ECOLOGY AND BIOGEOGRAPHY

Modern pollen–vegetation relationship of plant communities in the Uruguayan Atlantic coast

Silvana Masciadri · Silvina Stutz ·
Felipe García-Rodríguez

Abstract Modern pollen–vegetation relationships are the basis for any paleo-study and are especially needed to understand fossil pollen assemblages and their ecological inferences. Some authors have proposed that lakes and ponds represent the surrounding vegetation through pollen grains captured by the lake. The aim of this work was to establish the modern pollen–vegetation relationships of coastal plant communities and pollen spectra represented in the surface sediments of a coastal shallow lake, and to evaluate whether spatial heterogeneity was captured by the Lake Chaparral in *Perla de Rocha*, Rocha, Uruguay. Pollen grains of five surface sediment samples were analyzed and related with a stratified sampling of vegetation communities surrounding the lake. Correspondence analysis and *t* test were used to determine plant communities and analyze the diversity of pollen assemblages. Several plant species relevant to conservation were registered, and plant communities were differentiated: coastal forest, dunes, prairies, and wetlands. However, due to limitations in taxonomic identification level for the grains of graminoids (Poaceae, Cyperaceae) in pollen assemblages, herbaceous communities highly represented by these botanical families were inferred as open environments. Pollen spectra registered at Chaparral Lake represented local and nearby vegetation well, according to both old and new theoretical models of lakes as a catchment pollen system. Several pollen grains were good indicators of the coastal forest (*Myrsine* sp., *Ephedra tweediana* Fisch. & C. A. Mey., *Lithraea* sp. and *Tripodanthus acutifolius* (Ruiz & Pav.) Tiegh.), and dunes (Chenopodiaceae, and *Ambrosia* sp. and *Senecio* sp.). The modern pollen–vegetation relationship established in this work is similar to those registered for the southern coast of Brazil, due to a shared forest component in both vegetation and pollen spectra. These results constitute primary data for the area, and we think this system is very appropriate for the historic reconstruction of coastal vegetation, particularly the coastal forest.

S. Masciadri
Sección Limnología, Facultad de Ciencias, Instituto de Ecología y Ciencias Ambientales, UdelaR. Iguá 4225, 11400 Montevideo, Uruguay

S. Masciadri (✉)
Laboratório de Ecologia e Conservação da Biodiversidade, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Campus Universitário, Lagoa Nova, Natal, RN 59072-970, Brazil
e-mail: silvana.mb@gmail.com

S. Stutz
Laboratorio de Paleoecología y Palinología, IIMyC, FCEyN CONICET-Universidad Nacional de Mar del Plata, Funes 3250, 7600 Mar del Plata, Argentina
e-mail: silstutz@yahoo.com.ar

F. García-Rodríguez
Sección Oceanología, Facultad de Ciencias, Instituto de Ecología y Ciencias Ambientales, UdelaR. Iguá 4225, 11400 Montevideo, Uruguay
e-mail: felipe.garciarodriguez@gmail.com

Introduction

Pollen grains and spores are often used to reconstruct vegetation history and to develop paleoecologic and paleoclimatic hypotheses of changes over time in South

America (Cordeiro and Lorscheitter 1994; Lorscheitter and Dillenburg 1998; Behling et al. 2001; Lorscheitter 2003; Fontana 2005a; Stutz et al. 2006; Medeanic et al. 2009). It is widely recognized that establishing the modern pollen – vegetation relationship is the basis for any paleo-study and is a particular need for understanding fossil pollen assemblages and their ecological inferences. This is because pollen abundances cannot be directly extrapolated to abundances in plant communities, since pollen assemblages are strongly related to pollen production, dispersion, deposition, and preservation (Moore et al. 1991; Liu et al. 2008). In this way, several authors have attempted to explain how vegetation is represented by pollen assemblages in lakes and ponds as a pollen catchment system. Since Tauber (1965), who defined three major components, regional, extra-local, local, dispersion, and deposition models have been developed. Moore and Webb (1978) later recognized another input from local aquatic plants that is referred as the inside local input, which may also include inputs of older sediments by resuspension. Therefore, the interpretation of pollen assemblages contained in sediments should have a percentage of local, nearby local, extra-local, and regional vegetation. Jacobson and Bradshaw (1981) then related these different pollen contributions to distance, and on this basis other authors have tried to improve and fit pollen catchment models between the size of capture area (lakes and bogs) and the surrounding forest (Prentice 1985). Recently, simulation models have been developed by Sugita (2007a) that revealed a relationship between lake size and the surrounding plant communities represented in pollen spectra. These theoretical models (Sugita 1993, 2007b) propose that small lakes (up to 350 m radius: ≈40 ha) are more appropriate for studies of local vegetation as they better capture the spatial heterogeneity of the environment, while bigger lakes (750 m radius: ≈180 ha) are more suitable for studies of regional vegetation.

Located at the Southeast of South America, Uruguayan coastal ecosystems are situated at the confluence of the temperate and subtropical biozones, encompassing great environmental diversity comprising sandy beaches, rocky headlands, drifting sand dunes, wetlands, creeks, coastal lakes, and the Atlantic Ocean. This spatial heterogeneity supports a high diversity of flora, particularly herbaceous forms. These diverse plant communities have evolved over successive transgressions and regressions of the Atlantic Ocean in the late Holocene (García-Rodríguez et al. 2004, 2010; Bracco et al. 2005). However, due to an increase in poorly-planned urban and tourism development which have failed to take into account a highly dynamic coastal ecosystems, human actions have in some cases prompted the destruction of habitats and dramatic modification in others (GeoUruguay 2008). To achieve long-term conservation of

these threatened coastal plant communities, it is necessary to understand past events that have shaped them and changes that have taken place. For this purpose, it is essential to establish modern pollen – vegetation relationships of existing plant communities, not only for understanding historical changes in coastal vegetation, but also for contributing to palaeoenvironmental studies of Holocene sea-level change in the Atlantic Southeast coastal systems of Uruguay.

The aims of this work were to establish the modern pollen – vegetation relationship between existing threatened coastal plant communities and the pollen spectra represented in the surface sediments of a coastal lake, and to evaluate how the different coastal plant communities are represented by pollen assemblages at *Perla de Rocha*, Rocha, Uruguay. We describe specific and relative abundances of native coastal plant communities at this locality, and the relationships between species occurrences and environments. We also describe the modern pollen spectra through the palynological analysis of surface sediment samples at Lake Chaparral situated at this locality. Finally, we evaluate how pollen records reflect coastal plant communities and determine which taxa are likely to be used as indicators of each community; and investigate if the size of the lake relates with the surrounding environmental heterogeneity.

Materials and methods

Study area

We work at *Perla de Rocha*, Rocha, Uruguay (34°25.760′S, 53°52.535′W) (Fig. 1).The study was developed between December 2003 and March 2006. This area constitutes a relict of typical coastal biodiversity where all characteristic coastal plant communities are well represented, and is one of the few localities that still remains preserved along the Uruguayan Atlantic coast. Cattle and tourism are the main activities developed in the region, and areas that have been forested with exotic species of *Pinus* are located at a distance of 2 km. In order to obtain a good representation of the local heterogeneity of coastal native plant communities, a small coastal lake of 90 m radius within a coastal forest was selected for pollen analysis. Lake Chaparral has an area of 1.2 ha, with a maximum depth of 2.2 m and a mean depth of 1.6, and is classified as oligotrophic (Kruk et al. 2006). It is adjacent to coastal patches of forest interspersed in a grassland matrix at the East, West and North, with wetland discharging to the sea between the sandy dunes at the South (Fig. 2).

Mean annual precipitation registered at the Rocha meteorological station was 1,286, 1,250, and 1,335 mm in

Fig. 1 Study site, Perla de Rocha, Rocha, located at the Atlantic southeastern coast of Uruguay. It is adjacent to the protected area of Cabo Polonio, a vast area of coastal mobile dunes, native forests and rocky islands
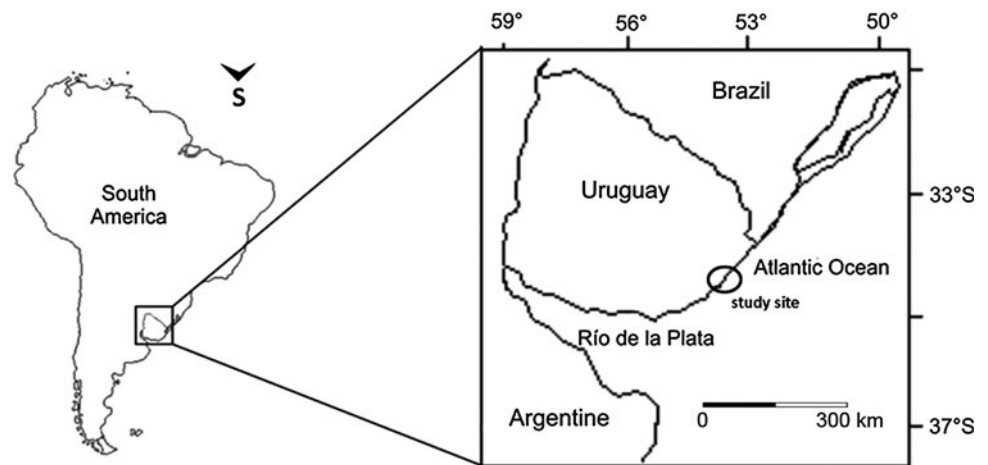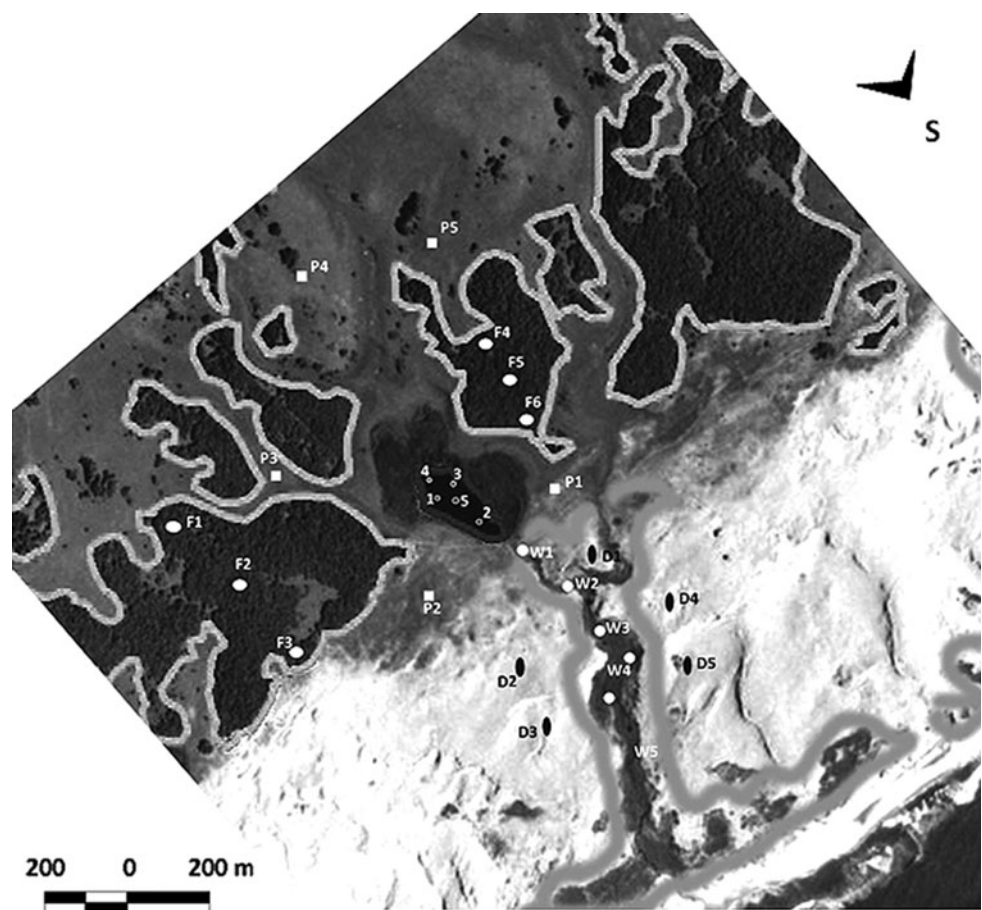

Fig. 2 Design and sites sampling of vegetation and pollen. Sampling points distributed in different vegetation environments at *Perla de Rocha* (Rocha, Uruguay): D dunes, W wetlands, P prairies, F forest, and pollen sampling points (numbers *1–5*) inside the lake

2003, 2004, and 2005, respectively. For the same years, annual mean temperature was 16.2, 13.5, and 16.8 °C.

Vegetation sampling

A stratified sampling method was selected due to the different plant communities observed in the area (Matteucci and Colma 1982). Linear plant cover by unit samples of 200 cm length was estimated in environments with herbaceous cover such as sandy dunes, prairies, and wetlands. In each environment, five transects of 30 m length were established in which four unit samples were obtained every 10 m, at 0, 10, 20, and 30 m. In the forest, richness and relative abundance of woody plants were estimated in six quadrants of 50 m², distributed along two transects in forest patches at both sides of the lake (Fig. 2). To establish minimal area size, accumulation rate of species richness was estimated for forest and open environments in area

(m^2) and lineal cover (cm), respectively (Matteucci and Colma 1982; Kent and Coker 1994). Minimal area and length was 32 m^2 for the forest and 150 m long for open environments, but samples of 50 m^2 and 200 cm length, respectively, were measured. The aquatic plant cover of Lake Chaparral was estimated by Kruk et al. (2006), where plant volume infested – PVI (Canfield et al. 1984) was estimated at 13 points distributed along four equidistant transects including the whole area.

Vegetation samples were collected and dried, and then processed and herborized at the Herbarium and Museum of the Botanical Garden of Montevideo, where voucher vegetation samples of the present study were deposited. Specimens were identified using the national and regional bibliography and national herbarium data (Cabrera 1953; Rosengurtt et al. 1970; Cabrera and Klein 1975; Dimitri 1978, 1980; Marzocca et al. 1979; Sánchez-Monge and Parellada 1981; Lombardo 1982, 1983, 1984; Izaguirre and Beyhaut 1998).

Pollen sampling

Five random samples of surface sediments were obtained at Lake Chaparral, with a 5 cm diameter corer, taking the upper 3 cm of the core. A volume of 50 cm^3 of sediment per sample was processed in the laboratory according to standard protocols used in palynology (Fægri and Iversen 1989), five *Lycopodium* L. tablets were added for control (Stockmarr 1972). Inorganic components (carbonates and silicates) were removed with hydrochloric and hydrofluoric acids under a fume hood. Afterward, acetolysis was used to remove organic compounds and highlight the pollen grains. Finally, the samples were resuspended in glycerin-phenol. Sediment samples were processed and deposited in the Laboratory of Palynology of the Faculty of Sciences in Montevideo. A minimum of 300 pollen grains was counted in each sample. Pteridophytes were not considered in this study. Counting and identifications were made on an Olympus BX40 microscope, and identification was based on the bibliography (Erdtman 1943, 1952; Markgraf and D'Antoni 1978) and reference collection of the Faculty of Sciences (FPA-UdelaR).

Data analysis

Specimens were identified and relatives' richness and abundances for each plant community were estimated. To establish the relationship between the open environments, sandy dunes, prairies and wetlands and the plant communities registered, a correspondence analysis was performed based on an abundance matrix of species and environments. To minimize the scale effect between extreme values of plant cover, data were log transformed as log

($x + 2$), with x being the estimated linear plant cover value in cm. For multivariate analysis, plant species and genera belonging to the botanical families Poaceae and Cyperaceae were analyzed at the family level, as family is the lowest taxonomic level to which their pollen grains are identifiable.

To analyze the diversity of pollen assemblages found in each sample, the Shannon index was calculated and differences were analyzed each pair of samples with Student t tests up to an error (α) of 0.05 (Zar 1999).

Results

Plant communities

The floristic composition of the study site has been monitored since 2001 (Delfino et al. 2005; Masciadri et al. 2006, 2007). In the coastal forest, 26 species of trees and shrubs belonging to 18 families were registered. The most abundant species were the tree *Rollinia maritima* Záchia (Annonaceae), and the shrub *Daphnopsis racemosa* Griseb. (Thymelaeaceae), followed by *Scutia buxifolia* Reissek (Rhamnaceae), *Lithraea brasiliensis* Marchand (Anacardiaceae), and *Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl. (Sapindaceae) (Fig. 3). Four species with conservation priority were registered in the forest, *R. maritima* (Annonaceae), *Sideroxylon obtusifolium* (Humb. ex Roem. & Schult.) T. D. Penn. (Sapotaceae), *Varronia curassavica* Jacq. (Boraginaceae), and *Bromelia antiacantha* Bertol. (Bromeliaceae) (SNAP 2009a).

By comparison, in the dunes, wetlands, prairies, and lakes (aquatic plants) 47, 15, 16, and 17 species were recorded belonging to 19, 8, 7, and 12 families, respectively. Forests and dunes showed more diversity than the other environments at the three taxonomic levels analyzed. Wetlands and prairies averaged 80 and 85 % of plant
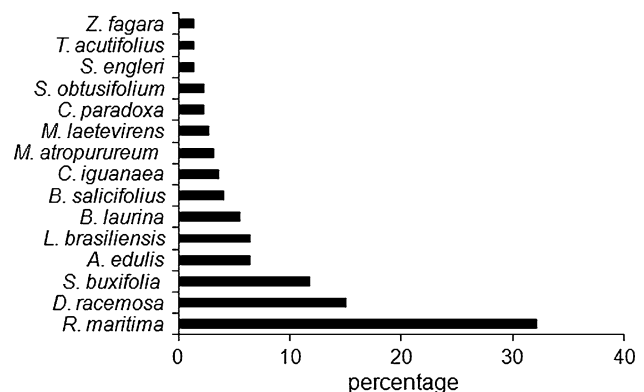

Fig. 3 Relative abundance distribution of tree species recorded at the coastal forest of *Perla de Rocha* (Rocha, Uruguay)

cover, while sandy dunes had 27 % cover, although despite their lower plant cover dunes had a more diverse flora than the other herbaceous environments, wetlands, prairies, and aquatic vegetation at the lake Chaparral. In wetlands and prairies, both Poaceae and Cyperaceae were the best represented Families, and *Ischaemum minus* J. Presl (Poaceae) was the most abundant species, with 37 and 55 % cover, respectively. However, in wetlands *Eleocharis* sp. (Cyperaceae) was the second most abundant species, while in prairies it was the exotic *Cynodon dactylon* (L.) Pers. (Poaceae) (Fig. 4). Cyperaceae is a botanical family that characterizes marsh and wetland environments in this grassland biome, while Poaceae is typical of prairies,
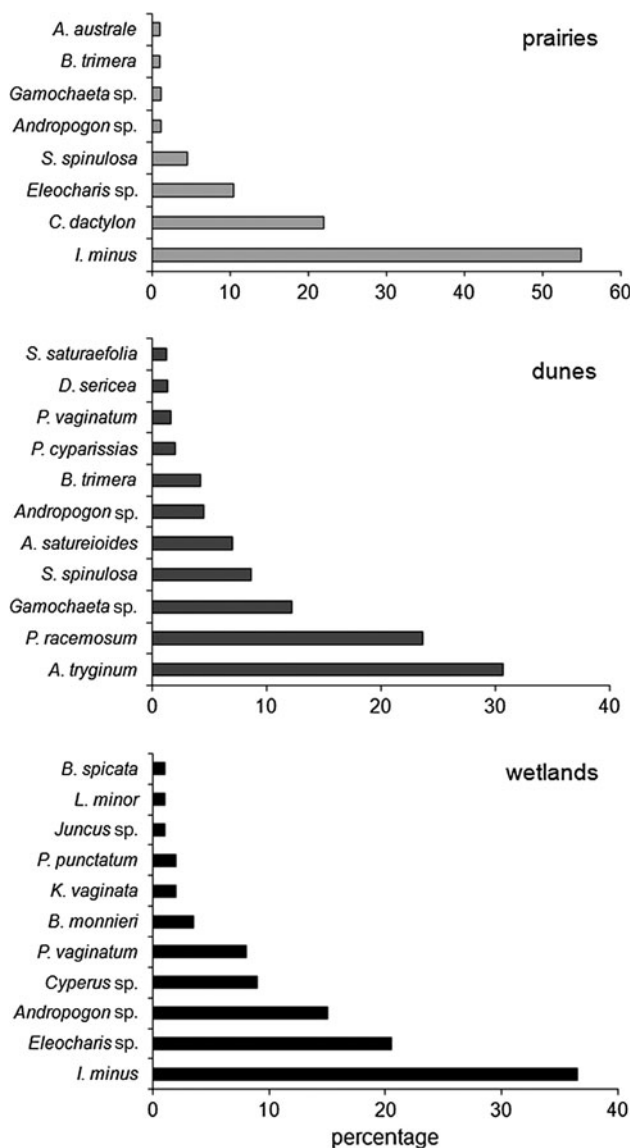
which is reflected in the greater abundance of Cyperaceae relative to Poaceae in damper environments.

Dunes were characterized by *Androtrichum trigynum* (Spreng.) H. Pfeiff. (Cyperaceae) and *Panicum racemosum* (P. Beauv.) Spreng. (Poaceae), but also by other less abundant Asteraceae, such as *Gamochaeta* Wedd. spp., *Sommerfeltia spinulosa* (Spreng.) Less. and *Achyrocline satureioides* (Lam.) DC. (Fig. 4). These Asteraceae, belonging to the Inuleae and Astereae tribes, were a distinct component of dunes.

In Lake Chaparral, *Cabomba caroliniana* A. Gray (Cabombaceae) accounted for 95 % of coverage, while *Ludwigia peploides* ssp. *montevidensis* (Spreng.) P. H. Raven (Onagraceae) accounted for only 20 % of coverage. Also recorded, without cover values, were *Sagittaria montevidensis* Cham. & Schltdl., *Hydrocleys nymphoides* (Willd.) Buchenau (Alismataceae), and *Ricciocarpos natans* (L.) Corda (Kruk et al. 2006).

In open environments, five species with conservation priority according to SNAP (2009a) were recorded: *Acicarpha obtusisepala* Marchesi (Calyceraceae), *S. spinulosa* (Asteraceae), *Porophyllum brevifolium* (Hook. & Arn.) Malme, and *Apium prostratum* Labill. (Apiaceae) *Phyla reptans* (Kunth) Greene (Verbenaceae) which are endemic of Uruguay and the adjacent region (South of Rio Grande do Sul in Brazil and East of Entre Ríos in Argentina). Also recorded were two endangered species *Eleocharis montevidensis* Kunth (Cyperaceae) and *Juncus capitatus* Weigel (Juncaceae) (SNAP 2009a).

Ordination analysis for open environments and species groups showed a good fit to the model (99.6 %), where the first two axes elucidate a good correspondence between species and environments (Fig. 5). Axis 1 explained 63 % of the variance while axis 2 explained 38 %. For axis 1, groups of species were associated with dunes on one hand and with wetlands to the other. For axis 2, prairies were differentiated from dunes and wetlands. Marsh species such as *Polygonum punctatum* Elliott (Polygonaceae), *Baccharis spicata* (Lam.) Baill. (Asteraceae) and *Lilaeopsis brasiliensis* (Glaz.) Affolter (Apiaceae) were associated to wetlands. Dune building species such as *Oenothera mollissima* L. (Onagraceae), *Dichondra sericea* Sw. (Convolvulaceae) and *Stevia satureiifolia* (Lam.) Sch. Bip. (Asteraceae), were associated with sandy dunes, and *Centella asiatica* (L.) Urb. (Apiaceae), *Eryngium nudicaule* Lam. (Apiaceae), and *Plantago* sp. (Plantaginaceae) were more related to prairies. Axis 1 could be explained as an environmental moisture gradient where sandy dunes are opposite to wetlands, with prairies located in an intermediate position sharing species associated with dunes on one hand, and species related to wetlands on the other. Poaceae and Cyperaceae were the best represented families and were present in all three open environments.

Fig. 4 Percent relative abundances of taxa recorded in wetlands, prairies, and dunes at *Perla de Rocha* (Rocha, Uruguay). Note the different *y* axis scales

Fig. 5 Relationship between species and environments. Graph of correspondence analysis showing the assemblages of species and environments at *Perla de Rocha* (Rocha, Uruguay). The variance explained by each factor is indicated in the *axis labels*
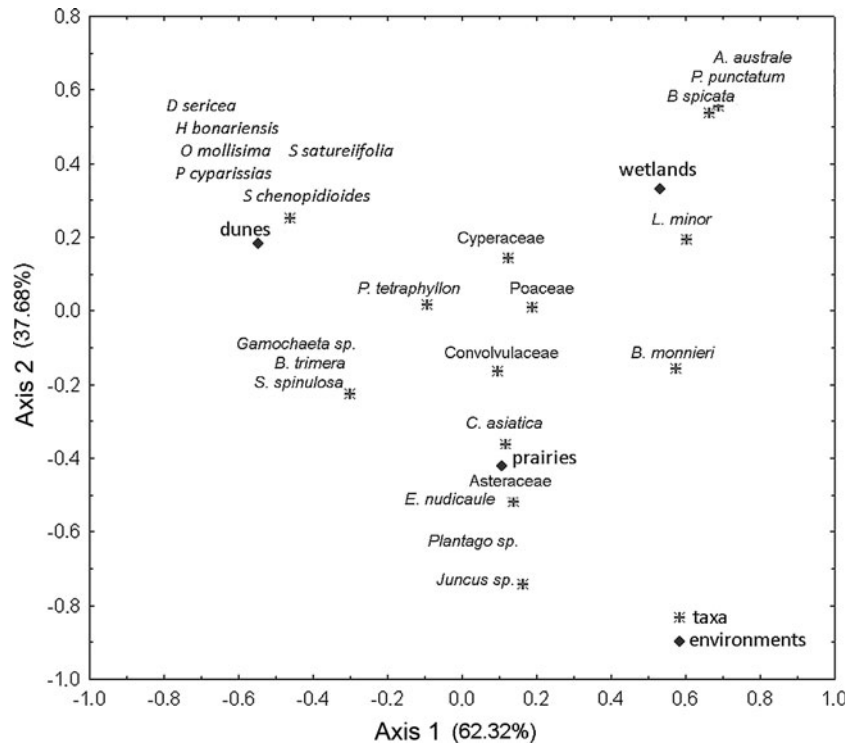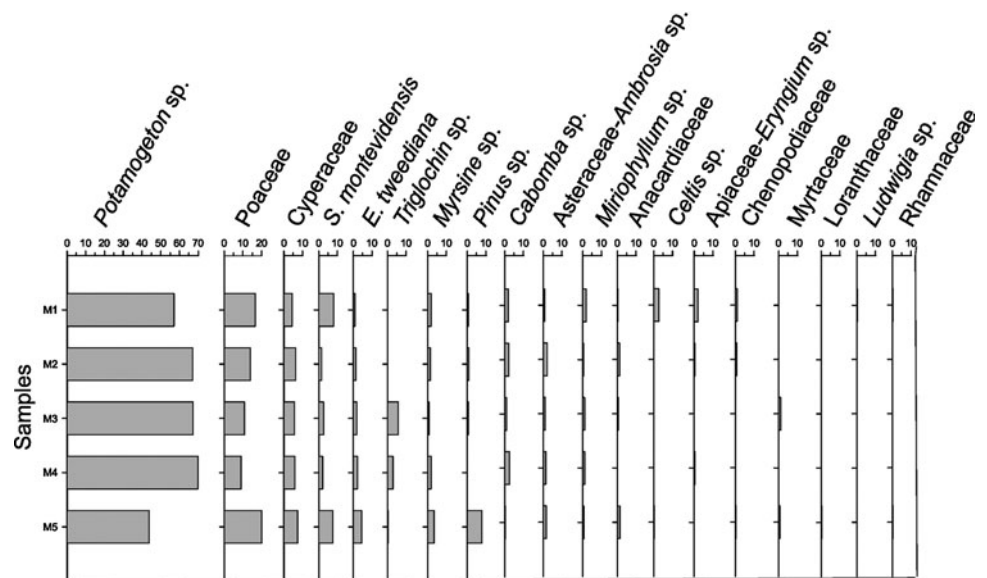

Fig. 6 Distribution diagram of pollen relative abundances recorded in the samples at Chaparral Lake in Perla de Rocha (Rocha, Uruguay)

Pollen assemblages

The number of pollen grains counted varied among samples, between a minimum of 383 (sample 1) and a maximum of 564 (sample 3). A total of 19 taxa where registered at the family, genus, and species level, where 12 taxa were shared among all samples and no taxon was exclusive to any one sample. Relative abundances of taxa recorded are shown in Fig. 6. The t test did not reveal significant differences ($P > 0.05$) in diversity values between the pairs of samples 2, 3, and 4. However, a significant difference was detected between samples 1 and 5 and the rest (2, 3, and 4) (Table 1).

When the percentage of pollen taxa were grouped according to their source, local pollen (aquatic plants) was the most abundant component with 67 %, followed by open environments with 18 %, with Poaceae, Cyperaceae, Apiaceae, as the next most represented. Forest represented primary by *Ephedra tweediana* Fisch. & C. A. Mey. (Ephedraceae) and *Myrsine* sp. accounted for 6 %. The

Table 1 Pollen samples diversity test. Pollen sample pairs and their respective t values (t) and associated P values (P)

Sample pair		t	P
m1	*m2*	*2.61*	*0.0091*
m1	*m3*	*2.38*	*0.017*
m1	*m4*	*2.711*	*0.0068*
m1	*m5*	*2.67*	*0.0077*
m2	m3	0.369	0.711
m2	m4	0.13	0.89
m2	*m5*	*−5.56*	*≪0.01*
m3	m4	0.5	0.61
m3	*m5*	*−5.47*	*≪0.01*
m4	*m5*	*−5.62*	*≪0.01*

Sample pairs with significant differences are italicized
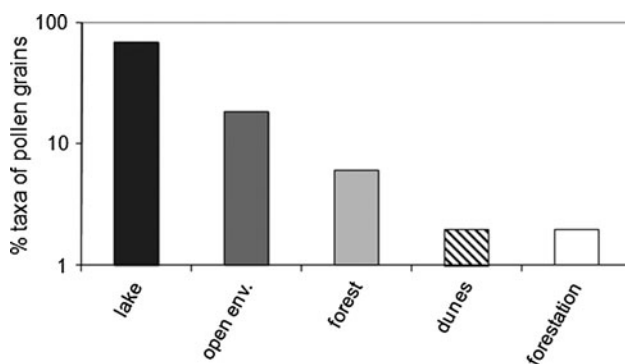
Fig. 7 Percentage of pollen taxa classified according to associated plant communities at Perla de Rocha (Rocha, Uruguay). The percentages values are presented with logarithmic scale for best visualization (*open env.* open environments)

Dunes characterized by Chenopodiaceae and Asteraceae (*Senecio* sp. and *Ambrosia* sp.) were represented by 2 % of the pollen, as well as a regional vegetation component, which was indicated by the exotic *Pinus* sp. (Fig. 7).

Pollen – vegetation relationship

In the coastal forest, only seven taxa were registered in the pollen assemblage, whereas 26 taxa were recorded in the vegetation. *Rollinia maritima* was the most abundant species in the forest, but it was not present in pollen samples. The other forest pollen grains recorded were *E. tweediana*, *Myrsine* sp. (Primulaceae), Anacardiaceae (*L. brasiliensis* and *Schinus* spp.), *Celtis* spp. (Cannabaceae), Rhamnaceae (*S. buxifolia* and *Colletia paradoxa* (Spreng.) Escal.), and *Tripodanthus acutifolius* (Ruiz & Pav.) Tiegh. (Loranthaceae), the last a native forest parasite species; all were present in both pollen and vegetation samples. Each of these could therefore serve as useful indicators of forest association. *Ephedra tweediana* and *Myrsine* sp. showed the highest percentages (Fig. 8), although *E. tweediana*

was not registered in the quantitative sampling; however, it had been previously recorded in the area (Delfino et al. 2005).

Because it is not possible to discriminate whether pollen grains of Poaceae or Cyperaceae come from dunes or wetland vegetation, the pollen–vegetation relationship of dunes, prairies and wetlands communities were grouped and analyzed together up to family level as open environments. Hence, four families were registered in pollen assemblages related to open environments (Poaceae, Cyperaceae, Asteraceae, and Apiaceae), corresponding to 50 % of the taxa registered to vegetation (Table 2a). However, these four families accounted for only 30 % of the taxa recorded in vegetation (Table 2b). Poaceae and Cyperaceae were the more important families in both pollen and vegetation (Fig. 8).

In Lake Chaparral, only two taxa out of five registered in pollen samples were recorded in the vegetation samples (Fig. 8): *C. caroliniana* (Cabombaceae) and *L. peploides* ssp. *montevidensis* (Onagraceae). *Potamogeton* sp. was the best represented pollen taxa with 62 %, but not was recorded in the vegetation samples, like *Myriophyllum* sp., which had a very low value (1 %).

Discussion

Vegetation

Knowledge of the coastal native plant communities of Uruguay is still in a descriptive state (Alonso Paz and Bassagoda 1999; Campo et al. 1999; Delfino and Masciadri 2005; Delfino et al. 2005; Fagúndez and Lezama 2005; Alonso Paz and Bassagoda 2006). To date, few studies exist referring to these coastal plant communities (Campo et al. 1999; Masciadri et al. 2006, Bartesaghi et al. 2007; Ríos et al. 2007). This research constitutes the first quantitative assessment of native coastal vegetation in the area. This area comprises one of the best preserved ecosystems of the Atlantic coast of Uruguay encompassing a relict of coastal native biodiversity. According to the results of the present study, dunes and forest are the more diverse environments, and despite the significantly lower plant cover of dunes relative to prairies, wetlands, and aquatic vegetation, dunes were more diverse. There are several factors in this area relevant to conservation. In total, 11 species registered in this work are of conservation priority, because of a national or regional endemism, or constitute populations in their southern limit of species distribution, both of which represent geographical patterns of significance to species conservation. Of these 11 species, two are endangered: *E. montevidensis* (Cyperaceae) and *J. capitatus* (Juncaceae). In addition, the study area is adjacent to Cabo Polonio, a
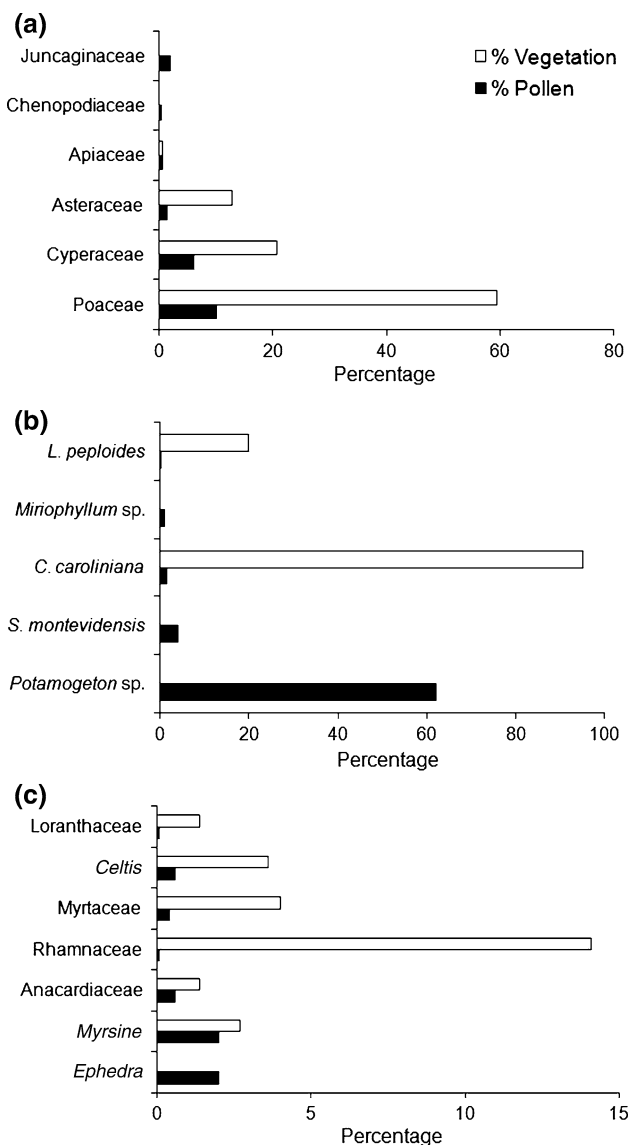
Fig. 8 Percentages of taxa represented in both pollen and vegetation at *Perla de Rocha* (Rocha, Uruguay). **a** Forest, **b** open environment (dunes, prairies and wetlands), **c** Chaparral Lake. Note the different *y* axis scales

protected coastal area encompassing mobile dunes, several species of trees, shrubs and herbs of conservation value priority, as well as important fauna species (Masciadri et al. 2006; SNAP 2009a).

In a regional context, the open environment plant communities described in this study show similar phytophisiognomy and composition to the herbaceous communities of lakes, dunes, wetlands, and prairies from coastal ecosystems of both the Province of Buenos Aires, Argentina (Mancini 1994; Stutz 2001; Fontana 2005b) southward, and Southern of Brazil northward (from Santa Catarina to Rio Grande do Sul) (Dillenburg et al. 1992; Medeanic 2004; Bertolin 2006; Klein et al. 2007). However, forest components are absent or restricted to

monospecific associations of *Celtis* sp. in the Province of Buenos Aires coast, which are a differently composed than the more diverse coastal forest described here. Moreover, several coastal forest species recorded in this study are characteristic of the Restinga forest of the southeastern coast of Brazil (*S. obtusifolium*, *R. maritima*, *B. antiacantha*, *Lithraea* spp., *Myrsine* spp., among others) (Pereira and Bauermann 2001; Fuhro et al. 2005; Scherer et al. 2005, Lima Batista et al. 2007) revealing a phytogeographic similarity. Plant communities described in this study, particularly the arboreal ones, present a more similar association with those reported from Restinga forests in the southeast of Brazil. On the other hand, some of the species recorded are in their limit of distribution (*R. maritima*, *S. obtusifolium*, *B. anthiacantha*), indicating a possible confluence of a biogeographic and climatic transition zone between the temperate and subtropical biota. This zone, called a node or ecotone, it is of particular interest to evolutionists and biogeographers, owing to the biota that converges through space and time (Morrone 2005). For example, despite its small size, Uruguay has 40 and 25 % of bird species documented for Argentina and Brazil respectively (SNAP 2009b). The southeastern coast of Uruguay is included in one of the 200 priority eco-regions to Global Programme of WWF, and recognized as one of the more productive ecosystems of the world (SNAP 2009b). In addition, the wetlands system is of international value for conservation, as they are included in the RAMSAR convention due to their biological, ecological, and productive value (RAMSAR 1971).

Pollen assemblages

Samples from the center of the lake (1 and 5) showed more equal diversity than the points sampled on the shoreline of Lake Chaparral. This is consistent with the general assumption that central samples better reflect the vegetation surrounding a lake, and also with other research results (Amami et al. 2010). Moreover, the local effect due to highly local pollen representation is minimized in central samples. In fact, there were no significant diversity differences between samples obtained near the shore, with *Potamogeton* sp. as the dominant taxon. The pollen assemblage was composed mainly of herbaceous components (92 %), whereas tree pollen grains were 8 %, of which 6 % corresponded to a coastal native forest origin [Anacardiaceae (*Schinus* spp. and *L. brasiliensis*), *E. tweediana*, *T. acutifolius* (Loranthaceae), Rhamnaceae, *Celtis* sp. and *Myrsine* sp.], and 2 % to an exotic *Pinus* L. sp. (Pinaceae) forest located 2 km away (Fig. 9). Hence, the pollen spectra show a large local component of aquatic plants (68.6 % *Potamogeton* sp., *S. montevidensis*, *M. aquaticum* and *C. caroliniana*), followed by 18.5 % of

Table 2 Taxon percentages of vegetation and pollen recorded

(a)	Percentage of taxa on vegetation	Presence of taxa in pollen assemblage
Dunes (9 taxa)		
Poaceae	82.6	1
Cyperaceae	6.8	1
Asteraceae	5.08	1
Scrophulariaceae	3.8	
Brassicaceae	0.65	
Plantaginaceae	0.5	
Apiaceae	0.42	1
Caryophyllaceae	0.12	
Convolvulaceae	0.03	
Prairies (9 taxa)		
Asteraceae	33	1
Cyperaceae	30.6	1
Poaceae	30	1
Polygalaceae	2.2	
Convolvulaceae	1.4	
Onagraceae	1	
Apiaceae	0.8	1
Solanaceae	0.5	
Caryophyllaceae	0.5	
Wetlands (8 taxa)		
Poaceae	67.8	1
Cyperaceae	25.6	1
Scrophulariaceae	2.7	
Polygonaceae	1.5	
Juncaceae	1	
Apiaceae	0.8	1
Caryophyllaceae	0.6	
Asteraceae	0.54	1

(b)	Percentage of taxa on vegetation	Percentage of taxa in pollen assemblage (4 taxa)
Open environments (14 taxa)		
Poaceae	59.5	10
Cyperaceae	20.8	5
Asteraceae	12.8	1.3
Scrophulariaceae	2.2	
Polygonaceae	1.2	
Polygalaceae	0.7	
Apiaceae	0.6	0.5
Convolvulaceae	0.5	
Caryophyllaceae	0.4	
Juncaceae	0.3	
Onagraceae	0.3	
Brassicaceae	0.2	
Plantaginaceae	0.2	
Solanaceae	0.2	

a Taxa of vegetation recorded in dunes, prairies, and wetlands at *Perla de Rocha* (Rocha, Uruguay). For pollen assemblage, the presence (1) of each taxon is indicated, *b* Relative percentages of taxon in both pollen and vegetation in sites grouped as open environments

open environment pollen grains (dunes, wetlands and prairies) composed largely of four families, Poaceae (10 %), Cyperaceae (5 %), Asteraceae (1 %), and Apiaceae (0.5 %). The lowest possible level of pollen taxonomic identification in open environments was to the family level. It was not possible to determine the plant

community source of those pollen grains (e.g.,: wetland, prairie), although it was just feasible to identify some pollen taxa related to dunes as *Ambrosia tenuifolia* Spreng. and *Senecio* sp. (Asteraceae), and *Chenopodium ambrosioides* L. (Chenopodiaceae), which represented 2 % of the pollen assemblage. In addition, Cyperaceae and Apiaceae are more related to wetlands, marshes or moist prairies, and it is therefore possible to establish a relationship between these taxa and more humid environmental conditions.

Pollen – vegetation relationship

The pollen assemblage recorded in the surface sediments of Lake Chaparral, resembles the native coastal plant communities and well represented local vegetation: the surrounding forest, the open environment including wetlands, dunes and prairies, and a minor component of regional vegetation indicated by the presence of *Pinus* sp. pollen grains. Local vegetation was the main component of pollen spectra (68.6 %), where *C. caroliniana*, *S. montevidensis* and *L. peploides* were recorded in both pollen and vegetation. However, *Potamogeton* sp., which was the dominant pollen taxon (62 %), was not recorded in vegetation, whereas *C. caroliniana* dominated the plant cover of aquatic vegetation (95 %). Several hypotheses could explain this discrepancy. Aquatic plants often have rapid colonization strategies and water level changes may have influenced the succession of dominant species in the lake. Water bodies can have different stable states dominated by vegetation or phytoplankton (Scheffer 1998), and move from one state to another over time. Considering that sediment pollen samples represent the last 30 years in the lake, several state changes could have occurred. Nevertheless, during this study, the presence and dominance of *C. caroliniana* was always observed. On the other hand, it is possible that these species inhabit different layers of the lake, in central or border zones, and the absence of *Potamogeton* sp. in the vegetation cover may be an artifact of the sampling technique for aquatic vegetation. In addition, the flower structure of *Potamogeton* sp. is in male spikes containing more abundant quantities of pollen than solitary flowers of *C. caroliniana*, and flowers of *Potamogeton* sp. are also more abundant than those of *C. caroliniana* (Masciadri *per obs*.). Further study and sampling over time is needed to conclusively determine the cause for the discrepancy between pollen and vegetation of these species.

Correspondence analysis showed different species compositions from wetlands, dunes, and prairies along a moisture gradient, but it was not possible to detect these different vegetation signals through the taxonomic identification level of pollen grains. The four families, Poaceae, Cyperaceae, Asteraceae, and Apiaceae, characterizing open environments both in vegetation (59.5, 20.8, 12.8, and 0.5 %) and pollen spectra (10, 5, 1.3, and 0.5 %), are also the most representative botanical families of Uruguayan flora (Marchesi 2004). Although similar difficulties in the determination of the species composition of Poaceae, Cyperaceae pollen grains were encountered in other studies (Stutz and Prieto 2003; Medeanic 2004; Fontana 2005b), generally, Poaceae, and Asteraceae are more related to dry environments (prairies), and Cyperaceae and Apiaceae to wetlands and marshes. Despite the differences in proportions of these taxa found in vegetation, is difficult to directly allocate to same proportions of taxa observed in the pollen. A Poaceae/Cyperaceae ratio may prove to be a useful tool to establish wetter or dryer environmental conditions. Moreover, as some taxa were exclusive to dunes, such as *A. tenuifolia*, *Senecio* sp. (Asteraceae) and Chenopodiaceae, could be establish as dune components.

The coastal forest had limited representation in pollen spectra (6 %), but several taxa were good indicators of this community [*Myrsine* sp., Anacardiaceae (*Schinus* sp. and *L. brasiliensis*), Rhamnaceaae, Myrtaceae, *Celtis* sp and *T. acutifolius* (Loranthaceae)], and were also represented in vegetation and pollen spectra. Other taxa, however, showed different pathways. The most abundant tree recorded, *R. maritima*, was not identified in pollen samples. Moreover, *E. tweediana* was not recorded in forest sampling but it was identified in vegetation (Delfino et al. 2005). This native gymnosperm had higher pollen percentages, and was a good indicator of coastal forest.

Other studies of coastal pollen–vegetation relationships in the region (the south of Brazil and the southeast of Argentina), also found discrepancies between the pollen spectra and vegetation cover, which were explained by differences in pollen productivity, dispersal and preservation (Medeanic 2004; Fontana 2005b). Fontana (2005b) found five different plant communities and two pollen assemblages in a Bahia Blanca coastal system. On the other hand, Medeanic (2004) found an equal proportion of plant communities and pollen assemblages in De Los Patos Lagoon and predominance of herbaceous plant communities over aquatic and tree pollen was recorded, matching with the pollen spectrum, which had a higher proportion of terrestrial herbaceous pollen (50 %) than aquatic (20 %) and tree (6 %) grains. Thus, modern pollen – vegetation relationships found in out study are more consistent with the results obtained from the southeast Brazilian coast, reflecting the greater environmental similarity between Uruguayan Atlantic and Brazilian southern coasts (Cordeiro and Lorscheitter 1994; Medeanic 2004), than with the coast of the Province of Buenos Aires in Argentina.

The pollen – vegetation relationship is affected by reasons related to differences between the production and dispersal of pollen grains, but also due to environmental heterogeneity of the site (Parsons and Prentice 1981;
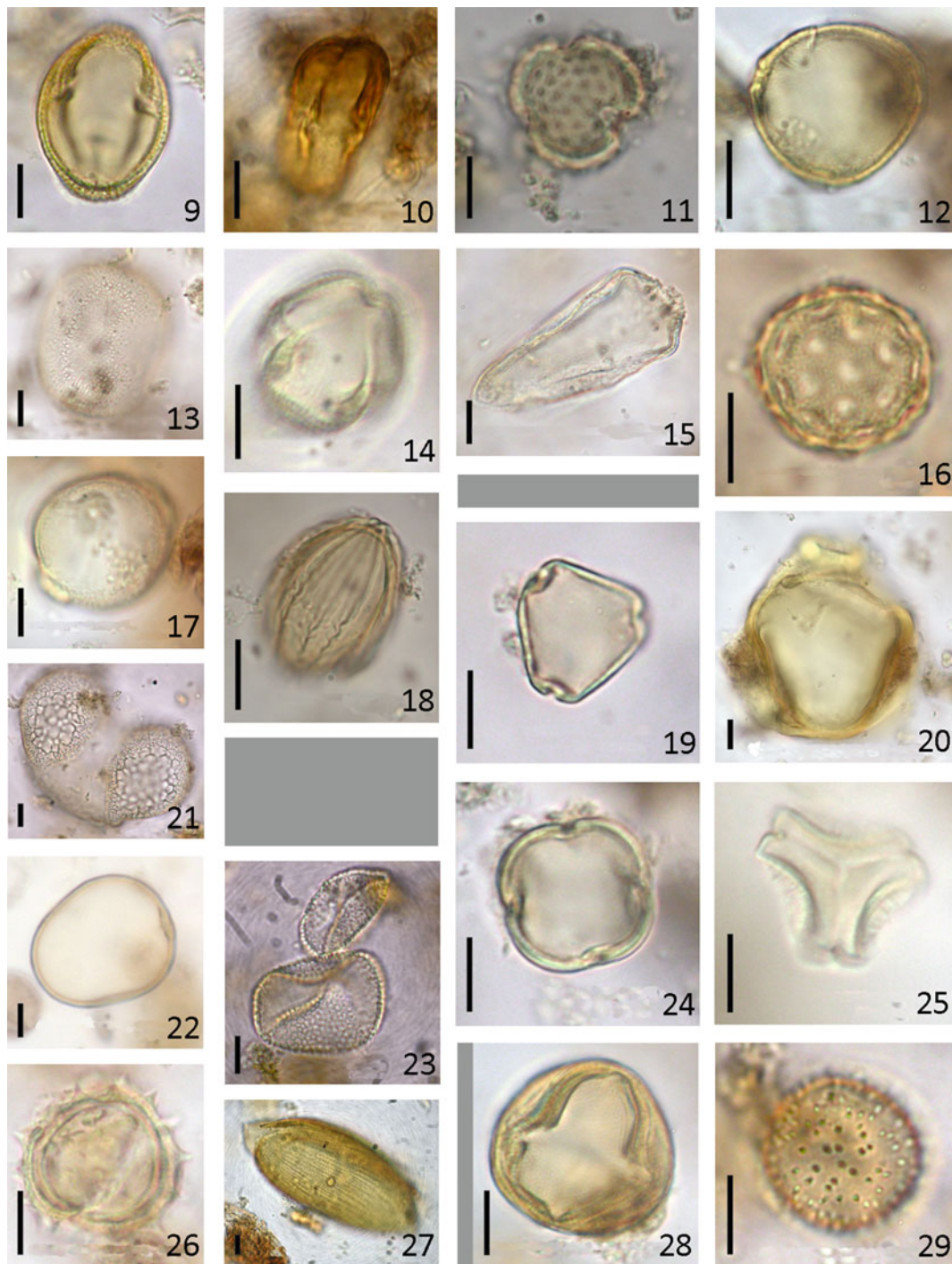
Figs. 9–29 Pollen grains observed in surface sediment samples of Lake Chaparral, Perla de Rocha, Rocha, Uruguay. Family, Genera or species are specified. **9** Anacardiaceae, *Lithraea* sp.; **10** Apiaceae, *Eryngium* sp.; **11** Asteraceae, *Ambrosia* tenuifolia; **12** Cannabaceae, *Celtis* sp.; **13** Juncaginaceae, *Triglochin* sp.; **14** Rhamnaceae; **15** Cyperaceae; **16** Chenopodiaceae; **17** Haloragaceae, *Miriophyllum* sp.; **18** Ephedraceae, *Ephedra tweediana*; **19** Myrtaceae; **20** Onagraceae, *Ludwigia* sp.; **21** Pinaceae, *Pinus* sp.; **22** Poaceae; **23** Potamogetonaceae, *Potamogeton* sp.; **24** Myrsinaceae, *Myrsine* sp.; **25** Loranthaceae, *Tripodanthus acutifolius*; **26** Asteraceae, *Senecio* aff.; **27** Cabombaceae, *Cabomba caroliniana*; **28** Anacardiaceae, *Schinus* sp.; **29** Alismataceae, *Saggitaria* sp. *Bar* 10 μm

Prentice 1985; Stutz et al. 2006; Sugita 2007a, b; Liu et al. 2008). Therefore, some taxa such as those with greater pollen production are overestimated, while others with lesser production tend to be underestimated. The high percentage of local pollen from aquatic species found in this study follows the capture model of a lake surrounded

Fig. 30 Schemes of pollen dispersion models. **a** Diagram of pollen transfer model for a forest area by Tauber ([1965](#)). *Cr* rain component, *Cc* canopy component, *Ct* internal component of the forest, *Cl* local component, *Cw* local component transported by water. **b** Jacobson and Bradshaw ([1981](#)) graphic diagram of the relationship between the size of site and the different sources of pollen
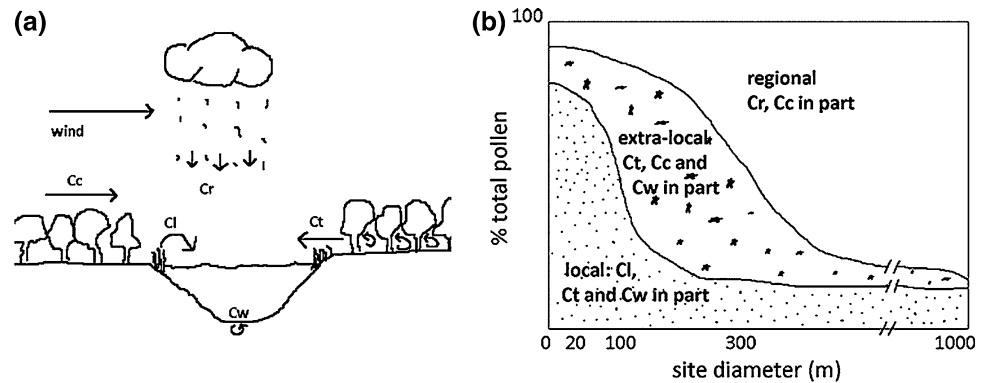
by a forest proposed by Tauber (1965) and later modified by Jacobson and Bradshaw (1981) (Fig. 30). Furthermore, the spatial heterogeneity of different plant communities was reflected in the pollen spectrum as predicted Sugita (2007a), where lakes smaller than 350 m better reflect environmental heterogeneity.

These are promising results for the reconstruction of the coastal forest history at *Perla de Rocha*, because sediment pollen samples were found to be well-preserved and reflected the nature of the vegetation in the study site, offering excellent conditions for future studies of coastal history vegetation changes.

Conclusions

The pollen spectra registered in Lake Chaparral represented the surrounding coastal plant communities, and also reflected the neighboring spatial heterogeneity, according to both old and new theoretical models of lakes as a catchment pollen system. We think this system is very appropriate for the historic reconstruction of coastal vegetation, particularly the coastal forest.

Pollen samples taken from the lake center are less influenced by local vegetation (macrophytes) than border samples, and so the best represent the terrestrial vegetation. *Myrsine* sp. and *E. tweediana* and, to a lesser degree, *Lithraea* sp. (Anacardiaceae), and *T. acutifolius* (Loranthaceae), were good indicators of the coastal forest. The dunes also have distinct pollen grains such as Chenopodiaceae and Asteraceae (*Ambrosia* sp. and *Senecio* sp.), but with low abundances.

The results of this study constitute a series of primary data for Uruguay, encouraging more research efforts in the area. The study of terrestrial surface samples in each environment can supplement and refine the modern pollen–vegetation relationship. Moreover, the comparison with

data from other localities on the coast will lead to an actual pollen–vegetation model for the Uruguayan Atlantic coast.

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