Research papers

Modern pollen and vegetation relationships in northeastern Patagonia (Golfo San Matías, Río Negro)

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ABSTRACT

The understanding of modern pollen is a critical component of palaeoecological research. The pollen assemblages reflect general patterns in vegetation distribution; however, pollen representation is biased by several factors such as differences in pollen production, dispersal and preservation. Therefore, this relationship cannot be applied directly in pollen records of the past. The aim is to study the relationship between modern pollen and vegetation and to apply this new information on the interpretation of Holocene pollen records. Classification of the vegetation into groups corresponding to different geomorphological units was carried out by cluster analysis. Discriminant analysis was applied on the surface samples to test if different vegetation types could be distinguished by their pollen assemblages. To evaluate the relationship between pollen assemblages and vegetation types, association (A), under-representation (U) and over-representation (O) indexes were calculated for all present taxa in both plant and pollen dataset. The main vegetation types are reflected in pollen assemblages but with greater differences in the proportions of Poaceae, *Hyalis argentea*, Chenopodiaceae, Asteraceae subf. Asteroideae and *Larrea divaricata*. Association and representation indexes provided information related to the production rate and pollen dispersal. This study helps to interpret Holocene vegetation and environmental changes from fossil pollen records of the study area.

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1. Introduction

The understanding of the relationship between modern pollen and vegetation composition is a critical component in the interpretation of palaeocological research. The pollen assemblages reflect general patterns in vegetation (Fontana, 2005), nevertheless, pollen representation is biased by several factors such as differences in pollen production, dispersal and preservation of taxa (Faegri and Iversen, 1992; Prentice, 1988). Therefore, this relationship cannot be applied directly in pollen records of the past.

Modern pollen–vegetation studies have been carried out in North America (Bradshaw and Webb, 1985; Calcote, 1995; Davis, 1963; Jackson, 1990) and in west Europe (Andersen, 1970; Prentice et al., 1987) among others. In Argentina, these studies have been performed in different environments of Patagonia by Markgraf et al. (1981), Mancini (1993, 1998, 2002), Mancini et al. (2011), Paez et al. (1997) and Heusser (2000), among others.

The association, under and over-representation indexes, as a tool to study the pollen–vegetation relationship, have been explored by Davis (1984), Islebe and Hooghiemstra (1995), Hjelle (1997), Berrío et al. (2003), Bunting (2003), and Fontana (2005). These indexes give additional information about production and

dispersion of the vegetation, improving the understanding of the modern pollen–vegetation relationship and the interpretation of Quaternary pollen records.

Palaeoecological reconstruction studies were performed by Schäbitz (1994, 1999, 2003) in Espinal Biogeographic Province and Schäbitz and Liebritcht (1998) in Patagonian Steppe. Only few studies (Schäbitz, 1994, 1999 and 2003) have been used modern pollen samples as a tool for interpreting the fossil record or to estimate paleoprecipitation values in northeast Patagonia.

Palaeoecological reconstructions and the relation with human occupation in northeast of Río Negro, Argentina, have been carried out by Marcos et al. (in review). However, in this region the pollen–vegetation relationship has not been studied yet. The Rio Negro coast is a complex ecosystem with high internal variation and extensive zonation of the vegetation across the shore line. In this sense, this research is relevant to better understand and interpret past pollen records.

The aim of this paper is to study the relationship between modern pollen assemblages obtained from sediment samples and vegetation on the North Coast of San Matias Gulf, Rio Negro, Argentina to apply this new information on the interpretation of Holocene pollen records.

We explored the relationship between modern pollen records (assemblages) and vegetation through association and representation indexes for different taxa. The relationship between species richness of vegetation and palynological richness has also been analysed.

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2. Study area and vegetation characteristics

Bajo de la Quinta (40° 55′ 42″ S, 64° 20′ 19″ W) is located in the north Patagonian coast of San Matias Gulf (Fig. 1). It is a fluvial and deflation basin eroded on tertiary (Miocene) rocks belonging to the Barranca Final Formation (Kaasschieter, 1965). The area also forms active sea cliffs—up to 15 m high—and shore platforms. On the coast and bordering Bajo de la Quinta, Holocene and Pleistocene sandy–gravel beach ridge are present (Favier Dubois and Kokot, 2011; Kokot et al., 2004). Ephemeral streams drain the Bajo de la Quinta basin, but this drainage towards the coast is impeded by the Holocene beach ridge and dunes. Then, although this semiarid region presents low rainfall, unusual rain storms generate a pond in the sector of interrupted drainage providing a source of fresh water for few days (Favier Dubois and Kokot, 2011).

The regional climate in northeastern Río Negro is semiarid; the temperature coincides with the 12 °C mean annual isotherm and the mean annual rainfall is about 250 mm (Labraga and Villalba, 2009).

The vegetation is a shrubland, belonging to the Monte Biogeographic Province, Southern District (Abraham et al., 2009; Roig et al., 2009; Roig-Juñent et al., 2001). The predominant geoforms and soil types in this landscape determine spatial heterogeneity of vegetation ranging from psammophytic community on the sand dunes along the coast to xerophytic shrublands to inland. So, water availability and different edaphic conditions are probably leading to this community differentiation. Monte shrub communities are organized as two-phase mosaic composed by a phase of perennial grasses and shrub-dominated patches alternating with sparse cover (Ares et al., 2003; Bertiller et al., 2004; Bisigato et al., 2009). In these communities, the dominant specie is *Larrea divaricata* Cav. forming the *jarillal* associated with *Prosopis alpataco* Phil, *Monttea aphyla* (Miers) Gay., *Condalia microphylla* Cav., *Senna aphylla* (Cav.) H.S. Irwin & Barneby and *Chuquiraga erinaceae* D. Don. Chenopodiaceae shrubs (*Atriplex lampa* (Moq) D. Diertr. and *Suaeda divaricata* (Moq)) dominate on depressions with salty soils (León et al., 1998).

3. Materials and methods

3.1. Vegetation analysis, pollen analysis and pollen–vegetation relationship

For vegetation analysis, four units were selected and sampled according to main geomorphological and physiognomical characteristics of the area (Mobile Dunes, Fixed Dunes, Fluvial Landscape and Ephemeral Pond, see Fig. 1). Four replicate plots were made in each geomorphological unit. Following minimum area methods 8×8 m plots were displayed in shrub and shrub-grass communities and 4×4 m plots were displayed in grass communities. All species were listed and cover-abundance values were estimated by Braun-Blanquet scale (1979).

The Shannon–Wiener index ($H' = -\sum p_i \log p_i$) was calculated to characterize the species relative diversity (Pielou, 1975; Whittaker, 1972) for each plot.

For pollen analysis ($N = 26$) surface soil samples following the multiple sub-sampling techniques were collected in each community vegetation. Each sample consists of five sub-samples of surface soil, randomly taken within the community.

In order that the pollen analysis represents a variety of the natural vegetation, 5 surface samples were collected in Psammophytic community, 5 in Psammophytic community–shrub steppe transition, 10 in shrub steppe and 6 in grass steppe.

Sediment samples were processed according to standard palynological techniques including hot KOH, HCl (10%), heavy liquid with ZnCl$_2$ ($\delta = 2$), HF and acetolysis (Faegri and Iversen, 1992; Gray, 1965). Three *Lycopodium clavatum* tablets were added to every weighted sample before treatment to estimate representative pollen sums; the samples were analysed under light microscope. According to Weng et al. (2006), during the early phase of pollen counting, the palynological richness increases rapidly, but the growth rate decreases gradually and eventually reaches a plateau (asymptote) of nearly zero change. However, the point where the asymptote is reached varies among samples from different communities. In samples from *Psammophytic*
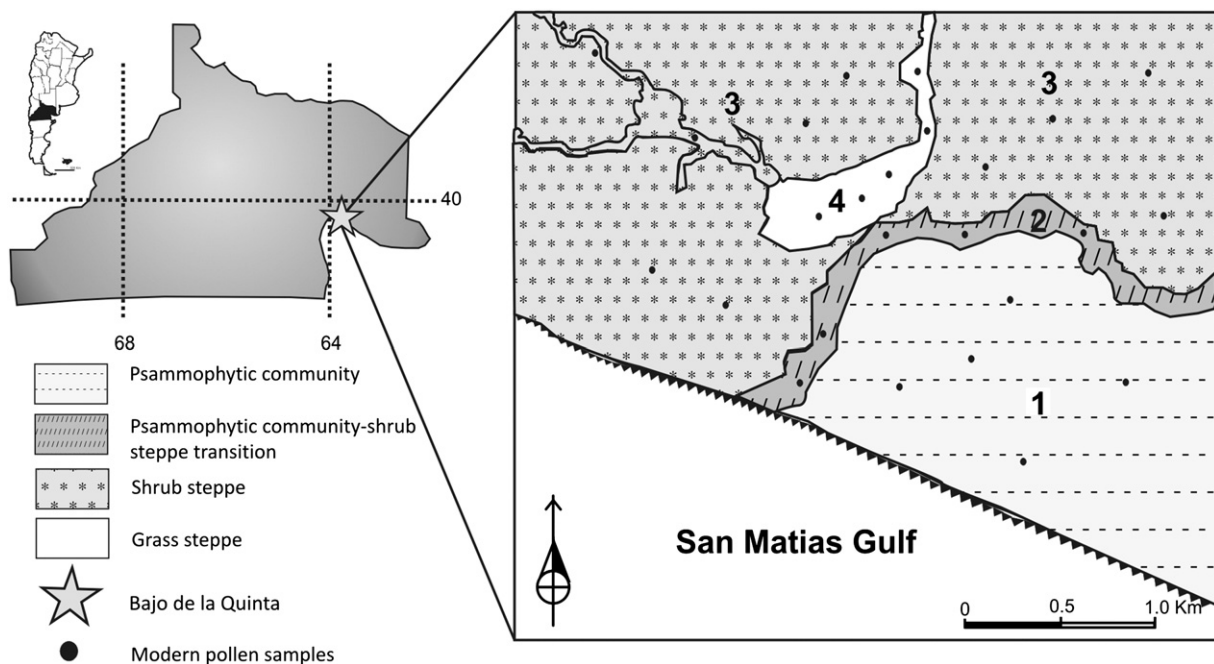

Fig. 1. Location of the study area, Bajo de la Quinta, Río Negro, Argentina, with main vegetation types and the surface samples used for pollen analysis. Geomorphological units: 1.Mobile Dunes, 2. Fixed Dunes, 3. Ephemeral Pond and 4. Fluvial Landscape.

community the asymptote was reached with a sum about 300 grains while samples from *Psammophytic community–shrubs steppe transition*, *Shrub steppe* and *Grass steppe*, with a high diversity, were reached when at least 500 grains were counted. Identifications were performed using the pollen reference collection of the Laboratory of Paleoecology and Palynology, University of Mar del Plata. The pollen types Asteraceae subf. Cichorioideae and *Rumex* (Disturbance taxa) were excluded from the pollen sum since their spatial distribution is related to disturbed areas. Species such as *Eucalyptus*, Brassicaceae and *Pinus* were excluded from the pollen sum because it is not pollen representation of native ecosystem. Additionally, Geraniaceae, Plumbaginaceae, Rosaceae, Convolvulaceae, Ranunculaceae and Malvaceae with low representation were grouped and called "herbs". Each taxon is expressed as a percentage of the total pollen sum. Pollen diagrams were plotted using TGView, 2.0.2 (Grimm, 2004).

Discriminant analysis (DA) was applied on the surface samples to test if different vegetation types present in Bajo de la Quinta can be distinguished by their pollen assemblages. This technique will contribute to the understanding of qualitative relationship between modern pollen and contemporary vegetation.

The DA requires an *a priori* classification of pollen surface samples into groups based on their vegetation types. All modern pollen samples were used to describe four groups based on their main vegetation types. Thus, four modern pollen samples groups corresponded to each community: *Psammophytic community*, *Psammophytic community–shrubs steppe transition*, *Shrub steppe* and *Grass steppe*. The variables that represent taxa characteristic of Monte vegetation were included in the analysis.

On the other hand, palynological richness (E (Tn)) was estimated by rarefaction analysis, based on 210 grain minimum pollen sum, using the software Psimpoll 4.10 (Bennett, 2003; Birks and Line, 1992).

The relationship between main vegetation types and geomorphological units was tested by cluster analysis with a minimum variance technique and Euclidean distance.

With the aim to study pollen–vegetation relationship for all taxa present, both plant and pollen dataset (Davis, 1984; Hjelle, 1997), surface pollen samples (N = 16) corresponding to the vegetation censuses were used for estimated indexes of association and representation. Three indexes (association (A), under-representation (U) and over-representation (O)) were calculated. The indexes are based on a comparison between pollen percentages and vegetation cover-abundance measured at the same time that the sediments were collected. All components of the vegetation (shrubs, dwarf-shrubs and herbs) were evaluated in this study. These indexes are defined as follows:

$$A = B_0(P_0 + P_1 + B_0)^{-1}$$
$$U = P_1(P_1 + B_0)^{-1}$$
$$O = P_0(P_0 + B_0)^{-1}$$

where B_0 = number of sample where pollen type and associated plant taxon are present, P_0 = number of sample where the pollen type is present in the surface sample but the plant taxa is not present in the vegetation, and P_1 = number of sample where the pollen type is not present in the surface sample but the plant taxa is present in the vegetation (Bunting, 2003).

The association index (A) is a measure of whether the presence of the pollen type in the surface sample is an indication of the presence of the associated plant in the local vegetation. The index can range from 1.0 for pollen types that are always present, but only if the plant taxon is present in the local vegetation, to 0.0 for pollen types that are present when the plant taxon is absent or that are absent when the plant taxon is present.

Pollen types can have low values for the association index for two reasons: the pollen may be present when the plant is absent in the local vegetation (over-representation), or the pollen may be absent in the surface sample even though the plant is present in the local vegetation (under-representation). The difference between these two types of "inaccuracy" is important to the interpretation of fossil pollen frequencies, so over and under-representation are measured with two additional indexes (Davis, 1984).

Table 3 summarises the representation and association indexes calculated for all taxa recorded. According to Bunting (2003), five groups of taxa are identified based on these scores. Strongly associated taxa have A values above 0.75 and moderate O values. Associated taxa have A values between 0.5 and 0.75, coupled with moderate O and U values. Taxa with A scores below 0.5 can be divided into three groups. Over-represented types have low A values, high O and zero U values. Weakly associated types have low A values and relatively high values for both U and O. Unassociated types have zero A values, and high O and U values.

Relationships between species diversity in contemporary vegetation and palynological richness were tested using the Spearman coefficient for simple linear correlation. Statistical analysis was carried out using R programs (2008).

4. Results

4.1. Vegetation analysis

Cluster analysis (Fig. 2) grouped vegetation censuses coinciding with the prior defined geomorphological units. Three major associations can be distinguished with a 0.6 Euclidean distance. Censuses from Ephemeral Pond constitute the first association. Fluvial Landscape and Fixed Dunes censuses formed the second association. The last association is composed by Mobile Dunes censuses.

Shannon–Wiener index is shown in Table 1.

Four main vegetation types in Bajo de la Quinta were identified based on the cover-abundance and the most representative species in each geomorphological unit.

(1) *Psammophytic community*. This type is characterized by open vegetation, cover varies between 25% and 50% and species richness is 3.25. Its dominant species are *Hyalis argentea* Hook &Arn and *Sporobolus rigens* (Trin) E. Des. This community is represented in Mobile Dunes.

(2) *Psammophytic community–shrubs steppe transition*. It is located in Fixed Dunes, vegetation cover varies between 25% and 75% and species richness is about 7. *Larrea divaricata* dominates the shrub layer with accompanying shrubs such as *Capparis atamisquea* Kuntze, *Prosopis alpataco*, *Ephedra ochreata* Miers, *Cereus aethiops* Haw and *Condalia microphylla*. The presence and cover of *Sporobolus rigens* (10–25%) difference this community from adjacent ones. This community represents a transition between xeric–psammophilous communities.

(3) *Shrub steppe*. Vegetation cover is around 75% and species richness is about 9. The dominant specie is *Larrea divaricata*, other shrubs and dwarf-shrubs such as *Geoffroea decorticans* (Gillies ex Hook & Arn) Burkart, *Condalia microphylla*, *Capparis atamisquea* (A. Gray) Mold., *Monttea aphylla*, *Acantholippia seriphioides*, *Senna aphylla* and *Chuquiraga erinaceae* are present. Grasses and herbaceous present low cover values (5–25% and 1% respectively). It is characteristic of the Fluvial Landscape.

(4) *Grass steppe*. This type is represented on the Ephemeral Pond. *Poa ligularis* Phil. and *Stipa tenuis* Phil. present high cover values upper to 75% and this community species richness is 4.5. The community is characterized by a poorly represented shrubby layer of *Larrea divaricata* and *Condalia microphylla*. Other herbs, such as *Hoffmanseggia glauca* (Ort.) Eifert, *Senecio subulatus* D. Don ex Hook & Arn and *Grindelia chiloensis* (Cornel) with patches of bare soil, also occur in this unit.

Table 1
Values species richness, evenness and diversity of each vegetation censuses, coordinates and soil type from Bajo de la Quinta.

Vegetation communities	Mobile Dunes A					Fixed Dunes B		
N° Censuses	1	2	3	4	5	6	7	8
Latitude (°S)	40°57′12″	40°57′05″	40°57′00′	40°56′50″	40°56′31″	40°56′28″	40°56′24″	40°56′21″
Longitude (°W)	64°21′12″	64°20′58″	64°20′59″	64°21′04″	64°21′20″	64°21′17″	64°21′25″	64°21′39″
Soil texture		Sandy				Sandy-clay		
Average species richness (S)		3.25				7		
Species richness (s)	4	3	2	4	7.5	6	6	8
Evenness	0.596	0.911	0.855	0.785	0.775	0.630	0.715	0.676
Diversity	0.826	1001	0.593	1089	1509	1128	1487	1405

Vegetation communities	Fluvial Landscape C					Ephemeral Pond D		
N° Censuses	9	10	11	12	13	14	15	16
Latitude (°S)	40°56′11″	40°56′09″	40°56′01′	40°55′50″	40°56′55″	40°56′08″	40°56′05″	40°56′20″
Longitude (°W)	64°21′07″	64°21′03″	64°21′07″	64°21′34″	64°21′16″	64°21′13″	64°21′10″	64°21′00″
Soil texture		Clay-slimy				Slimy		
Average species richness (S)		9				4.57		
Species richness (s)	6	10	10	10	3	3	7.5	5
Evenness	0.612	0.619	0.777	0.629	0.707	0.708	0.665	0.654
Diversity	1097	1426	1788	1448	0.777	0.777	0.295	1052

4.2. Pollen analysis

Pollen percentage data from surface samples are shown in Fig. 3 and indicate the presence of 4 groups related to local and regional vegetation communities.

Psammophytic communities characterized by high percentages of *Hyalis argentea* (10–40%) and Poaceae (10–55%) together with Calyceraceae (5–10%), Chenopodiaceae (5–20%) and Asteraceae subf. Asteroideae (5–60%). Among shrubs, *Larrea divaricata*, *Prosopis* sp., Fabaceae and *Ephedra* sp. are present. The lowest value (E (Tn)) was 7.67 with ranges between 6 and 9 pollen types.

Psammophytic communities–shrub steppe transition is characterized by high values of Poaceae (5–40%), Chenopodiaceae (10–30%) together with moderate percentages of *Larrea divaricata* and *Prosopis* sp. (5–10%). Other shrubs such as Asteraceae subf. Asteroideae, *Condalia microphylla*, *Schinus* sp., Verbenaceae, Fabaceae, Caesalpinoideae, Scrophulariaceae, and Nyctaginaceae, among others, and psammophytic taxa (*Hyalis* and *Calycera* sp.) are present. (E (Tn)) reaches values around 20 pollen types, the lowest value was 12.45.

Shrub steppe is characterized by entomophilous shrubs such as, *Larrea divaricata* (3–7%) and *Prosopis* sp. (5–20%) together with other shrubs such as *Condalia microphylla* (5–15%), *Schinus* sp. (5%), Verbenaceae (<5% with 20% in one sample), Caesalpinoideae (5–20%) and *Chuquiraga* sp. (5–10%), among others. Chenopodiaceae reaches values up to 80% throughout the group. Poaceae shows values of approximately 5–25%. The lowest value of (E (Tn)) was 9 with values that range between 15 and 20 pollen types.

Grass steppe is dominated by Asteraceae subf. Asteroideae (80%) and Poaceae (5–20%). Chenopodiaceae shows values of 5–10% approximately with an increment of 15% at the base of the group. Others shrubs with low values (<5%) such as *Larrea divaricata*, *Prosopis*, Rhamnaceae, *Schinus*, Verbenaceae, Fabaceae, Caesalpinoideae, Scrophulariaceae, Nyctaginaceae, *Bougainvillea*, *Chuquiraga* and *Lycium* are present.

Ephedra sp. reaches values about 5–20%. The lowest value of (E (Tn)) was 8.31 with a range of pollen types between 7 and 10.

4.2.1. Discriminant analysis

The results of this analysis show that the discrimination between pollen assemblages of the four vegetation types was highly significant (*Wilks'Lambda = 0.0092*; *F = 7.38*; *p<0.0001*). The variables that contribute the most to the overall discrimination were (Table 2), *Hyalis argentea*, Asteraceae subf. Asteroideae, *Larrea divaricata*, Rhamnaceae and Poaceae. The first and second discriminant functions (*R canonical: 0.957 and 0.896*) were statistically significant and explained 69% and 26% of the total variance respectively. In both functions, the four units analysed were clearly differentiated (Fig. 4). *Psammophytic community* and *Grass steppe* units reach the greatest power of discrimination. However, many similarities occur between *Psammophytic community–shrubs steppe transition* and *Shrub steppe*, reflecting the transitional character of both pollen assemblages.

These results suggest that the four geomorphological units have different pollen spectra, except for some similarities between *Psammophytic community–shrubs steppe transition* and *Shrub steppe*.

4.3. Pollen–vegetation relationship

The most representative pollen taxa recorded in the main vegetation types on Bajo de la Quinta and their comparison with associated vegetation are shown in Fig. 5. The same representative pollen taxa and vegetation were present; however, the pollen assemblages differ considerably in the diversity and proportions of taxa in relation to vegetation. Some of the largest discrepancies are due to the differences between pollen percentages and vegetation cover of *Hyalis argentea*, *Larrea divaricata*, *Prosopis alpataco*, Chenopodiaceae and Asteraceae subf. Asteroideae. Pollen from non-local sources (*Nothofagus* and *Celtis*) was also found.

The *Psammophytic community* (Mobile Dunes) showed similar pollen and vegetation taxa while pollen assemblages of *Psammophytic community–shrubs steppe transition* (Fixed Dunes) and *Shrub steppe* (Fluvial Landscape) present high diversity of the pollen assemblages in relation to vegetation (Fig. 5). In these vegetation types, *Larrea divaricata*, the main component of Monte vegetation, presents high values cover (60% and 70%) in vegetation. However, its pollen values range between 10% and 7%. On the other hand, the *Shrub steppe* exhibits an important contribution of Chenopodiaceae pollen which taxa were not recorded in the vegetation censuses. Finally, the *Grass steppe* (Ephemeral Pond) is represented by equal pollen and vegetation associations but differing in their proportions and diversity (Fig. 5).

Poaceae and *Hyalis argentea* are strongly associated with values of 0.87 and 0.83 A respectively. *Larrea divaricata* and Rhamnaceae were associated with values of 0.61 and 0.60. The over-represented taxa were *Prosopis*, Asteraceae subf. Asteroideae, *Ephedra*, *Lycium*, Fabaceae and Chenopodiaceae with values of 0.75, 0.86, 0.87, 1, 0.77 and 1 respectively. The weakly associated taxa were Verbenaceae

Table 2
Significant variables in discriminant function analysis, p-level<0.01.

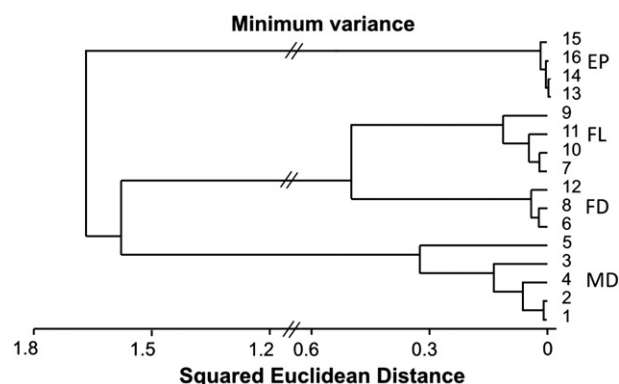|	Wilks' Lambda	p-Level	F
Hyalis argentea	0.034	0.000148	13,619
Asteraceae subf. Asteroideae	0.003	0.00038	11.34
Larrea divaricata	0.021	0.0052	6.4
Rhamnaceae	0.018	0.00957	4.77
Poaceae	0.014	0.0096	4.53

Fig. 2. Dendrogram of vegetation censuses from four geomorphological units. MD: Mobile Dunes, MF: Fixed Dunes, EP: Ephemeral Pond and FL: Fluvial Landscape.

and Caesalpinoideae with low values of 0.14 and 0.16. Finally, Calyceraceae was unassociated.

The correlation between species diversity and palynological richness was not significant (r: 0.379, p: 0.506).

5. Discussion

Pollen assemblages reflect the vegetation of Bajo de la Quinta according to geomorphological units and differences in pollen production/ dispersion.

The pollen–vegetation relationship in *Psammophytic community* and *Grass steppe* is determined by edaphic conditions such as sand mobility and silting of the pond, respectively. Although Asteraceae subf. Asteroideae is not highly represented in vegetation, the pollen assemblages from the *Grass steppe* show high percentage. This difference can be attributed to pollen contribution from a patch of *Baccharis spartoides* (Hook & Am ex Dc. J.Rémy). The patch is located in the eastern border of the pond and both plant abundance and pollen production are over-represented in the area. Other taxa present in the pollen assemblage of *Psammophytic community* and *Grass steppe* belong to Monte shrubs.

Pollen assemblages and vegetation from *Psammophytic community–shrubs steppe transition* and *Shrub steppe* communities represent Monte vegetation related to climatic arid conditions at regional scale. The pollen assemblages are characterized by the highest palynological richness and by the shrub taxa of Monte, such as *Larrea divaricata*, *Prosopis alpataco*, and *Condalia microphylla*, among others. Besides, xerophytics and psammophytic elements from *Psammophytic community–shrubs steppe transition* unit represent a transition between *Shrub steppe* and *Psammophytic community units*.

Although *Larrea divaricata* is the dominant specie of Monte vegetation, it presents low pollen percentages in *Psammophytic community–shrubs steppe transition* and *Shrub steppe*. Its dominance is under-represented in the pollen assemblages because of its entomophilous dispersion. Other shrubs such as *Prosopis alpataco*, Rhamnaceae, Verbenaceae, Fabaceae, Caesalpinoideae, and Scrophulariaceae, also

present this dispersion type and were under-represented in pollen assemblage.

Chenopodiaceae shows anemophilous dispersion, reflected by high pollen percentage in all units, mainly in *Shrub steppe*. This pattern can probably be explained by the fact that the samples analysed were situated in a currently dry meander. Sporadic rainfalls could generate flood-drought periods in the meander and salinization of substrate favoring the Chenopodiaceae establishment and growing on the ephemeral streams.

Differences in pollen proportions on the main vegetation types of Bajo de la Quinta are linked with the production and dispersion characteristics of the main representative taxa. Also, different flowering phenology between years is likely to be influenced by climatic characteristics, such as seasonality and temperature variation; water availability can affect production and pollen dispersion (Tadey et al., 2009).

Pollen diversity differs from plant diversity owing to the lower taxonomic precision of pollen identification and "silence" of many species, which are not represented in pollen spectra (Faegri and Iversen, 1992). In this study, the low taxonomic resolution on pollen identification of Poaceae, Asteraceae subf. Asteroideae and Chenopodiaceae species appears to be the major cause for the poor correlation between species diversity and palynological richness.

Pollen analyses in temperate and semi-arid regions are based almost exclusively on anemophilous taxa, which comprise the dominant source of pollen assemblages in sediments. Nevertheless, entomophilous taxa should not be excluded in diversity studies, because they are important elements of many vegetation types (Weng et al., 2006). The A, O, and U values also provide information on the type of pollen production and dispersion (Davis, 1984; Hjelle, 1997). Strongly associated taxa have good pollen dispersal and/or open blossoms with anthers more or less exposed (Hjelle, 1997). In this analysis Poaceae and *Hyalis argentea* were strongly associated. Pollen of Poaceae is found in all main vegetation types probably due to its anemophilous dispersion. Although both the plant and the pollen were found in few samples, *Hyalis argentea* shows a strong association index. Its blossoms with few exposed anthers may explain the good association found. Furthermore, the pollen grain size of *Hyalis argentea* (>40 μm) does not favor a wide dispersion (Faegri and Pijl, 1979).

According to Hjelle (1997), taxa with entomophilous dispersion but with anthers more or less exposed and pollen grain size less than 40 μm have relatively good association (A<0.75). That may be the case of *Larrea divaricata* and Rhamnaceae whose presence is recorded in several units of vegetation.

Over-represented taxa have generally characteristics such as anemophilous dispersion, pollen grain size less than 40 μm and open flowers with numerous exposed anthers. In this group are *Ephedra*

Table 3
Indexes of association and representation of pollen assemblage.

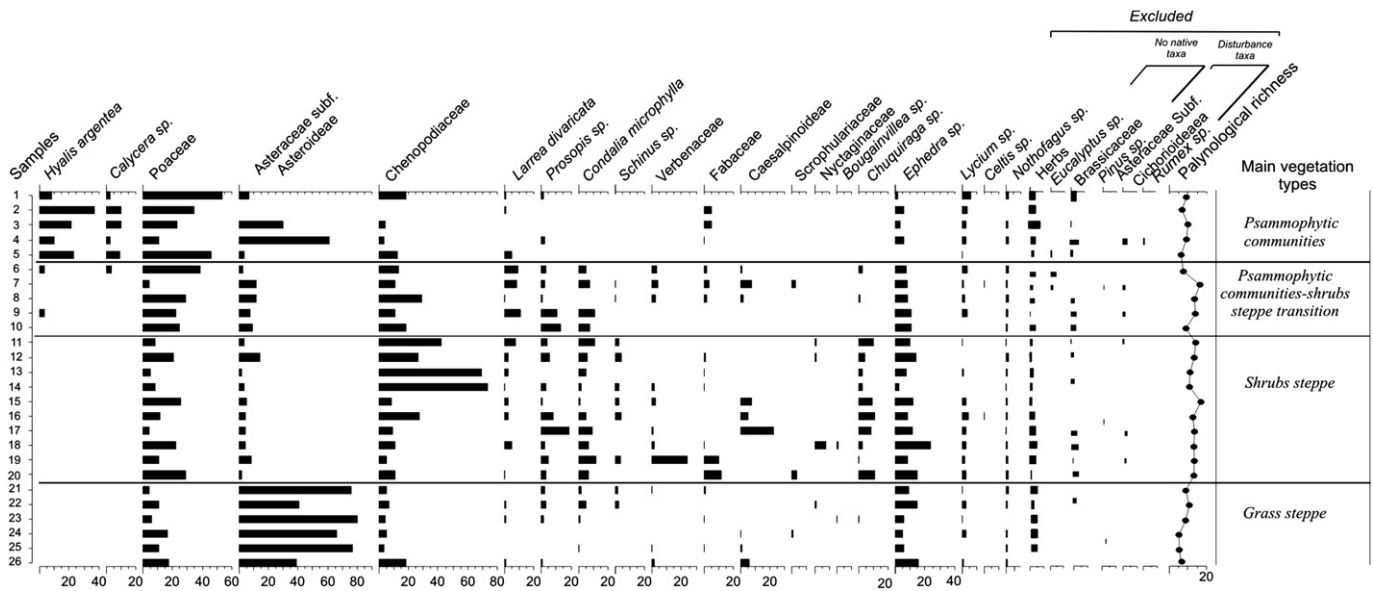| Taxa	A	U	O
Strongly associated types			
Poaceae	87	0	0.125
Hyalis argentea	0.83	0	0.16
Associated types			
Larrea divaricata	0.61	0.2	0.27
Condalia microphylla	0.60	0	0.23
Over-represented types			
Prosopis	0.25	0	0.75
Asteraceae subf. Asteroideae	0.13	0	0.86
Ephedra	0.125	0	0.87
Lycium	0	0	1
Fabaceae	0.22	0	0.77
Chenopodiaceae	0	0	1
Weakly associated types			
Verbenaceae	0.14	0.75	0.75
Caesalpinoideae	0.16	0.66	0.75
Unassociated types			
Calyceraceae	0	1	1

Fig. 3. Percentage pollen diagram and palynological richness from surface sediment samples.

with anemophilous dispersion, and Asteraceae subf. Asteroideae as *Baccharis spartoides* that presents numerous exposed anthers. Although *Prosopis* presents entomophilous dispersion, its flowers have exposed anthers which favor the relatively good pollen dispersion.

Particularly, in the *Shrub steppe*, high pollen percentage of Chenopodiaceae may be correlated with high pollen production and good pollen dispersion. Good dispersion properties are seen in the high over-representation index for anemophilous species. However, the low taxonomic resolution in pollen identification was a limiting factor for the index calculation at specie level.

Another factor to explain the occurrence of pollen when the plant was absent (*Lycium* and Fabaceae) is the fact that surface sediment samples may represent several years of pollen accumulation. Plants not growing at the site today may have grown there in the recent past (Davis, 1984).

Taxa with low pollen production always have low pollen percentages, independently of the absence or presence of plants (e.g. Caesalpinoideae and Verbenaceae) and show a weak association or unassociation (Calyceraceae).

Other taxa that are not recorded in vegetation are *Nothofagus* and *Celtis*, which come from Sub-Antarctic forest and Espinal respectively, with extra-regional origin.

6. Conclusions

Vegetation zonation at Bajo de la Quinta is regulated by geomorphology, substrate type and water availability, reflecting a vegetation change from psammophytic to xerophytic communities. Main vegetation types are represented in the pollen assemblages characterized by the dominance of *Larrea divaricata*, *Prosopis*, Poaceae, *Hyalis argentea* and Asteraceae subf. Asteroideae and presence of Rhamnaceae, *Ephedra*, *Calycera crassifolia*, and *Schinus*, among others. However, Poaceae, Chenopodiaceae, Asteraceae subf. Asteroideae and *Larrea divaricata* show the greatest differences in the pollen percentage in relation to vegetation. Moreover, pollen and vegetation relationships in Bajo de la Quinta are determined by local/regional conditions and differences in pollen production and dispersion.

Nothofagus and *Celtis* with low pollen percentage are an example of long distance pollen transport from source populations.

In this paper, the association–representation indexes and different pollen proportions provided information related to the production rate and pollen dispersal. In addition, these indexes helped in the interpretation of pollen–vegetation relationship. However, the estimation of indexes at species level was difficult due to low pollen morphological variability of Poaceae, Asteraceae subf. Asteroideae and Chenopodiaceae.

Environmental Holocene reconstructions require the interpretation of fossil pollen spectra in terms of past vegetation composition. Thereby, this study improves the insight of the pollen–vegetation relationship in this arid region so it can be applied in the interpretation of fossil pollen data in terms of past vegetation landscape.
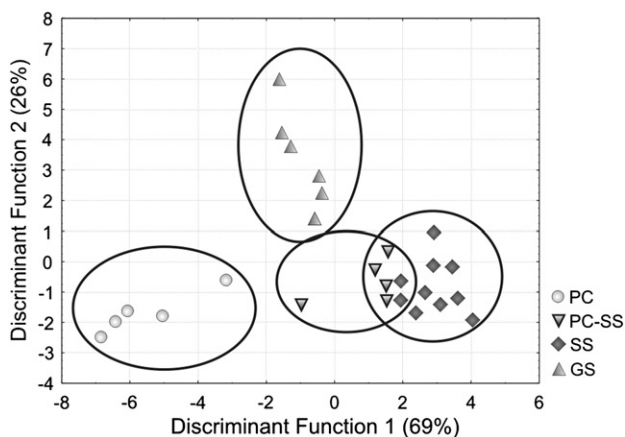
Fig. 4. Discriminant analysis of the surface samples (N = 26) from four main vegetation types. (PC) Psammophytic community, (PC–SS) Psammophytic community–shrub steppe transition, (SS) Shrub steppe, (GS) Grass steppe.
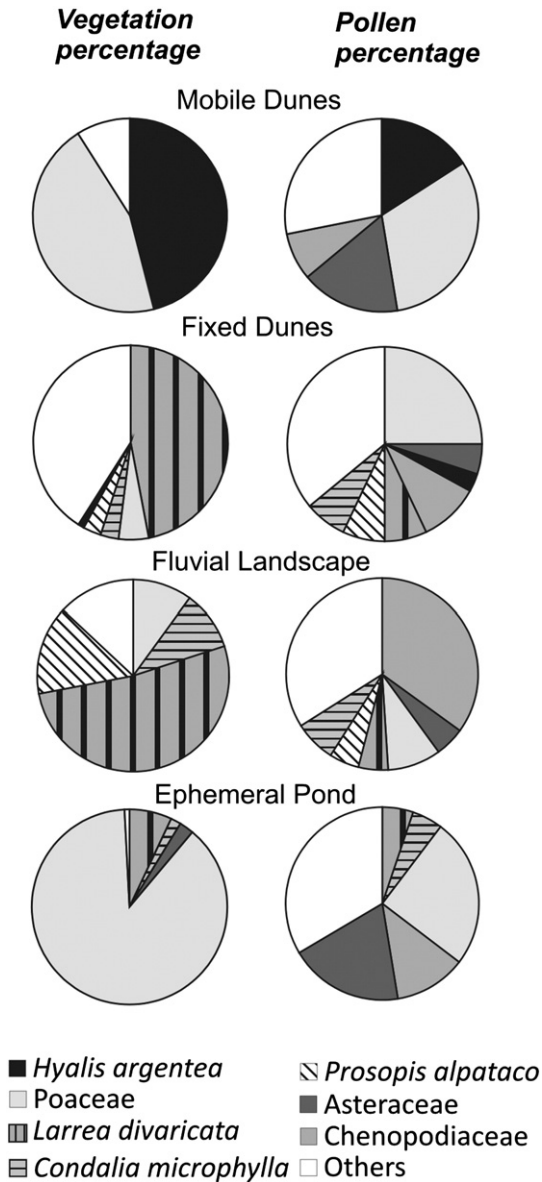
Fig. 5. Pollen–vegetation comparison for the different vegetation types of Bajo de la Quinta. Values are given as percentage coverage of each vegetation community census (N = 16) and percentage coverage of each surface pollen sample (N = 16) corresponding to vegetation censuses.

References

Abraham, E., del Valle, H.F., Roig, F., Torres, L, Ares, J.O., Coronato, F., Codagnone, R., 2009. Overview of the geography of the Monte Desert biome (Argentina). Journal of Arid Environments 73, 144–153.

Andersen, S.T., 1970. The relative pollen productivity and pollen representation of north Eropean trees, and corrections factors for tree pollen spectra. Danmarks Geologiske Undersogelse. Series II, 96, pp. 1–99.

Ares, J., Bertiller, M.B., Bisigato, A.J., 2003. Modeling and measurement of structural changes at a landscape scale in dryland areas. Environmental Modeling & Assessment 8, 1–13.

Bennett, K.D., 2003. "psimpoll" and "pscomb": C programs for analysing pollen data and plotting pollen diagramsAvailable online from Uppsala University Quaternary Geology program at URL http://www.kv.geo.uu.se/psimpoll.html2003.

Berrío, J.C., Arbeláez, M.V., Duivenvoorden, J.F., Cleef, A.M., Hooghiemstra, H., 2003. Pollen representation and successional vegetation change on the sandstone plateau of Araracuara, Colombian Amazonia. Review of Palaeobotany and Palynology 126, 163–181.

Bertiller, M.B., Bisigato, A.J., Carrera, A.L., del Valle, H.F., 2004. Estructura de la vegetación y funcionamiento de los ecosistemas del monte Chubutense. Boletín de la Sociedad Argentina de Botánica 39 (3–4), 139–158.

Birks, H.J.B., Line, J.M., 1992. The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. The Holocene 2, 1–10.

Bisigato, A.J., Villagra, P.E., Ares, J.O., Rossi, B.E., 2009. Vegetation heterogeneity in Monte Desert ecosystems: a multi-scale approach linking patterns and processes. Journal of Arid Environments 73, 182–191.

Bradshaw, R.H.W., Webb, T.I.I.I., 1985. Relationships between contemporary pollen and vegetation data from Wisconsin and Michigan, USA. Ecology 66, 721–737.

Braun-Blanquet, J., 1979. Fitosociología. Bases para el estudio de las comunidades vegetales. In: Blume, H. (Ed.), , p. 820. Madrid.

Bunting, M.J., 2003. Pollen–vegetation relationships in non-arboreal moorland taxa. Review of Palaeobotany and Palynology 125, 285–298.

Calcote, R., 1995. Pollen source area and pollen productivity: evidence from forest hollows. Journal of Ecology 83, 591–602.

Davis, M.B., 1963. On the theory of pollen analysis. American Journal of Science 261, 897–912.

Davis, O.K., 1984. Pollen frequencies reflect vegetation patterns in a great basin (U.S.A.) mountain range. Review of Palaeobotany and Palynology 40, 295–315.

Faegri, K., Iversen, J., 1992. Textbook of Pollen Analysis, 4 ed. John Wiley & Sons, Chichester.

Faegri, K., Pijl, L., 1979. The Principles of Pollinitation Ecology. Pergamon Press, London. 244 pp.

Favier Dubois, C.M., Kokot, R.R., 2011. Changing in the Bajo de la Quinta (San Matías Gulf, Northern Patagonia, Argentina): impact of geomorphologic processes in subsistence and human use of coastal habitats. Quaternary International. doi:10.1016/j Quaint.2011.03.051.

Fontana, S.L., 2005. Coastal dune vegetation and pollen representation in south Buenos Aires Province, Argentina. Journal of Biogeography 32 (7), 19–35.

Gray, J., 1965. Palynological Techniques. W. H. Freeman, San Francisco, CA. 471–587.

Grimm, E., 2004. Tilia Software. Illions State Museum. Research and Collection Center, Springfield, IL.

Heusser, C., 2000. Pollen fallout in the Araucaria region of the Argentina Andes (39° S) and downslope in Patagonia to the Atlantic Ocean. Regensburger Geographische Schriften 33, 157–168.

Hjelle, K.L., 1997. Relationships between pollen and plants in human-influenced vegetation types using presence–absence data in western Norway. Review of Palaeobotany and Palynology 99, 1–16.

Islebe, G.A., Hooghiemstra, H., 1995. Recent pollen spectra of highland Guatemala. Journal of Biogeography 22, 1091–1099.

Jackson, S.T., 1990. Pollen source area and representation in small lakes of the Northeastern United States. Review of Palaeobotany and Palynology 63, 53–76.

Kaasschieter, J.P.H., 1965. Geología de la cuenca del Colorado. Actas Segundas Jornadas geológicas Argentinas, Buenos Aires, Vólumen III, pp. 251–269.

Kokot, R.R., Codignotto, J.O., Elissondo, M., 2004. Vulnerabilidad al ascenso del nivel del mar en la costa de la provincia de Río Negro. Revista de la Asociación Geológica Argentina 59 (3), 477–487.

Labraga, J.C., Villalba, R., 2009. Climate in the Monte Desert: Past trends, present conditions, and future projections. Journal of Arid Environments 73, 154–163.

León, R.J.C., Bran, D., Collantes, M., Paruelo, J.M., Soriano, A., 1998. Grandes unidades de vegetación de la Patagonia extra andina. Ecología Austral 8, 125–144.

Mancini, M.V., 1993. Recent pollen spectra from forest and steppe of South Argentina: a comparison with vegetation and climate data. Review of Palaebotany and Palynology 77, 129–142.

Mancini, M.V., 1998. Vegetation changes during the Holocene in Extra-Andean Patagonia, Santa Cruz Province, Argentina. Palaeogeography, Palaeoclimatology and Palaeoecology 138 (1–4), 207–219.

Mancini, M.V., 2002. Vegetation and climate during the Holocene in Southwest Patagonia, Argentina. Review of Palaeobotany and Palinology 122, 101–115.

Mancini, M.V., de Porras, M.E., Bamonte, F.P., 2011. Southernmost South America Steppes: vegetation and its modern pollen-assemblages representation. Steppe Ecosystems: Dynamics, Land Use and Conservation. Nova Science Publishers, Hauppauge, NY, USA. ISBN: 978-1-61122-765-9.

Markgraf, V., D'Antoni, H.L., Ager, T.A., 1981. Modern pollen dispersal in Argentina. Palynology 5, 43–63.

Paez, M.M., Villagrán, C., Stutz, S., Hinojosa, F., Villa, R., 1997. Vegetation and pollen dispersal in the subtropical-temperate climatic transition of Chile and Argentina. Review of Palaeobotany and Palynology 96, 169–181.

Pielou, E.C., 1975. Ecological Diversity. Wiley Interscience, New York.

Prentice, I.C., 1988. Records of vegetation in time and space: the principles of pollen analysis. In: Huntley, B., Weeb III, T. (Eds.), Vegetation History. Kluwer, The Hague, pp. 17–42.

Prentice, I.C., Berglund, B.E., Olsson, T., 1987. Quantitative forest-composition sensing characteristics of pollen samples from Swedish lakes. Boreas 16, 43–54.

R. Development Core Team, 2008. R: A Language and Environment for Statistical Computing. The R Foundation for Statistical Computing, Viena, Austria3-900051-07-0http://www.R-project.org.

Roig, F.A., Roig-Juñent, S., Corbalán, V., 2009. Biogeography of the Monte Desert. Journal of Arid Environments 73, 164–172.

Roig-Juñent, S., Flores, G., Claver, S., Debandi, G., Marvaldi, A., 2001. Monte Desert (Argentina): insect biodiversity and natural areas. Journal of Arid Environments 47, 77–94.

Schäbitz, F., 1994. Holocene climatic variations in northern Patagonia, Argentina. Palaeogeography, Palaeoclimatology, Palaeoecology 109, 287–294.

Schäbitz, F., 1999. Paläoökologische Untersuchungen an geschlossenen Hohlformen in den Trockengebieten Patagoniens. Bamberger Geographische Schriften 17, 1–239.

Schäbitz, F., 2003. Estudios polínicos del cuaternario en las regiones áridas del sur de Argentina: Rev. Museo Argentino de Ciencias Naturales 5 (2), 291–299.

Schäbitz, F., Liebricht, H., 1998. Landscape and climate development in the south-eastern part of the "Arid Diagonal" during the last 13,000 years. Bamberger Geographische Schriften Bd 15, 371–388.

Tadey, M., Tadey, J.C., Tadey, N., 2009. Reproductive biology of five native plant species from the Monte Desert of Argentina. Botanical Journal of the Linnean Society 161, 190–201.

Weng, C., Hooghiemstra, H., Duivenvoorden, J.F., 2006. Challenges in estimating past plant diversity from fossil pollen data: statistical assessment, problems and possible solutions. Diversity Research 12, 310–318.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 21.-251.