coastal shrublands.

Table 1

Description of the vegetation types (Chebataroff, 1960; del Puerto, 1969, 1987; León, 1991; Alonso-Paz and Bassagoda, 1999, 2002a; Fagúndez and Lezama, 2005; Brussa and Grela, 2007; Geymonat and Rocha, 2009; Lezama et al., 2011)
and the associated modern pollen samples in the *campos* region of Uruguay.

Vegetation type	Habitat	Vegetation frequent taxa	Surface samples: characteristic pollen taxa
Grasslands	Flat and gently-rolling relief, hills, gentle hills and low mountains	*Stipa* spp., *Aristida* spp., *Andropogon* spp., *Briza* spp., *Erianthus* spp., *Piptochaetium* spp., *Paspalum* spp., *Axonopus* spp., *Panicum* spp. (Poaceae), *Baccharis* spp., *Eupatorium* spp. (Asteraceae), *Eryngium* spp. (Apiaceae), *Trifolium polymorphum* Poir., *Adesmia bicolor* (Poir.) DC. (Fabaceae), *Dichondra sericea* Sw. (Convolvulaceae), *Oxalis* spp. (Oxalidaceae), *Glandularia* spp. (Verbenaceae).	Samples 30 to 32; 34 to 45. Poaceae, Asteraceae subf. Asteroideae, Cyperaceae, Apiaceae, Monocotyledoneae.
Grasslands with palm individuals	Lowlands and flooding plains Sandy soils	Poaceae, *Butia capitata* (Mart.) Becc. (Arecaceae). Poaceae, *Butia yatay* (Mart.) Becc. (Arecaceae).	Samples 33 and 46. Poaceae, Cyperaceae, Apiaceae, *Butia*.
Riparian forests	Margin of rivers and water streams	Hydrophilous trees: *Sebastiania commersoniana* (Baill.) L.B. Sm. & Downs (Euphorbiaceae), *Erythrina cristi-galli* L. (Fabaceae), *Phyllanthus sellowianus* (Klotzsch) Müll. Arg. (Phyllanthaceae), *Cephalanthus glabratus* (Spreng.) K. Schum. (Rubiaceae), *Salix humboldtiana* Willd. (Salicaceae), *Pouteria salicifolia* (Spreng.) Radlk. (Sapotaceae). Mesophilous trees: *Lithraea molleoides* (Vell.) Engl., *Schinus longifolius* (Lindl.) Speg. (Anacardiaceae), *Celtis ehrenbergiana* (Klotzsch) Liebm. (Celtidaceae), *Ocotea acutifolia* (Nees) Mez, *O. Pulchella* (Nees) Mez (Lauraceae), *Myrsine laetevirens* (Mez) Arechav. (Myrsinaceae), *Blepharocalyx salicifolius* (Kunth) O. Berg, *Myrceugenia glaucescens* (Cambess.) D. Legrand & Kausel, *Myrcianthes cisplatensis* (Cambess.) O. Berg (Myrtaceae), *Scutia buxifolia* Reissek (Rhamnaceae), *Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl. (Sapindaceae).	Samples 18 to 29. Poaceae, Cyperaceae, Asteraceae subf. Asteroideae, *Sebastiania*, *Salix humboldtiana*, *Phyllanthus sellowianus*, Myrtaceae, *Myriophyllum*, *Polygonum*, *Nymphoides indica*.
Low mountain shrublands-forests	Hills, rocky slopes	Trees: *Lithraea molleoides*, *S. lentiscifolius* Marchand, *S. Longifolius* (Lindl.) Speg., *S. Molle* L. (Anacardiaceae), *Celtis ehrenbergiana* (Celtidaceae), *Myrsine coriacea* (Sw.) R. Br., *M. laetevirens* (Mez) Arechav. (Myrsinaceae), *Scutia buxifolia* (Rhamnaceae). Shrubs: *Baccharis* spp., *Heterothalamus alienus* (Spreng.) Kuntze (Asteraceae), *Croton* spp. (Euphorbiaceae), *Mimosa* spp. (Fabaceae), *Colletia paradoxa* (Spreng.) Escal. (Rhamnaceae), *Dodonaea viscosa* Jacq. (Sapindaceae), *Daphnopsis racemosa* Griseb. (Thymelaeaceae).	Samples 7 to 17. Poaceae, Cyperaceae, Asteraceae subf. Asteroideae, *Lithraea/Schinus*, Myrtaceae, *Myrsine*, Rhamnaceae in some samples.
Psammophilous forests	Sandy soils in coastal zones	Trees: *Lithraea brasiliensis* Marchand, *Schinus longifolius* (Anacardiaceae), *Ficus luschnathiana* (Miq.) Miq. (Moraceae), *Myrsine laetevirens*, *M. parvifolia* A. DC. (Myrsinaceae), *Blepharocalyx salicifolius* (Myrtaceae), *Scutia buxifolia* (Rhamnaceae), *Sideroxylon obtusifolium* (Roem. & Schult.) T.D. Penn. (Sapotaceae). Shrubs: *Rollinia maritima* Záchia (Annonaceae), *Varronia curassavica* Jacq. (Boraginaceae), *Ephedra tweediana* Fisch. & C.A. Mey. emend. J.H. Hunz. (Ephedraceae), *Colletia paradoxa* (Rhamnaceae), *Daphnopsis racemosa* (Thymelaeaceae).	Samples 4 to 6. Poaceae, Cyperaceae, *Lithraea/Schinus*, *Myrsine*, Rhamnaceae, *Ephedra tweediana*.
"Candela" coastal shrublands	Mobile and semi-fixed dunes in coastal zones	Shrubs: *Dodonaea viscosa* (Sapindaceae), *Baccharis* spp., *Eupatorium buniifolium* Hook. & Arn. (Asteraceae).	Samples 1 to 3. *Dodonaea viscosa*, Poaceae, Asteraceae subf. Asteroideae.

layer coverage is variable, based primarily on their topographic position on the hills which is related to the water availability. Thereby, at the bottom of the hills slope, trees have a better development due to the higher water availability and wind protection, whereas at the top of the slope the trees have shrubby growth habit and shrubs are dominant (Brussa and Grela, 2007). Between these forests and shrublands there is a gradual transition where forest circular patches develop between shrubby grasslands. Some climbers, parasitic plants and ferns also develop in these patches.

The psammophilous forests occur in sandy soils along the Atlantic Ocean coasts, in small fragmented patches. Their species have a shrubby growth habit due to the effects of strong winds. The exclusive species *Rollinia maritima*, *Varronia curassavica* and *Sideroxylon obtusifolium* link them with the "restinga" vegetation of southern Brazil (Alonso-Paz and Bassagoda, 2002b; Delfino et al., 2011). On the other hand, the "Candela" coastal shrublands develop in small fragmented patches on mobile and semi-fixed dunes along the Río de la Plata coast. They are dominated by a shrub, *Dodonaea viscosa*, which common name is "Candela".

3. Materials and methods

3.1. Field work

An extended dataset of 46 surface soil samples were collected from November 2008 to October 2009 following Adam and Mehringer (1975) sampling strategy. Soil samples were collected by taking five subsamples of the upper 2 cm of the surface on the tip of a trowel from an area of relatively uniform vegetation with an estimated area of 100–200 m². The subsamples were sealed in plastic bags and mixed thoroughly before extraction. A total of 15 samples were recorded in grasslands, 12 in riparian forests, 11 in low mountain shrublands-forests, 3 in psammophilous forests, and 3 in "Candela" coastal shrublands (Fig. 1; Table 1). In the coastal area, finding suitable sampling sites proved to be a challenging task, because the psammophilous forests and "Candela" coastal shrublands develop in very small patches that are surrounded by urbanizations and plantations. This explains the low number of samples that we could collect for this study in those coastal areas. However, the interest of including them has phytogeographical implications, taking into account their probable original distribution range and their linkages with the neighboring regions.

The sample sites are principally located in the eastern part of Uruguay because: (1) it concentrates a large number of different vegetation types than the eastern part; (2) it has minor human disturbance; and (3) it has water bodies where Holocene sedimentary sequences have been cored for palynological studies (Mourelle, in prep.). In the field, a qualitative vegetation survey was made at each sampling site. The brief description consisted of a general floristic inventory in order to control the correspondence with the vegetation types previously analyzed by botanists (Alonso-Paz and Bassagoda, 1999; Fagúndez and Lezama, 2005; Brussa and Grela, 2007; Lezama et al., 2011) and to facilitate the subsequent identification of pollen content in surface soil samples.

3.2. Laboratory work

Surface pollen samples were dried at 60 °C for 24 h. Subsamples of 5 to 15 g dry sediment were used for pollen analysis (except in "Candela" coastal shrubland samples where 50 to 60 g of fine sand was used). Sediment samples were sieved trough a 110 μm screen to remove coarse particles and then were processed according to standard palynological techniques including warm KOH, HCl, heavy-liquid separation with ZnCl₂, HF and acetolysis (Gray, 1965; Fægri and Iversen, 1989). Three *Lycopodium clavatum* spore tablets were added to every weighted sample before treatment to estimate representative pollen sums. Pollen grains and spores were counted using a microscope with 1000× magnification. Identifications were performed using the pollen reference collection of the Laboratory of Palaeoecology and Palynology, Universidad Nacional de Mar del Plata, Argentina; of the Laboratory of Palynology, Universidad de la República, Uruguay; with the reference pollen collection obtained from the herbarium material of the Museo y Jardín Botánico "Profesor Atilio Lombardo" (MVJB), Montevideo, Uruguay; and from flowers collected during the fieldwork, and were supplemented by published keys and photographs (Markgraf and D'Antoni, 1978; Prieto and Quattrocchio, 1993). Pollen nomenclature followed the nomenclature system of the Institute of Botany Darwinion, Argentina (http://www.darwin.edu.ar) and of the Missouri Botanical Garden (http://www.tropicos.org/).

In Uruguay there is a high abundance of native species of Myrtaceae, but also *Eucalyptus* plantations are spread throughout the country. In consequence, as it was necessary to differentiate *Eucalyptus* pollen grains from the other Myrtaceae taxa, we studied the pollen morphology of the main cultivated species of *Eucalyptus* (*E. grandis* W. Hill ex Maiden, *E. globulus* Labill. and *E. camaldulensis* Dehnh.) and separate them in the pollen counts. The multi-member myrtle family was undifferentiated.

Due to difficulties in distinguishing morphologically the pollen genera *Schinus* and *Lithraea*, they were grouped as *Lithraea/Schinus*, which only includes the trees *Lithraea molleoides*, *L. brasiliensis*, *Schinus longifolius*, *S. lentiscifolius*, *S. molle*, *S. engleri* F.A. Barkley and *S. ferox* Hassl. (Brussa and Grela, 2007).

Rhamnaceae family is represented in Uruguay by the trees *Scutia buxifolia* and *Condalia buxifolia* Reissek, the shrubs *Colletia paradoxa*, *C. spinosissima* J.F. Gmel. and *Discaria americana* Gillies & Hook. (Brussa and Grela, 2007) and the climber *Gouania ulmifolia* Hook. & Arn. that is frequent in the riparian forests of the Uruguay River (M. Bonifacino, personal communication, 2011). Their pollen grains could not be differentiated and thereby they were joined to the family level. However, considering the list of species of the qualitative vegetation surveys of the areas sampled and the species distribution range (Brussa and Grela, 2007), it was defined a priori that Rhamnaceae pollen grains from the riparian forest samples considered in this study could correspond exclusively to *Scutia buxifolia*, while the presence of them in samples from the other vegetation types could be from any species belonging to this family.

Due to the low taxonomic resolution of Asteraceae pollen grains, they were grouped as Asteraceae subf. Asteroideae and Asteraceae subf. Cichorioideae. The former includes shrubs and herbs.

Pollen grains of *Butia capitata* and *B. yatay* are indistinguishable (Bauermann et al., 2010) and, for that reason, they were clustered as *Butia*.

Acacia pollen represents native taxa as the shrub *A. bonariensis* Gillies ex Hook. & Arn. However, in coastal samples, *Acacia* represents the exotic species *A. longifolia* (Andrews) Willd. which was introduced during the mid-twentieth century to diminish dune erosion. *A. caven* (Molina) Molina is a native species that naturally develops along the coast, but their pollen morphology differs from *A. longifolia* and it was not recorded in pollen counts.

Due to the over-representation of Poaceae in grassland samples, 300 pollen grains excluding Poaceae were counted in order to obtain a good representation of the subordinated taxa.

A total of 67 pollen and spore taxa were represented in the original database (Table 2). The total pollen sum varied between 278 and 1740 grains, and includes pollen from herbs and aquatic herbs (herbaceous pollen), shrubs (shrubby pollen), trees (arboreal pollen) and climbers. Introduced and long distance pollen, ferns and bryophytes, and both undetermined pollen and spores were counted and expressed as percentages of the total palynomorphs (pollen and spore) sum. Undetermined refers to palynomorphs which botanical affinities are unknown or were broken or crumpled.

Numerical analyses were performed to determine whether the vegetation types are associated with characteristic pollen spectra from which the parent vegetation can be identified. Pollen variables were selected for numerical analyses if: (1) the mean value of each

Table 2
List of the 67 identified pollen and spore taxa in the 46 modern pollen samples of the *campos* region of Uruguay. A: Anemophilous pollen; Z: Zoophilous pollen. Pollination characteristics according to Fægri and Pijl (1979), Bazzurro (1998), Navarro et al. (1998), Kinoshita et al. (2006), Martins and Batalha (2006, 2007) and Araújo et al. (2009).

Herbs	Shrubs	Introduced
Apiaceae (Z)	*Abutilon* (Z)	*Casuarina cunninghamiana*
Asteraceae subf. Cichorioideae (Z)	*Acacia* (Z)	Cupressaceae
Brassicaceae (Z)	*Daphnopsis racemosa* (Z)	*Eucalyptus*
Caryophyllaceae (Z)	*Dodonaea viscosa* (Z)	Juglandaceae
Chenopodiaceae/Amaranthaceae (A-Z)	*Ephedra tweediana* (A)	*Ligustrum*
Cyperaceae (A)	*Maytenus ilicifolia* (Z)	*Lonicera japonica*
Echium-type (Z)	*Pavonia* (Z)	*Pinus*
Fabaceae subf. Faboideae (Z)	*Phyllanthus sellowianus* (Z)	
Galianthe-type (Z)		Long distance
Lythraceae (Z)	Shrubs and trees	*Alnus*
Monocotyledoneae (A-Z)	Rhamnaceae (Z)	*Nothofagus dombeyi*-type
Oxalis (Z)		
Plantago (A)	Trees	Ferns
Poaceae (A)	*Allophylus edulis* (Z)	*Anemia*
Polygalaceae (Z)	*Butia* (Z)	Aspleniaceae/Dryopteridaceae
Ranunculaceae (Z)	*Celtis* (Z)	*Blechnum*-type
Sida-type (Z)	*Ilex paraguayensis* (Z)	*Isoetes*
Urticaceae (A)	*Lithraea/Schinus* (Z)	*Lycopodiella*
Verbenaceae (Z)	*Myrsine* (Z)	*Ophioglossum*
	Myrtaceae (Z)	Polypodiaceae
	Ocotea (Z)	*Pteris*
	Pouteria salicifolia (Z)	Other pteridophytes
Aquatic herbs	*Salix humboldtiana* (Z)	
Myriophyllum (A)	*Sapium* (Z)	Bryophytes
Nymphoides indica (Z)	*Sebastiania* (Z)	*Anthoceros*
Polygonum (Z)		*Phaeoceros*
	Climbers	Ricciaceae
Herbs and shrubs	*Cissus* (Z)	
Asteraceae subf. Asteroideae (Z)	*Tripodanthus acutifolius* (Z)	

variable in percentage was higher than 1.5%; or (2) if the variable has a value higher than 5% in at least one sample. Even though *Tripodanthus acutifolius* encompass these requirements, it was excluded for the numerical analyses because it is a hemiparasite species that frequently grows on the native forest trees but also on the introduced ones, planted overall the *campos*. As a result, 23 pollen types were selected for numerical analyses: *Acacia*, *Allophylus edulis*, Apiaceae, Asteraceae subf. Asteroideae, *Butia*, *Celtis*, Chenopodiaceae/Amaranthaceae, Cyperaceae, *Daphnopsis racemosa*, *Dodonaea viscosa*, *Ephedra tweediana*, *Lithraea/Schinus*, Monocotyledoneae, *Myrsine*, Myrtaceae, *Oxalis*, *Phyllanthus sellowianus*, Poaceae, *Pouteria salicifolia*, Rhamnaceae, *Salix humboldtiana*, *Sebastiania* and Urticaceae. *Acacia* pollen was excluded for numerical analyses in the coastal samples (psammophilous forests and "Candela" coastal shrublands) because it represents the introduced *Acacia longifolia*.

The percentage data were square root transformed prior to numerical analyses in order to stabilize their variances. Pollen samples were classified into groups using Cluster Analysis unconstrained (Birks and Gordon, 1985) with Euclidean distance (Overpeck et al., 1985). To assess whether to apply linear- or unimodal-based numerical techniques (ter Braak, 1986), the data set was first analysed by Detrended Correspondence Analysis (DCA) to estimate the length of the composition gradient (ter Braak and Prentice, 1988), choosing the options detrended-by-segments and downweighting of rare taxa. According to ter Braak and Prentice (1988), linear ordination methods perform better for short gradients (<1.5 SD units) and unimodal methods are more suitable for long gradients (>3 SD units), whereas both methods may be appropriate for intermediate gradient lengths. As the gradient length of the pollen assemblage is 1.68 SD units along the first axis, we used DCA to ordinate the data. Ordination analyses were implemented with CANOCO version 4.5 program (ter Braak and Ŝmilauer, 2003). Pollen percentages were calculated and pollen diagrams were drawn using TGView 2.0.2 program (Grimm, 2004).

Pollen types were characterized according to their pollination characteristics in anemophilous and zoophilous. Those pollen types which taxonomic resolution was at the family, sub-family or genera

level were classified considering the predominant pollination type of those species present in the local plant communities (Table 2).

4. Results

4.1. Cluster Analysis (Figs. 3 and 4)

The Cluster Analysis of the selected pollen taxa split the five vegetation types into four groups of pollen assemblages (Figs. 3 and 4). Group I represents grasslands. Their pollen assemblages are dominated by herbs (70–95%), mainly represented by Poaceae (50–85%) and Cyperaceae (<20%); except in sample 42 where Cyperaceae represents 40%, Poaceae 20% and Urticaceae 13%. Minor proportions of Apiaceae and Monocotyledoneae (<10%) are also well represented. Asteraceae subf. Asteroideae pollen frequencies are also high (<30%). However, pollen of woody taxa appears scarcely (<5%), mostly represented by Myrtaceae, *Celtis*, *Myrsine*, *Allophylus edulis* and *Lithraea/Schinus*. *Butia* pollen is present only in samples 33 and 46 (with 0.5 and 8%, respectively). Anemophilous pollen dominates (60–90%).

Group II represents "Candela" coastal shrublands vegetation, characterized by shrubs (40–65%) associated with herbs (25–40%) and Asteraceae subf. Asteroideae (<20%). The former are mainly represented by *Dodonaea viscosa* (35–55%), whereas the herbs correspond principally to Poaceae (20–35%). Percentages of arboreal pollen taxa reach up to 15%, represented principally by *Celtis* and Myrtaceae. *Myrsine* is overrepresented in sample 2 (7%). Zoophilous pollen dominates (60–80%).

Group III comprises samples from low mountain shrublands-forests and psammophilous forests. Pollen assemblages are co-dominated by herbs (30–75%), Asteraceae subf. Asteroideae (<45%) and trees (<30%). Climbers pollen is frequent, reaching up to 20%. Zoophilous pollen taxa dominates in most of the samples (>50%). This group is divided into two sub-groups. Sub-group IIIa comprises eight low mountain shrublands-forests samples, characterized by high pollen frequencies of herbaceous pollen (35–75%), mostly represented by Poaceae (20–55%) and Cyperaceae (<20%) and minor proportions of Monocotyledoneae, Apiaceae, *Oxalis* and Chenopodiaceae/Amaranthaceae (<5%). Asteraceae
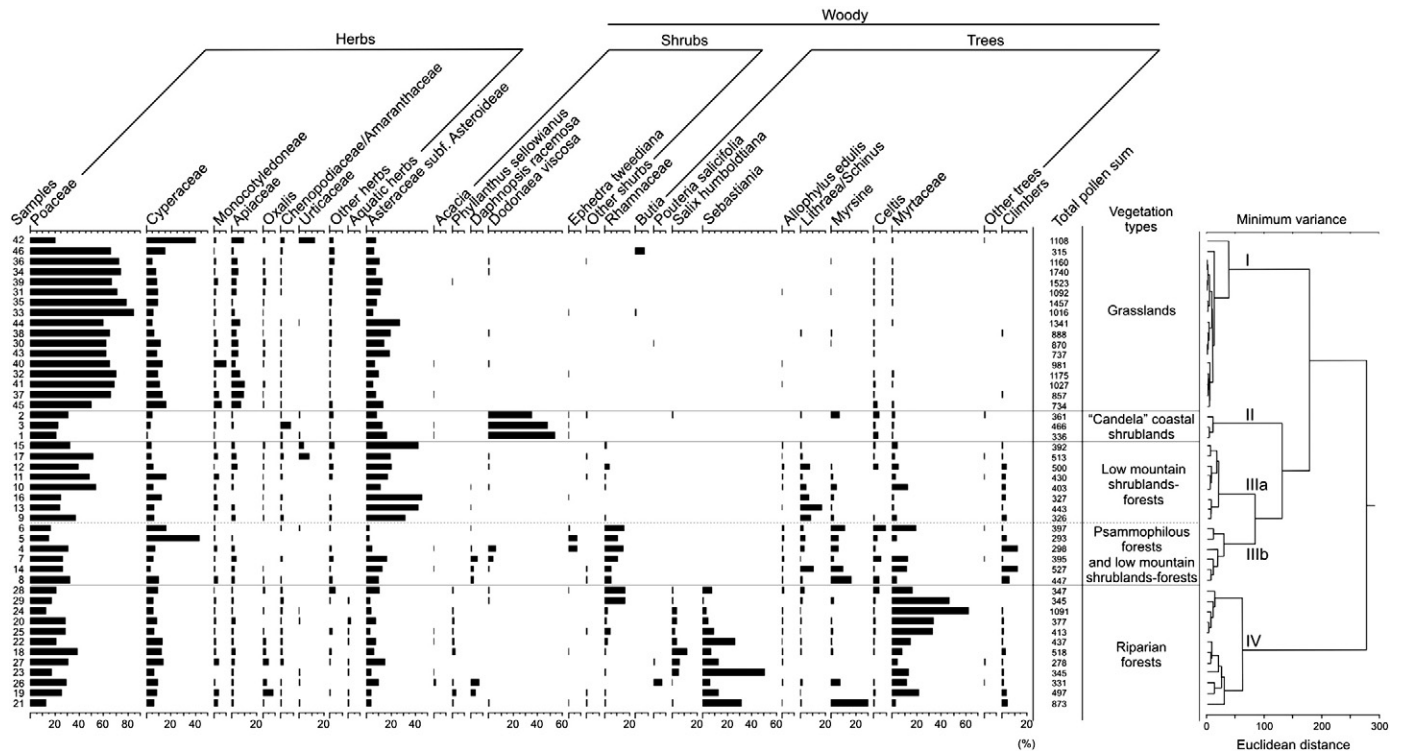
Fig. 3. Pollen diagram of the 46 surface soil samples in percentages ordered according to the Cluster Analysis unconstrained results.

subf. Asteroideae pollen is also well represented (10–45%), whereas arboreal pollen is less frequent (<25%), mainly represented by *Lithraea/Schinus* (<20%) and Myrtaceae (<15%). Other contributors are Rhamnaceae and the shrubs *Dodonaea viscosa* and *Daphnopsis racemosa* (<5%). Sub-group IIIb includes three samples from low mountain

shrublands-forests and three from psammophilous forests. These samples are characterized by higher values of arboreal pollen (<45%), Rhamnaceae and shrubby pollen (<20%) than sub-group IIIa. Arboreal pollen are represented by *Myrsine* and Myrtaceae (<20%), associated with *Celtis*, *Lithraea/Schinus* (<10%), *Allophylus edulis* (<5%) and
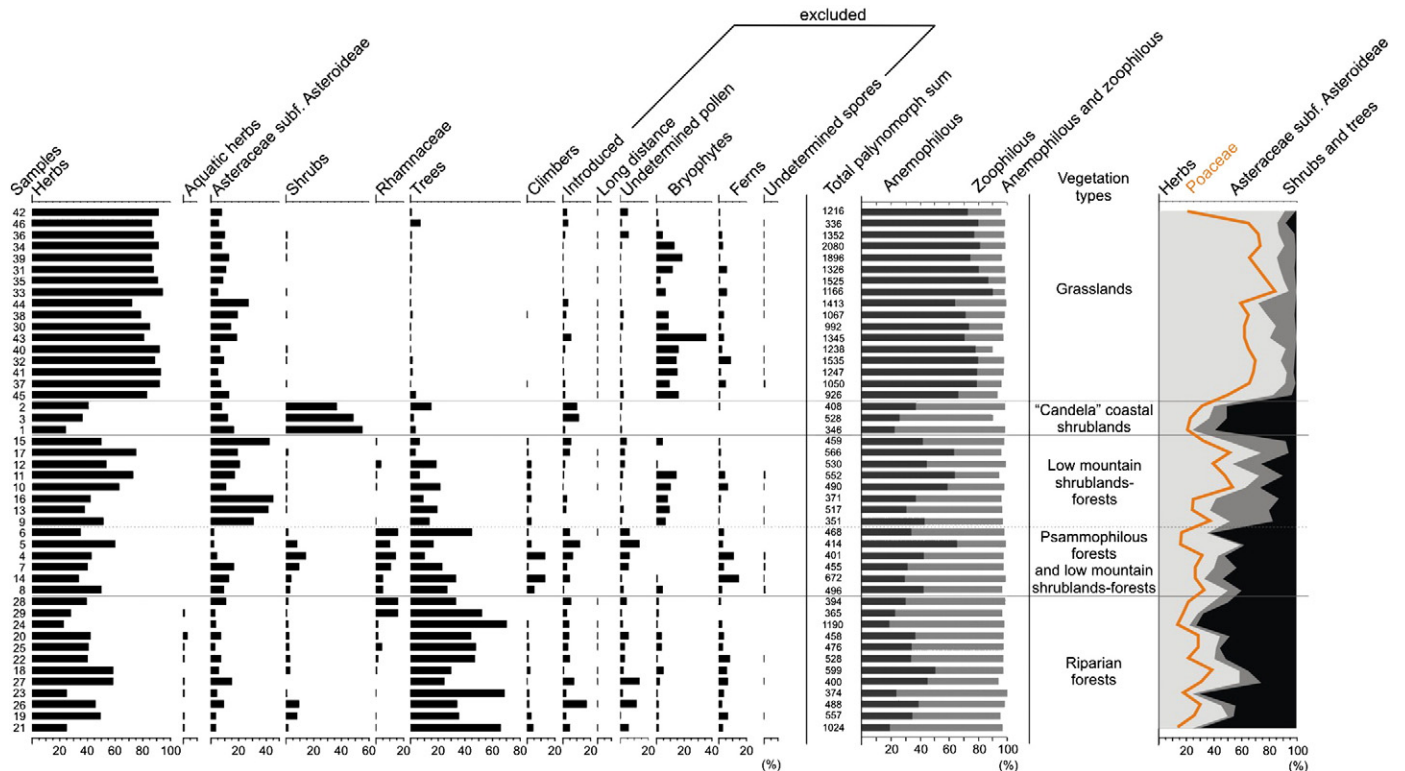

Fig. 4. Summary percentage pollen and spore diagram of the 46 surface soil samples, including total palynomorph sum, the anemophilous and zoophilous pollen and the ecological groups. The samples are ordered according to the Cluster Analysis unconstrained results.

shrubby pollen (*Dodonaea viscosa* and *Daphnopsis racemosa*,<5%). Herbaceous pollen are mostly represented by Poaceae (<35%) and Cyperaceae (<15%). Samples of low mountain shrublands-forests have higher values of Asteraceae subf. Asteroideae than psammophilous forest ones (<20% and <5%, respectively), and only in the latter ones *Ephedra tweediana* is present, reaching up to 10%.

Group IV represents riparian forests vegetation and is characterized by some exclusive taxa: *Sebastiania, Salix humboldtiana, Phyllanthus sellowianus, Pouteria salicifolia* and aquatic herbs. Pollen assemblages are co-dominated by arboreal (25–75%) and herbaceous (20–60%) pollen. The former are mostly represented by maximum values of Myrtaceae, reaching up to 65%, accompanied by *Sebastiania* (<50%) and *Salix humboldtiana* (<15%), and by minor proportions of Rhamnaceae, *Myrsine, Lithraea/Schinus, Allophylus edulis* and *Celtis*. Herbaceous pollen are represented by Poaceae (10–40%) and Cyperaceae (<15%), accompanied by *Oxalis* (<10%), Monocotyledoneae, Apiaceae and Chenopodiaceae/Amaranthaceae (<5%). Asteraceae subf. Asteroideae and shrubby pollen reach values up to 15%, the latter represented by *Phyllanthus sellowianus* (<5%) and in some samples by *Acacia* and *Daphnopsis racemosa*. Zoophilous pollen dominates (>50%).

Long distance pollen are represented in some samples by very low amounts of *Alnus* and *Nothofagus dombeyi*-type (<0.5%). Introduced pollen are represented in all samples, reaching up to 11%, principally due to *Pinus* (<11%) and *Eucalyptus* (<9%). The *Acacia* pollen found in coastal samples (psammophilous forests and "Candela" coastal shrublands) represents the introduced species *Acacia longifolia*. Ferns are represented in samples from all vegetation types (<15%), whereas bryophytes are well represented in grasslands and in low mountain shrublands-forests (<20%).

4.2. Detrended Correspondence Analysis (DCA) (Fig. 5)

The DCA revealed a composition gradient of 1.68 standard deviations units along the first axis, indicating that unimodal-based numerical methods are appropriate to analyse the data. The first two DCA-axes account 36.3% of the total variance. The DCA separates the samples into five groups (Fig. 5) consistent with the different vegetation types. The DCA results suggest a major separation on the first axis (25.4%), with hydrophilous tree species as *Sebastiania, Salix humboldtiana* and *Phyllanthus sellowianus*, exclusive from the riparian forest (scores less than −0.75), in contrast to Poaceae, Apiaceae,

Asteraceae subf. Asteroideae and *Butia* pollen, characteristic of different grasslands (scores higher than 1.25). The second axis (10.9%) separates some shrubby and arboreal pollen (*Ephedra tweediana*, Rhamnaceae, *Myrsine* and *Celtis*) and *Dodonaea viscosa*, characteristic of psammophilous forests and low mountain shrublands-forests, and of the "Candela" coastal shrublands, respectively, from the other pollen types that characterize the other vegetation types. Herbaceous pollen (Poaceae, Apiaceae, Monocotyledoneae and Cyperaceae), Asteraceae subf. Asteroideae and arboreal pollen (*Myrsine, Celtis, Lithraea/Schinus, Allophylus edulis* and Myrtaceae) are present in the low mountain shrublands-forests and occupy an intermediate position in both the first and second axes, showing that they share many taxa with the other vegetation types.

5. Discussion

Pollen analyses from modern surface samples revealed the good relation between modern pollen assemblages and the principal vegetation types of the *campos* region of Uruguay, and provided useful data for the interpretation of Holocene pollen sequences from the east and southeast of Uruguay. According to the numerical analyses, surface samples can be divided into five groups which correspond to (1) grasslands, (2) riparian forests, (3) low mountain shrublands-forests, (4) psamophilous forests, and (5) "Candela" coastal shrublands.

The samples ordination in DCA on the first axis (Fig. 5) suggests a gradient related to the substrate water availability, reflecting the major availability in riparian forests and minor in grasslands. Samples progressively separated along the second axis probably reflect the substrate-type and topography.

The occurrence of *Pinus* and *Eucalyptus* in most samples can be explained by the fact that these plants are widespread throughout the forestations in Uruguay. Therefore, although we chose sample sites distant from forested areas, pollen grains of these species reach all the samples under study. Moreover, other introduced pollen grains were also recorded due to their dispersion from the roads (that are generally surrounded by introduced trees) and country houses.

Nothofagus dombeyi-type represents wind pollen transported for more than 1000 km from the Subantarctic *Nothofagus* forests that develop on the foothills of the Andes, south of latitude 37 °S. On the other hand, *Alnus* is not present in Uruguay, and so its pollen grains also represent long distance transport, probably from the *pampas*,
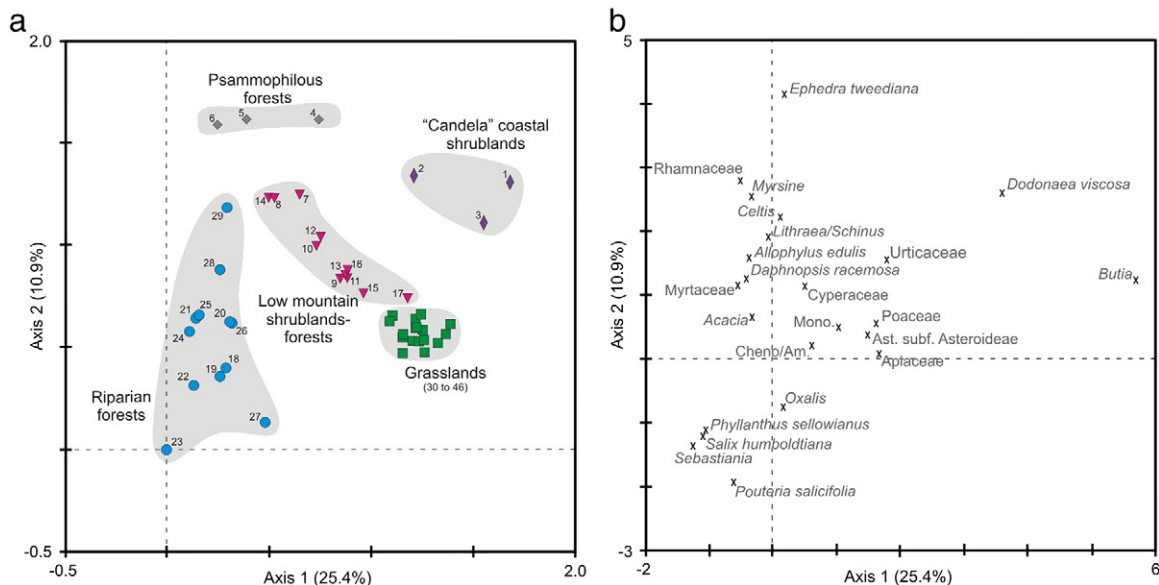

Fig. 5. DCA ordination of the (a) 46 surface soil samples and (b) the 23 pollen types considered for numerical analyses along the first and second ordination axis. Cheno/Am.: Chenopodiaceae/Amaranthaceae; Mono.: Monocotyledoneae.

where it has been introduced as exotic tree, or from the "Yungas" forests of northwestern Argentina.

5.1. Grasslands

Poaceae, Cyperaceae and Asteraceae dominate the pollen assemblages of grasslands. Poaceae represents species of the genera such as *Stipa, Aristida, Paspalum, Piptochaetium* and *Briza*, whereas Cyperaceae represents *Carex, Cyperus, Eleocharis, Kyllinga* and *Bulbostylis*. The dominance of Cyperaceae pollen in some samples represents small local communities related to higher substrate water availability. In consequence, these samples can be used to identify local communities in the grasslands, as it happens in the *pampas* (Stutz and Prieto, 2003; Fontana, 2005).

On the other hand, although Asteraceae subf. Asteroideae plants are zoophilous and produce much less pollen than other wind-pollinated species, the high values of Asteraceae subf. Asteroideae recorded can be explained by the relatively high frequency of this family in natural grasslands. Most of the Asteraceae subf. Asteroideae pollen grains probably derived from both herbs (*Gamochaeta* spp., *Sencio* spp. and *Achyrocline* spp.) and shrubs (*Baccharis* spp. and *Eupatorium buniifolium*).

Apiaceae is also well represented in pollen assemblages, principally due to *Eryngium* sp., a taxon very common in the grasslands vegetation. Other frequent graminoid herbs in grasslands are also present in the pollen assemblages. Monocotyledoneae corresponds to various families such as Juncaceae, Amaryllidaceae and Iridaceae. *Oxalis* represents many species widely dispersed in the *campos*. Fabaceae, mostly represented by species of the genera *Trifolium, Adesmia* and *Vicia*, occur more frequently in vegetation than in pollen assemblages. This underrepresentation could be related to the zoophilous pollinitation. The same was also observed in modern samples of the *campos* of Rio Grande do Sul, Brazil (S. Bauermann, personal communication, 2011). The absence of Lamiaceae in pollen grassland samples could also be explained by the family pollination strategy (zoophilous) associated with low pollen productivity.

All these taxa are frequent components of the grasslands but the limited taxonomic resolution of their pollen grains did not make it possible to classify them in more detail and did not allow us to detect floristic variations present in the grasslands vegetation. For example, samples from *northern* and *southern campos* were undifferentiated by pollen analysis, as well as the samples from grasslands of the southeast hills of Uruguay, which are more heterogeneous than others areas. These results confirm previous modern pollen analyses in the *pampas* that have demonstrated the difficulty to separate the grasslands into different vegetation units (Prieto, 1992; Tonello and Prieto, 2008, 2009). Nevertheless, different proportions of pollen types that accompanied Poaceae in some areas of the *pampas* have allowed the identification of different local plant communities (Stutz and Prieto, 2003; Fontana, 2005). In this study, *Butia* pollen suggests the development of palms interspersed among grasslands. Values <0.5% represent six *B. capitata* individuals/ha, whereas values up to 8% represent 160 *B. yatay* individuals/ha (samples 33 and 46, respectively). Although palms are zoophilous and do not flower every year, further research is needed in reference to their pollination vectors, particularly in *B. capitata* (Molina Espinosa, 2001). Also, wind-pollination has to be considered because Arecaceae pollen grains have been found in aerobiological samplers (Gattuso et al., 2003).

On the other hand, the lack of taxonomic precision in pollen identification implies being unable to differentiate between native plants and weeds. In consequence, it is necessary to consider that various pollen types that constitute this modern pollen–vegetation analogue include pollen grains of weed taxa that could not be separated from native ones, as it happens in the *pampas* (Prieto, 1992).

No significant differences between the parameters of Poaceae grains from the *campos* and the *pampas* were observed in fossil Poaceae pollen grains (Schüler and Behling, 2011). However, the RPG grass pollen grains were considerably smaller compared to the ones from the other grassland regions (Schüler and Behling, 2011). Since the lack of taxonomic resolution causes subsequent loss of ecophysiological information, additional proxies with which to compare the pollen data, like phytoliths and isotopes, are needed for paleoecological reconstruction and modeling of grass-dominated ecosystems (Wooller and Beuning, 2002).

Arboreal pollen representation is somewhat limited in the pollen assemblages. In the *campos*, forests are local vegetation types that develop in restricted areas. They are dominated by trees, which have low pollen production and dispersal because most of them are zoophilous. In consequence, very small amounts of arboreal pollen grains reach the grasslands, regardless the closeness of both vegetation types: grassland sample sites were at a distance of 250 to 4500 m in respect of any forest. Although grassland surface samples of the northern limit of the *campos* in Brazil are also dominated by similar proportions of Poaceae, Cyperaceae and Asteraceae subf. Asteroideae, arboreal pollen of Myrtaceae, *Myrsine* and *Schinus* are present in higher values (12–20%), probably related to the closest proximity of the sample sites with forests (<100 m) (Behling et al., 2001; Jeske-Pieruschka et al., 2010). Herbaceous pollen values in the grasslands of the *campos* are similar to the values reported by Tonello and Prieto (2008) for the grasslands biome of the *pampas*, where Poaceae dominates the pollen assemblages (40–70%) accompanied by Asteraceae subf. Asteroideae, Cyperaceae and Apiaceae. However, Asteraceae subf. Cichorioideae and Chenopodiaceae reach values up to 25% in the grasslands biome of the *pampas* (Tonello and Prieto, 2008), whereas in the *campos* they represent less than 2.5%. Asteraceae subf. Cichorioideae pollen with values between 10 and 20% has been interpreted by Prieto et al. (2004) as an indicator of soils that have been tilled over several years.

Bryophytes are dominated by *Phaeoceros*, which develop in humid soils (Hässel de Menéndez, 1962). Ferns correspond principally to *Ophioglossum* and *Isoetes*: the former represents *O. crotalophoroides* Walter, *O. nudicaule* L. f. and *O. opacum* Carmich., and the latter represents *I. weberi* Herter (Brussa and Grela, 2005).

5.2. Riparian forests

Riparian forest pollen samples are distinguished from the other ones due to the occurrence of some exclusive pollen from hydrophilous trees such as *Sebastiania, Salix humboldtiana* and *Phyllanthus sellowianus* and aquatic herbs such as *Myriophyllum, Polygonum* and *Nymphoides indica*. On the other hand, species as *Cephalanthus glabratus* and *Erythrina crista-galli*, which occur frequently in this vegetation type, were not recorded in the surface samples. Additionally, few pollen grains of *Pouteria salicifolia* and *Ocotea* were found, even though these plants are very common in the riparian vegetation. Interspecific differences in pollen production and dispersion could be responsible for this under-representation (Behling and Negrelle, 2006), together with taphonomic processes that could cause a poor preservation of pollen grains. For example, *Ocotea* pollen grains are very fragile and are not usually found in pollen assemblages (Behling and Negrelle, 2006).

The riparian forest samples are also characterized by Myrtaceae, which reaches the highest values of the pollen spectra (up to 65%) and represents species as *Blepharocalyx salicifolious, Myrcianthes cisplatensis* and *Myrceugenia glaucescens*, and other ones more distant from the water bodies as *Eugenia uniflora* L., *E. uruguayensis* Cambess. and *Myrrhinium atropurpureum* Schott. Unfortunately, the high diversity of this family in the vegetation is not truly expressed in modern surface pollen assemblages because of the low taxonomic resolution of their pollen grains that disables their differentiation at genus or species level. The arboreal pollen with minor pollen values mainly represents the mesophilous species of the riparian forest vegetation. In these riparian forests, Rhamnaceae represents *Scutia buxifolia*

exclusively. Shrubby pollen is mainly represented by *Phyllanthus sellowianus*, but also by species that principally develop in areas with reduced water availability, such as *Acacia bonariensis* and *Daphnopsis racemosa*. Although the trees and shrubs are mainly zoophilous, the local vegetation of the riparian forests is very well represented in the pollen assemblages (Fig. 4), and the dominance of grasslands in the *campos* is masked by the local pollen signal of the riparian forest in these samples. These results are very important because in the *campos* some water bodies, where fossil sequences have been cored for further studies, are surrounded by riparian forests and so their sediments are probably unable to document grassland changes in the large surroundings, by masking and underrepresenting the regional pollen signal. The herbaceous pollen of riparian forest samples mainly corresponds to the forest understorey, principally composed of Poaceae and Cyperaceae species, but also of the grass pollen dispersed from the edge of the forest, such as *Paspalum quadrifarium* Lam. and *Coleataenia prionitis* (Nees) Soreng, and some Asteraceae shrubby species, as *Baccharidastrum* spp. and *Baccharis* spp. Probably pollen grains from the neighboring grasslands reach the forest interior but in minor proportions.

Both bryophytes and ferns were recorded in riparian forest samples. Bryophytes are mainly represented by *Phaeoceros*, frequent in the margins of rivers and streams (Hässel de Menéndez, 1962). Ferns are represented by *Isoetes* and Polypodiaceae: *Isoetes* spp. develops in humid areas, whereas Polypodiaceae is a family with wide distribution range in Uruguay, composed of various species from genera such as *Campyloneurum*, *Pleopeltis* and *Microgramma*.

5.3. Low mountain shrublands-forests

In low mountain shrublands-forests, trees grow in small circular patches surrounded by shrubby grasslands. This vegetation physiognomy allows an important development of the herbaceous forest understorey and facilitates the entrance of pollen from the surrounding shrubs and grasses into the forest. As a consequence, the herbaceous pollen and Asteraceae subf. Asteroideae in these samples represent the understorey and the shrubby grasslands, respectively, and they co-dominate the pollen assemblages together with arboreal pollen from the forest patches. In spite of being zoophilous, the high frequency of Asteraceae subf. Asteroideae pollen can be explained by the high frequency of these plants in those shrubby grasslands, represented by many *Baccharis* species, *Heterothalamus alienus* and *Eupatorium buniifolium*. Also, this results in a co-dominance of anemophilous and zoophilous pollen taxa in these samples.

The pollen types found in the low mountain shrublands-forests samples are shared with all the other vegetation types. Asteraceae subf. Asteroideae represents taxa as *Heterothalamus alienus* and *Baccharis* spp. that are accompanied by shrubs as *Dodonaea viscosa* and *Daphnopsis racemosa*, all characteristics of the shrublands that develop around the forest patches. The trees are mainly represented by *Lithraea/Schinus* and Myrtaceae. *Lithraea brasiliensis* is one of the most abundant species in those forests patches (Brussa and Grela, 2007); *Schinus* represents *S. longifolia*, *S. molle* and *S. lentiscifolius*; and *Blepharocalyx salicifolius*, *Myrrhinium atropurpureum*, *Myrcianthes cisplatensis*, *Eugenia* spp. and *Myrceugenia glaucescens* are the main Myrtaceae taxa that develop in those patches.

In particular, in the top of the Miriñaque hill (sample 17) a population of *B. paraguayensis* (Barb. Rodr.) L.H. Bailey develops, but its pollen grains are not represented. This absence prevents us to interpret this as an absence of palms in the vegetation. By the contrary, when *Butia* pollen is present in pollen assemblages (see Section 5.1) implies that palms are present in local vegetation, very close to the sampled site. This is an important observation as it makes clear the signal of the palm pollen on fossil records.

As in the grassland samples, bryophytes and ferns are present and mainly represent *Phaeoceros*, and *Ophioglossum* and *Isoetes*, respectively.

5.4. Psammophilous forests

According to the Cluster Analysis, psammophilous forest samples were joined with some low mountain shrublands-forests ones (subgroup IIIb, Figs. 3 and 4). However, the DCA divided these samples into two discrete groups according to each vegetation type (Fig. 5): the differences between these two groups of samples may be related to the higher values of *Ephedra tweediana* and Rhamnaceae, and minor of Asteraceae subf. Asteroideae in psammophilous forest samples. *Ephedra tweediana* is the only native gymnosperm of Uruguay and it has a major development in coastal environments with respect to the inland ones, which is clearly reflected in the surface pollen samples. Rhamnaceae represents *Scutia buxifolia* and *Colletia paradoxa*, abundant species in this vegetation.

Pollen grains from the characteristic species of the psammophilous forest vegetation were not present in the pollen assemblages. Its absence may be related to the fact that *Rollinia maritima* has cleistogamous flowers and its development is favored far from the sea coast, in humid areas and protected from the strong coastal winds (Ríos, 2007); *Varronia curassavica* develops irregularly in the shrubby strip closest to the sea (Delfino et al., 2011); and *Sideroxylon obtusifolium* is represented by few large long-lived individuals in fixed dunes (Delfino et al., 2011). In consequence, although both vegetation types present the same pollen grains in their pollen assemblages, their proportions were different enough only to the DCA to separate the sample according to each vegetation type.

Fern spores mainly represent Polypodiaceae, which corresponds to *Microgramma vacciniifolia* (Langsd. & Fisch.) Copel. and *Pleopeltis hirsutissima* (Raddi) de la Sota.

5.5. "Candela" coastal shrublands

Dodonaea viscosa dominates the pollen spectra from "Candela" coastal shrublands. Asteraceae subf. Asteroideae pollen is also well represented, mainly due to shrubs such as *Baccharis* spp. and *Eupatorium buniifolium*, and herbs as *Senecio* spp. The herbaceous layer is dominated by grasses such as *Panicum racemosum* (P. Beauv.) Spreng., *Aristida circinalis* Lindm., *Andropogon selloanus* (Hack.) Hack. and *Schizachyrium microstachyum* (Desv. ex Ham.) Roseng., B.R. Arrill. & Izag. Arboreal pollen, mainly represented by *Celtis*, Myrtaceae and *Myrsine*, is originated from communities that develop at distances shorter than 650 m from the sample sites. Although *Myrsine* pollen is zoophilous, their overrepresentation in one sample (2) might be explained by its relatively high pollen dispersal (Behling and Negrelle, 2006).

A considerable difference between shrubland and forest soils exists. Shrublands are developed on soils with coarse sand, low humidity and water availability for plants, as well as low levels of organic matter and nitrogen (Bartesaghi, 2007). These conditions hinder the development of many taxa, mainly trees, ferns and bryophytes.

In the coastal dunes of the southwestern *pampas*, some local communities dominated by the shrub *Discaria americana* (Fontana, 2005) have pollen assemblages similar to the "Candela" coastal shrublands ones: *Discaria americana* dominates, accompanied by Poaceae and Asteraceae. Despite the shrub dominant species is different, the situation could be considered as analogous concerning the RPG coast.

6. Conclusions

The results show distinctive palynological assemblages which characterized the main vegetation types of the *campos* region of Uruguay. According to numerical analysis, the 46 soil surface samples can be divided into five groups: (1) grasslands; (2) riparian forests; (3) low mountain shrublands-forests; (4) psamophylous forests; and (5) "Candela" coastal shrublands. The results suggest that the modern pollen assemblages are representative of the different vegetation types and reflect the vegetation heterogeneity at landscape scale.

Pollen-derived information on the composition and distribution of the vegetation along the *campos* region, indicate that they are mainly related to the substrate water availability, substrate-type and the macro-relief. Different grassland units could not be recognized probably because of the low taxonomic resolution of their main pollen grains, and this confirms previous results for the *pampas* (Prieto, 1992; Tonello and Prieto, 2008, 2009).

Pollen assemblages of the grasslands represent the regional vegetation of the *campos*, where herbaceous anemophilous pollen dominates the assemblages and the small amounts of arboreal and shrubby pollen represent the local forests that develop nearby, in restricted areas. Samples belonging to grasslands where palm individuals grow were differentiated from the others by the presence of *Butia* pollen.

The presence of shrubby and arboreal pollen in the *campos* differentiates its pollen assemblages from those of the *pampas*, where these taxa are absent. The dominance of grasslands in the *campos* is masked in the local forests and shrublands, where the zoophilous pollen of their characteristic species dominates, representing each local vegetation type. Large amounts of Asteraceae subf. Asteroideae are very frequent in the *campos* pollen assemblages, despite of being zoophilous, especially in the grasslands and low mountain shrublands-forests, in the latest related to its particular vegetation physiognomy. On the other hand, bryophytes appeared to be a significant indicator for grasslands and low mountain shrublands-forests, and so it is important to take bryophytes into account when interpreting pollen results from paleorecords.

This pollen dataset completes the information available for the Río de la Plata grasslands and will help to interpret Holocene fossil pollen sequences in progress in the scarcely investigated *campos* region of Uruguay and southern Brazil.

Acknowledgments

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