



STUDYING POLLEN REPRESENTATION OF VEGETATION AND PLANT RICHNESS FROM PAMPEAN COASTAL DUNES (ARGENTINA, SOUTH AMERICA): EXPLORING FROM LOCAL TO LANDSCAPE QUANTITATIVE LINKAGES

ESTUDIO DE LA REPRESENTACIÓN DEL POLEN DE LA VEGETACIÓN Y LA RIQUEZA DE PLANTAS DE LAS DUNAS COSTERAS PAMPEANAS (ARGENTINA, AMÉRICA DEL SUR): EXPLORANDO LAS RELACIONES CUANTITATIVAS DESDE LO LOCAL AL PAISAJE

Carolina Vásquez¹, Gonzalo Sottile^{1,2*}, Víctor Merino-Campos¹ & Silvina Stutz¹

SUMMARY

1. Grupo de Paleoecología y Palinología, Facultad de Ciencias Exactas y Naturales, Instituto de Investigaciones Marinas y Costeras (Universidad Nacional de Mar del Plata - CONICET), Mar del Plata, Argentina

2. Grupo de Biología y Ecodiversidad vegetal, Facultad de Ciencias Exactas y Naturales, Instituto de Investigaciones Marinas y Costeras (Universidad Nacional de Mar del Plata - CONICET), Mar del Plata, Argentina

*gonzalo_sottile@yahoo.com.ar

Citar este artículo

VÁSQUEZ, C., G. SOTTILE, V. MERINO-CAMPOS & S. STUTZ. 2024. Studying pollen representation of vegetation and plant richness from Pampean coastal dunes (Argentina, South America): exploring from local to landscape quantitative linkages. *Bol. Soc. Argent. Bot.* 59: 507-527.

DOI: <https://doi.org/10.31055/1851.2372.v59.n4.44793>

Recibido: 17 Abr 2024
Aceptado: 24 Jul 2024
Publicado en línea: 31 Dic 2024
Publicado impreso: 31 Dic 2024
Editor: Gonzalo J. Márquez¹

ISSN versión impresa 0373-580X
ISSN versión on-line 1851-2372

Background and aims: Studying plant dynamics through past pollen records may contribute to a better understanding of long-term changes in plant communities. Thus, this study aims to establish whether surface pollen composition and richness of the Argentinean Coastal Dune System reflect landscape heterogeneity in coastal dune environments.

M&M: Twenty-four sediment surface samples were collected in small lagoons. Landscape-scale heterogeneity up to 2000 m was mapped and classified in landscape units. Multivariate analyses were used to classify pollen samples and compare them to landscape unit coverage (%). Also, we evaluate plant species and pollen richness relationship by linear regression models.

Results: The relationship between plant and pollen richness is influenced by taxonomic smoothing, pollen production and taphonomic constraints (dispersal and preservation). The pollen assemblages and pollen richness from surface sediments of small lagoons and interdune slacks reflect plant richness and vegetation heterogeneity at the landscape scale (ca. 1000-2000 m). The main contributors to pollen richness are anemophilous pollen types, although some entomophilous pollen types are useful to infer some local heterogeneity.

Conclusions: We report the first quantitative analysis on pollen-vegetation relationship of coastal ecosystems showing that pollen records reflect landscape vegetation attributes, encouraging the study of past plant diversity and landscape variability based on pollen records.

KEY WORDS

Coastal dune vegetation, landscape heterogeneity, pollen, quantitative pollen-vegetation relationship.

RESUMEN

Antecedentes y objetivos: Estudiar la dinámica de la diversidad vegetal mediante registros polínicos puede contribuir a entender patrones de cambio de largo plazo. Para ello es necesario estudiar cómo la composición y riqueza del polen superficial de los sistemas de Dunas Costeras argentinas reflejan la heterogeneidad del paisaje.

M&M: Se recolectaron 24 muestras de superficie de sedimentos de pequeñas lagunas. Se mapeó y clasificó la heterogeneidad vegetal hasta 2000 m en unidades de paisaje y mediante análisis multivariados y agrupamiento se comparó el contenido polínico y la cobertura de las unidades de paisaje (%). Se modeló la relación entre riqueza específica y riqueza polínica, desde la escala local hasta la de paisaje mediante regresiones lineales.

Resultados: La relación entre la riqueza específica y polínica está influenciada por el sesgo taxonómico, la producción polínica y limitaciones tafonómicas (dispersión y preservación de polen). Las asociaciones y riqueza de polen superficial reflejan la riqueza específica y heterogeneidad vegetal a escala de paisaje (ca. 1000-2000 m). Los principales contribuyentes a la riqueza polínica son anemófilos. Algunos tipos de polen entomófilos son útiles para inferir cierta heterogeneidad local.

Conclusiones: El modelado cuantitativo de la relación polen-vegetación en término de unidades de paisaje y riqueza polínica demuestra el alto potencial para la aplicación de estos modelos en la reconstrucción de la dinámica de la vegetación en este tipo de ambientes a partir de registros polínicos.

PALABRAS CLAVE

Heterogeneidad del paisaje, polen, relación cuantitativa polen-vegetación, vegetación de dunas costeras.

INTRODUCTION

Coastal Dune Systems (CDS) are landforms of regional extension, consisting mainly of mobile dunes and dune ridges fixed by vegetation, in which a mosaic of environments has been formed with plant communities adapted to different landforms. They are abundant on the Argentinian coast, and according to Isla *et al.* (1996, 2001) and Codignotto *et al.* (2012) developed during the late Holocene between *ca.* 3070 and 540 yrs. BP. These systems are highly dynamic and diverse, in terms of vegetation cover and composition. They include endemic species and provide multiple ecosystem services of economic and environmental value Celsi (2016). Since the XIX century, they have been threatened by several factors, including afforestation with exotic species of *Acacia* Mill., *Populus* L., *Eucalyptus* L'Hér., and *Pinus* L. genera, which dispersion now represents one of the main threats to conservation in the area. Invasions of woody species have been considered to affect severely large areas of grassland causing variations in the dominant life forms, disturbing the dynamics of vegetation and changing the distribution patterns of species and increasing ecosystem patchiness (Alberio & Comparatore, 2014). Invasion rates and its impacts on biodiversity have been characterized spatially and seasonally, nevertheless, long term effects (decadal or longer time lags) have not been recorded for Argentinian CDS ecosystems.

Pollen assemblages preserved in sediments of CDS lagoons and interdune slacks can be used as a proxy for past plant richness as they record the dynamics of plant taxa through both, space and time. However, pollen assemblages studies are limited by low taxonomic resolution, pollen production, and taphonomic processes (transport, deposition, and preservation). Moreover, pollen-based species richness estimates are sensitive to source area size, missing taxa, and pollen count sizes (Van der Sande *et al.* 2021) which may decrease the accuracy with which pollen represents vegetation communities (Goring *et al.* 2013). For these reasons, pollen abundance cannot be directly translated into plant abundance when interpreting past pollen assemblages (Fontana, 2005a). To understand fossil pollen assemblages and make ecological inferences, it is necessary to calibrate modern pollen-vegetation diversity relationships in

surface samples (e.g. Goring *et al.*, 2013; Meltsov *et al.*, 2011; Matthias *et al.*, 2015; Felde *et al.*, 2015; Gosling *et al.*, 2018; Reitalu *et al.*, 2019; Abraham *et al.*, 2020; Papadopoulou *et al.*, 2022).

Modern pollen-vegetation studies in Argentinean CDS have been carried out on the coast of San Matías Gulf (north Patagonia) (Marcos & Mancini, 2012), and in the southwest and southeast coast of Buenos Aires Province (Fontana, 2003, 2004, 2005b; Stutz & Prieto, 2003; Latorre *et al.*, 2010; Monserrat *et al.*, 2012). These studies mainly focused on the relationship between vegetation distribution and pollen dispersal. Fontana (2005a) emphasized that pollen representation was influenced both by differences in pollen production, dispersal, and preservation of individual taxa, as well as by the spatial distribution of vegetation and topography of the CDS and by wind pattern.

Since the pioneers of quantitative analysis of modern and past pollen-vegetation relationships, Prentice (1985), Sugita (1994, 2007a, b) and Bunting & Middleton (2005, 2009), many works have been carried out, mainly in northern hemisphere forests and steppe ecosystems. Pollen richness or rarefied palynological richness was first interpreted as a proxy of past plant diversity (e.g. Birks & Line, 1992; Bennett *et al.*, 1992; Bunting, 1994; Andersen, 1995; Giesecke *et al.*, 2012), however, during the last twenty years, some quantitative approaches have explored the relationship between modern vegetation and modern pollen assemblages from surface samples to discuss the performance of these modeling and appliance to past palynological records (e.g. Burry *et al.*, 2001; Goring *et al.*, 2013; Masciadri *et al.*, 2013; Felde *et al.*, 2015; Matthias *et al.*, 2015; Reitalu *et al.*, 2019; Li *et al.*, 2022; Senn *et al.*, 2022). These studies warned about the spatial scale-dependence and the floristic composition of specific ecosystem effects on the capacity of this proxy to reconstruct past plant diversity dynamics. Disentangling between natural and human forcing of past Coastal Dune System vegetation dynamics demands calibrating modern pollen-vegetation representation models since a quantitative approach.

The CDS presents a large number of interdune slacks, which have a high potential for pollen trapping and preservation, as well as a mixture of landscape units with vegetated and pristine areas and some areas invaded by exotic forests, particularly in the northern section of the CDS, which makes it

an ideal area for performing paleoenvironmental reconstructions of past vegetation changes (Vásquez *et al.*, 2023). Previous studies based on fossil pollen records of Faro Querandí (northern area of the CDS) registered changes in wetland and dune vegetation over the last 500 years and they recorded also the first expansion of exotic forests in the CDS (Vásquez *et al.*, 2023). However, these pollen-based qualitative reconstructions have not discussed long-term changes in plant diversity. Thus, modeling between modern plant and pollen richness and pollen-vegetation representation in a quantitative dimension would encourage future past vegetation and diversity changes in quantitative reconstructions.

The aim of this work is to establish whether pollen composition and richness reflect the landscape heterogeneity, considering both vegetation patterns and geomorphological characteristics of the CDS. We plan to evaluate the relationship between plant and pollen richness in relation to pollen production, taxonomic and taphonomic (dispersal and preservation) constraints, at local and extra-local scales.

MATERIALS AND METHODS

Study area

The study area corresponds to the Faro Querandí Municipal Nature Reserve (FQNR), located in the Coastal Dune Systems (CDS) of the southeast of Buenos Aires Province, Argentina, which preserves a valuable area of the Pampa plain ecoregion, characterized mainly by the presence of grassland vegetation (Fig. 1). The CDS constitutes an almost uninterrupted extensive coastal dune fields with a width, from the sea towards the mainland, ranging from hundreds of meters to 8 km (Celsi, 2016). These dunes are generally parabolic to pyramidal, although there are also transverse dunes, barchans (crescent-shaped), and star-shaped dunes (Bértola *et al.*, 2002). Specifically, the FQNR comprises about 5000 ha with an aeolian morphology, and dunes are mainly transversal, with a general southwest-northeast orientation (Codignotto *et al.*, 2012). The pronounced topographic and edaphic variations at the CDS drive noticeable changes in vegetation cover and floristic composition. Psammophytic plant types cover mobile and semifixed dunes

while hydrophytic plants grow in flooded lowlands (lagoons and interdune slacks) (Celsi, 2016).

The vegetation of the CDS is characterized mainly by psammophytic species that are distributed according to the geomorphology heterogeneity (Cabrera, 1941; Stutz & Prieto, 2003; Celsi, 2016; Marcomini *et al.*, 2017). According to Fontana (2005a) this heterogeneity can be zoned in different landscape units. These landscape units include a strip of beach free of vegetation and the back shore, the adjacent area with permanent sand, salt spray, and water droplets carried by the wind in storms. Only a few halophytic plant species (<5% coverage), such as *Sporobolus coarctatus* (Trin.) P.M. Peterson & Saarela, grow under such environmental conditions. Mobile dunes, active dunes with a strong substrate movement due to wind action, expand toward the mainland, with <10-30% coverage. This zone is characterized by pioneer species such as *Panicum racemosum* (P. Beauv.) Spreng., *Calycera crassifolia* (Miers) Hicken, *Senecio crassiflorus* (Poir.) DC. and the exotic *Cakile maritime* Scop. Inward to the continent, the vegetation cover increases, stabilizing dunes sediments favoring the formation of humus. These semifixed (>30% coverage) and fixed dunes (>75% coverage) are covered by grasslands and psammophytic shrublands dominated by *Poa lanuginosa* Poir., *Tessaria absinthioides* (Hook. & Arn.) DC., and *Achyrocline satureioides* (Lam.) DC. Herbaceous plants such as *Ambrosia tenuifolia* Spreng., *Adesmia incana* Vogel, and *Hydrocotyle bonariensis* Lam. are subordinated components joint with some shrub species, *Baccharis genistifolia* DC., *Margyricarpus pinnatus* (Lam.) Kuntze, and *Discaria Americana* Gillies & Hook., and the exotics *Centaurium pulchellum* (Sw.) Druce, *Blackstonia perfoliata* (L.) Huds., *Medicago lupulina* L., *Melilotus indicus* (L.) All., and *M. albus* Desr. The interdune slacks (ca. 100% coverage) are intermediate depressions frequently flooded covered by species of the genus *Typha*, other hydrophytic such as *Schoenoplectus* spp. and *Eleocharis* spp., *Juncus* sp. and other herbaceous dicots, *Bacopa monnieri* (L.) Wettst., and *Eryngium* spp. *Cortaderia selloana* (Schult. & Schult. f.) Asch. & Graebn. grow on the edges of the interdune slacks and can also form large tall grasslands in the semifixed dunes or even patches on mobile dunes slopes. Temporary or permanent lagoons develop due to the contribution of rainwater

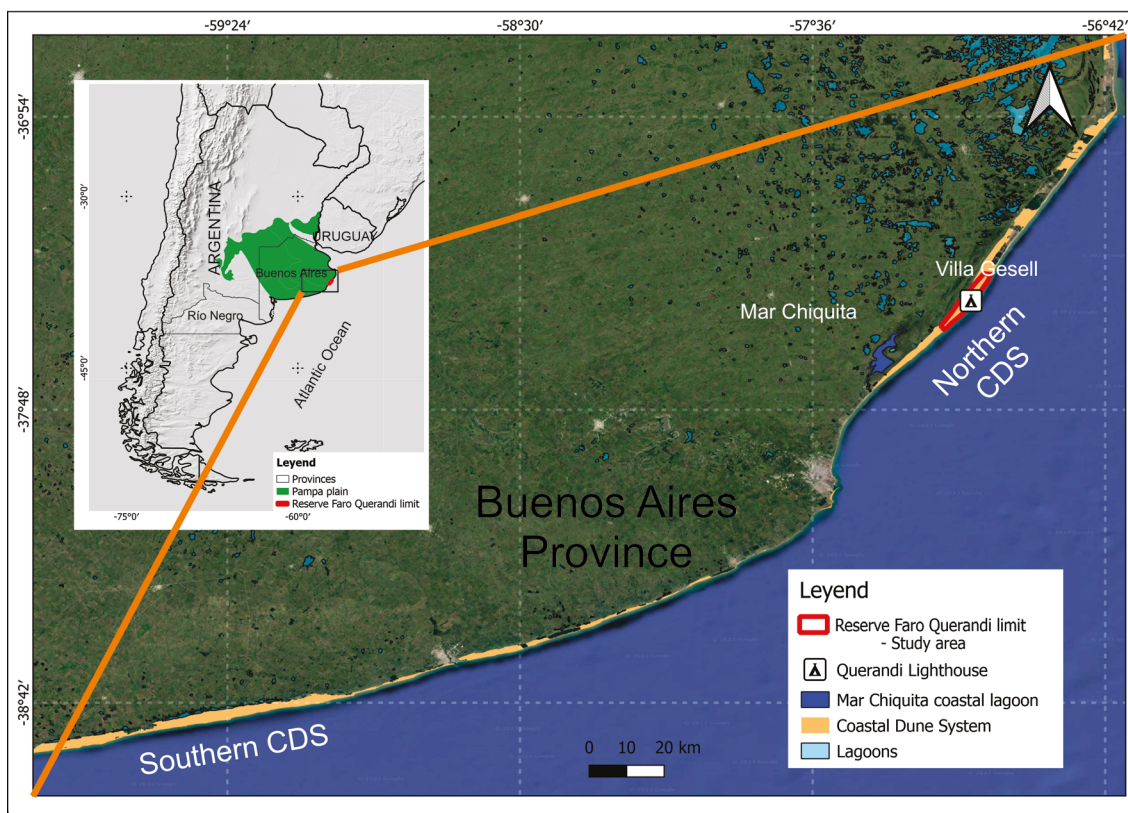


Fig. 1. Map of study area in Pampa plain (according to Oyarzabal *et al.*, 2018) showing the location of Reserve Faro Querandí and other sites mentioned in the text.

or water table raising, where dense hydrophytic vegetation grows, as species of the Cyperaceae and Juncaceae families, *Potamogeton* spp, *Polygonum punctatum* Elliott, *Utricularia gibba* L., among others.

Since the early 20th century, exotic trees were introduced to fix mobile dunes in the area of Villa Gesell village and to place the Querandí lighthouse, like pines, eucalyptus, cypresses, poplars, acacias, tamarisks, and various fruit trees (Benseny, 2011; Provendola, 2013). As a result, at present wide areas have been invaded mainly by *Populus alba* L., *Pinus* spp., and *Acacia* spp., particularly in the northern and central sector of the FQNR. Other exotic trees (*Betula pendula* Roth, *Casuarina* sp., *Juglans nigra* L., *Araucaria araucana* (Molina) K. Koch and *A. angustifolia* (Bertol.) Kuntze, *Cedrus* spp.) are widely spread across the gardens of some countryside residences neighboring the FQNR (Stutz, 2001).

The climate is humid temperate with a mean annual temperature of 14 °C, with marked seasonality; the average yearly precipitation is 930 mm and the mean annual humidity is greater than 75% (Estación Meteorológica Aeródromo de Villa Gesell 37°14' S, 57°01' W, Servicio Meteorológico Nacional). The most frequent winds are those coming from the north, but the most intense are those coming from the southeast, south, and southwest (Bértola *et al.*, 1999).

Sampling and vegetation surveys

Between December 2019 and March 2023, 24 sediment surface samples, henceforth sampling sites, were collected in lagoons and interdune slacks of the CDS, between 37°32' S 57°11' W and 37°22' S 57°3' W (Fig. 2), with a spatula or a Gravity-corer type sampler, depending on the presence of water during the sampling.

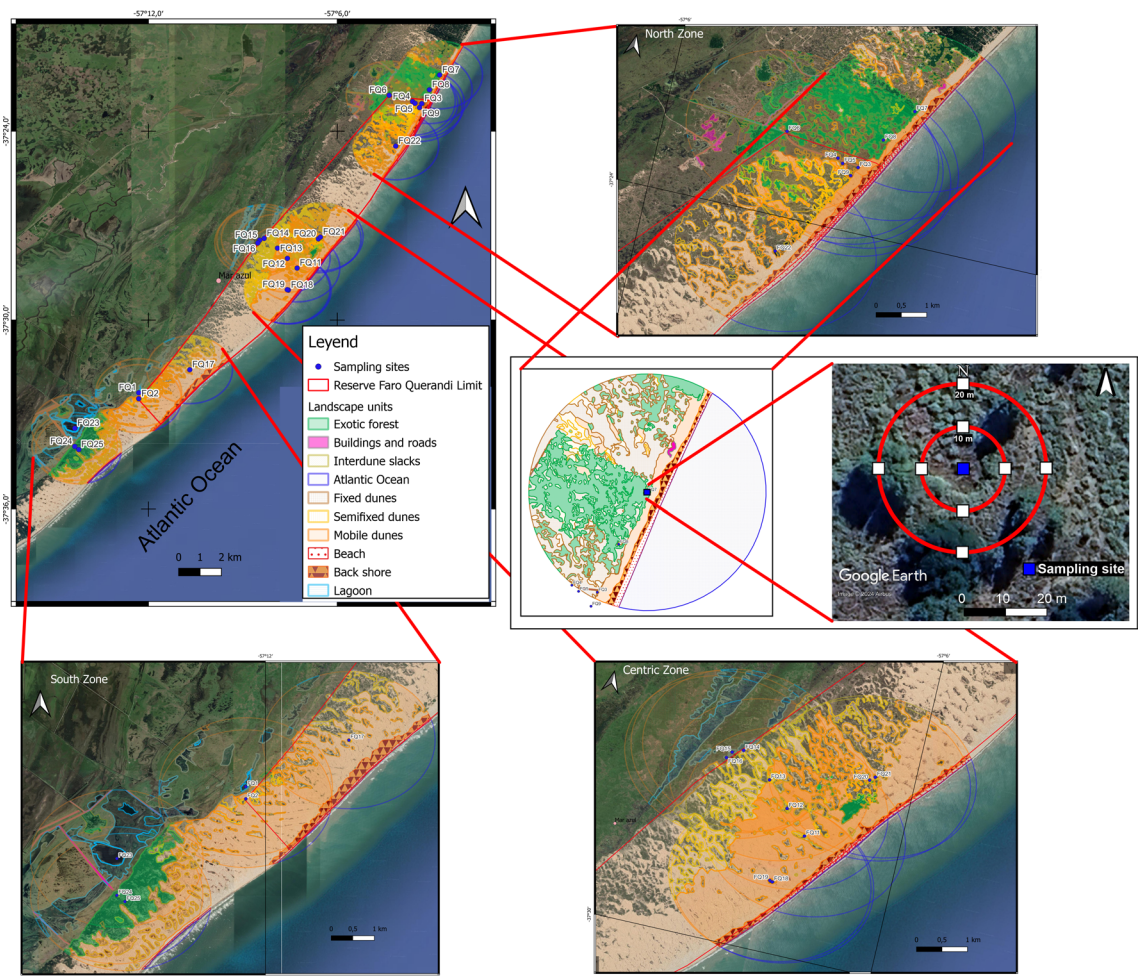


Fig. 2. Location of the sampling sites and surrounding landscape units of the Faro Querandí Municipal Nature Reserve, in a 2000 m radius: A close-up of the sampling sites in the southern, central and northern zones of the FQNR, a detail of the Landscape units of a sampling site and of scheme of the vegetation surveys method (adapted from Bunting *et al.*, 2013), are shown. Squares (=quadrat) shows vegetation survey sampling plot (5 m²) and the distances to the central point of the circumference (central point, 10 m and 20 m). Notice the 10 m and the 20 m radii plots are distributed following the main four cardinal directions.

To characterize the vegetation at a local scale, concentric censuses were carried out concerning each sampling site, at 10- and 20-meter radii, distributed following the four main cardinal directions (adapted from Bunting *et al.*, 2013). According to Prentice (1985), the term ‘local’ refers to pollen input within 20 m of the basin edge, ‘extra-local’ refers from 20 m to 2 km, ‘regional’ refers from 2 to 200 km, and ‘extra-regional’ from beyond 200 km. Cover, as percentages, of every vascular plant species was measured at different

5x5 m plots inside the circumference. A total of 9 plots per sampling site, one of them placed at the center of the circumference, 4 plots placed at 10m radius and other 4 plots placed at 20 m radius were measured (Fig. 2). A total of 216 vegetation surveys were obtained.

To evaluate pollen representation of extra-local vegetation, we mapped landscape scale heterogeneity up to 2000 m radii from the sampling site. We summarized landscape scale heterogeneity data by defining ten different landscape units,

following Fontana (2005a), vegetation and geomorphological features (see Study area section), using 2020 Google Earth images by visual interpretation, and field observations. The identified landscape units were: exotic forest, interdune slacks, fixed, semifixed and mobile dunes, beach, back shore, lagoons, buildings and roads, and Atlantic Ocean (Fig. 2). The area of each landscape unit was calculated within the 1000 and 2000 m radii (extra-local scales) using QGIS software (version 3.22.11).

Pollen analysis

Surface sediment samples were processed following the standard protocol for palynomorph extraction (Bennet & Willis, 2001). Two *Lycopodium* spore tablets were added before treatment. We tried to reach a minimum 300 pollen grain sum without counting Wetlands and Exotic taxa, and, in addition, due to the overrepresentation of Poaceae in grasslands samples, 100 pollen grains other than Poaceae were counted. Pollen identification was performed using the pollen reference collection of the Paleocology and Palynology Lab (IIMyC, CONICET- Universidad Nacional de Mar del Plata) and published palynological atlases. Identified pollen types were grouped into Dunes, Grasslands, Exotics, and Wetlands (Supplementary material, Appendix 1).

Pollen - Vegetation relationships analysis

Pollen samples were classified using unconstrained Cluster Analysis (CONISS, TILIA 2.6.1) with square root transformation. The pollen types were organized according to habitat's plant species; the Wetlands group (considered as strictly local pollen), *Podocarpus*, and *Nothofagus t. dombeyi*, considered an extra-regional type, were excluded from this analysis.

In the pollen diagram, some genera or species were grouped into family categories because some pollen types do not enable the pollen identification to a lower taxonomic level (see Supplementary material, Appendix 1). Non-native species of Argentinean flora were considered Exotics (Fig. 3 and Supplementary material, Appendix 1) according to Cabrera & Zardini (1953), Zuloaga *et al.* (2019), and Instituto de Botánica Darwinion (2020). In Appendix 1 of Supplementary material the different species that have been reported for

the study area or its surroundings are recorded, list elaborated according to vegetation surveys between 2019 and 2023 and literature review (Cabrera, 1941; Alberio, 2010; Benseny, 2011; Stutz, 2000; Stutz, 2001; Alberio & Comparatore, 2014; Celsi, 2016), about the different pollen types recorded in the pollen counts. It is shown to which group each pollen type was assigned, and data such as the habit and pollination type of the plant are added.

Pollen diagrams were plotted using TILIA 2.6.1 (Grimm, 2020). Each pollen type grouped in Dunes and each pollen type grouped in Grasslands was calculated as a percentage of the Dunes plus Grasslands pollen sum ($\Sigma D+G$); each pollen type grouped in Wetlands were calculated as a percentage of the Dunes plus Grasslands plus Wetlands pollen sum ($\Sigma D+G+W$). Finally, percentages of each pollen type grouped in Exotics are based on the total pollen sum ($\Sigma D+G+W+E+Extra\text{-regional}$). Results are presented as pollen percentages and include the value of pollen richness. Rarefied total pollen richness was performed using the minimum count size (536 pollen grains) with the Vegan package (Oksanen *et al.*, 2017) for R (R Development Core Team, 2021). Only *Podocarpus* and *Nothofagus t. dombeyi* (extra-regional) were excluded from the complete dataset, to calculate rarefied pollen richness.

Pollen vs. Landscape-scale heterogeneity analysis

Landscape units cover (%) at a 2000 m radius of each sampling site were compared using cluster analysis (CONISS, TILIA 2.6.1) results. This comparison implied a two-step dimension. First, different landscape unit covers were summed as: a) low or no vegetation cover units, (<30% coverage) b) moderate to high vegetation cover units (>30% coverage), and c) exotic forest cover. Second, detailed landscape units were graphed for each sample site to distinguish the main landscape unit contributor to pollen assemblages'.

Ordination analysis was performed to disentangle and quantify the main pollen types influencing pollen sample variance. To determine which ordination method is the most appropriate for the data analysis, a Detrended Correspondence Analysis - DCA was performed. According to Legendre & Birks (2012), linear ordination methods work best for short gradients (<1.5 SD units) and unimodal methods for long gradients (>3 SD units), while both methods

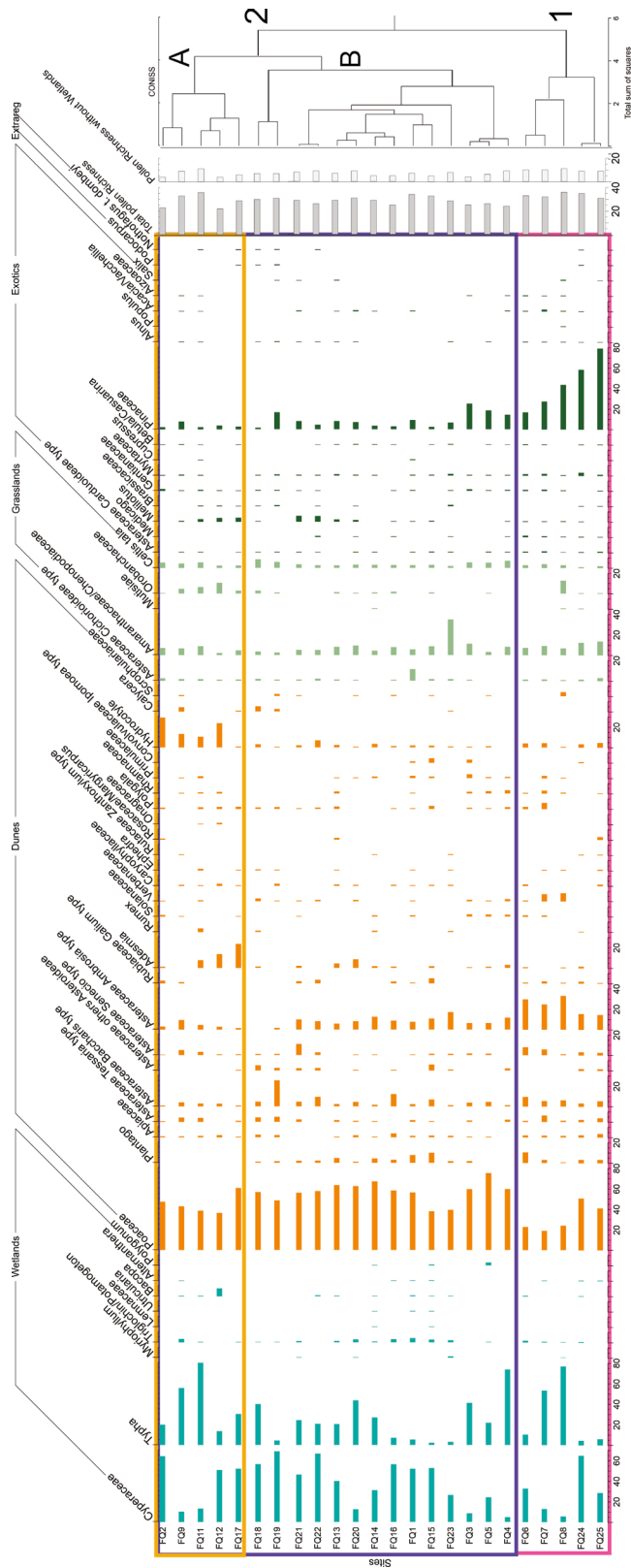


Fig. 3. Pollen diagram for surface samples at Faro Querandí Municipal Nature Reserve. Pollen richness and CONISS analysis (dendrogram) are shown. 55 pollen types were identified and organized according to plant's habitats. Asteroideae refers to Asteraceae subf. Asteroideae.

can be used on intermediate gradients. In this paper, we used Principal Component Analysis (PCA) because the length of the first DCA axis is 1.67 units of standard (SD) (closer to 1.5) therefore suggests unimodal data.

Pollen richness versus local and landscape plant species richness modeling

A linear regression model was applied between local plant species richness vs. local plant species richness transformed into pollen types (PSRPT), to evaluate the effect of taxonomic smoothing. Local plant species richness was calculated considering all the different species registered at every plot included at a 20 m radius of each sampling site. PSRPT was calculated by smoothing the plant data to pollen equivalents (plant species were assigned to pollen taxa as shown in Appendix 1 of Supplementary material).

Different linear regression models were performed between Rarefied total pollen richness (henceforth pollen richness), as well as for anemophilous and entomophilous taxa, vs. PSRPT from plant surveys performed at 0, 10, and 20 m radii, to evaluate possible taphonomic attributes (transport and deposition, and preservation) and pollen production that affect PSRPT and pollen richness relationship.

To extend the analysis of pollen contribution and its relationship with plant richness from local (0-20m) to landscape scale (0-1000 m and 0-2000 m - extra-local pollen source areas), we calculate a Landscape plant richness Index (LPRI) following this equation:

$$R_{Landscape}(i) = \sum_{n=1}^s (\bar{r}V_a COV_{i,xm})$$

$R_{Landscape}(i)$: Estimated landscape plant richness at site i
 s : Number of landscape units

$\bar{r}V_a$: Maximum plant richness calculated for landscape unit type a at local scale

$COV_{i,xm}$: Ratio cover (from 0 to 1) of landscape unit type at x meters radii from site i

a : Semifixed dunes / Fixed dunes / Mobile dunes / Lagoon / Exotic forest / Interdune slacks

We first characterize the maximum plant richness of a landscape unit type (a) as the number of different species registered considering the total plots surveyed for landscape unit type (a) (see the

list of maximum plant richness values for every landscape unit type in Table 1). Then, we calculate the estimated landscape plant richness at the site (i) as the sum of the maximum plant richness of every landscape unit type (a), multiplied by its individual cover at 1000 and 2000 m radii from each sampling site (i).

A linear regression model was applied between the values of the LPRI obtained at 1000 m and 2000 m vs. Pollen richness for each site, total as well as for anemophilous and entomophilous taxa.

Finally, a linear regression model was applied between the values of axis 1 of the PCA obtained according to the pollen assemblages of sediment samples vs. pollen richness values, as a measure to relate pollen-landscape unit composition with sediment pollen richness values.

Table 1. Maximum plant richness registered by landscape unit. ^a5x5 m plots. Note: Atlantic Ocean, beach, back shore and buildings and roads did not registered plant cover so they were not considered for this table.

Landscape units	Maximum richness (spp. number)	Vegetation surveys ^a per Landscape unit
Interdune slacks	35	89
Semifixed dunes	25	35
Mobile dunes	18	19
Fixed dunes	37	35
Exotic forest	23	18
Lagoon	28	21

RESULTS

Pollen - Vegetation relationships analysis

Cluster Analysis of pollen samples showed two large pollen assemblages, Group 1 and Group 2 (Fig. 3). Group 1 presented high percentages of Pinaceae (16.2-78.7%) and Asteraceae subf. Asteroideae *Ambrosia* type (14.2-32.6%, henceforth Asteroideae *Ambrosia* type), as well as the lowest to intermediate values for Poaceae (18.6-50.2%). Also, this group showed the highest richness of exotic pollen types (10 of the 14 exotic pollen types registered for the complete pollen dataset).

Group 2 was mainly characterized by high percentages of Poaceae (35.9-74.6%) and *Adesmia* (0.3-23.1%). This group was further subdivided into two groups (A and B). Subgroup A was also characterized by the highest presence of *Hydrocotyle* (0.5-28.8%) and Orobanchaceae (*Agalinis/Castilleja*) (0.3-10.2%). Subgroup B, in addition to Poaceae (37.3-74.6%), is characterized by Pinaceae (1.1-24.6%) and presented the greatest variety of pollen types. The sites FQ3 to FQ5, recorded intermediate values of Pinaceae (13.8-24.6%) and high values of Poaceae. Despite the presence of species like *Juncus acutus* L., *Ceratophyllum* sp., *Triglochin striata* Ruiz & Pav. in vegetation surveys (Appendix 1), no or lower than expected pollen grains were recorded in the surface samples.

Pollen vs. Landscape-scale heterogeneity analysis

To obtain a general picture of pollen percentages and landscape vegetation cover relationship, we showed the information of landscape units at the stacked column graphs summed as three main cover types. Units with low or no vegetation cover (buildings and roads, Atlantic Ocean, beach, back shore, and mobile dunes) vs. moderate to high native vegetation cover (semifixed and fixed dunes, interdune slacks and lagoons), and exotic forest (Fig. 4). When comparing the results of Cluster Analysis to the different landscape composition at every site, for a 2000 m radius (Fig. 4A-B), Group 1 registered the highest percentages of exotic forest (16.77-25.52%); and high values of low or no vegetation cover units (11.36-51.08%) and fixed dunes (17.27-45.95%).

Landscape units with low or no vegetation cover were highly represented in Subgroup 2A (48.12-69.76%, including mobile dunes coverage between 10.40-42.73%, Fig. 4A-B) with almost no exotic forest cover. Exotic forest cover was below 23.75% at subgroup 2B (Fig. 4A-B) with the highest values at FQ3, FQ4, FQ5, and FQ23. There was also a mixture of landscape units with a greater representation of interdune slacks in some sites and fixed dunes in others.

The PCA (Fig. 5) showed two large groups mostly consistent with Cluster Analysis. PC1 axis (eigenvalue 0.29) described 29% of the

variation of the pollen data. It was explained mainly by the variables Pinaceae, followed by Asteroideae *Ambrosia* type (positive values), *Adesmia*, and Poaceae (negative values). Group 1 sites presented mainly positive PC1 values. The positive values also correspond to the sites with the highest percentage of exotic forest cover, as opposed (negative values) to the sites with the highest percentages of units with low or no vegetation cover (Fig. 4).

PC2 axis (Fig. 5, eigenvalue 0.12) explained 12% of variance and it was related with Poaceae (positive values), and *Hydrocotyle* and Orobanchaceae (*Agalinis/Castilleja*, negative values). Subgroup 2A sites presented mainly negative PC2 values meanwhile Subgroup 2B sites presented mainly positive PC2 values.

Pollen richness versus local and landscape plant species richness modeling

When we graphed Plant species richness vs. plant species richness transformed into pollen types (PSRPT) (Fig. 6A), we observed strong correspondence between the raw data. The analysis of taxonomic smoothing (Plant species richness vs. PSRPT regression, see Fig. 6B) showed a positive relation ($r^2= 0.57$, $p\text{-value}=1.067e-05$) suggesting that the estimation of plant species richness by pollen richness may be possible at the Coastal Dune Systems (CDS). The slope estimate ($\beta=0.38$) is considerably lower than 1, thus pollen richness values represent only ca. 40% of actual plant richness.

The regressions parameters between pollen richness (total, anemophilous, and entomophilous) vs. PSRPT (5, 10, and 20 m) and LPRI -Landscape plant richness Index- (1000 m and 2000 m) are shown in Table 2. The r-squared estimate from pollen richness vs. PSRPT regression models was positive and significant at 20 m, as well as at the extra-local scale (pollen richness versus LPRI). This pattern suggests that these models fit best assuming a Relevant Pollen Richness Source Area (RPRSA) ca. 1000 m (extra-local scale). Even though 64% of total plant species recorded in this study present entomophilous pollination, entomophilous pollen richness versus plant richness relationship was not significant at any of the scales, while anemophilous pollen richness versus plant richness relationship presented

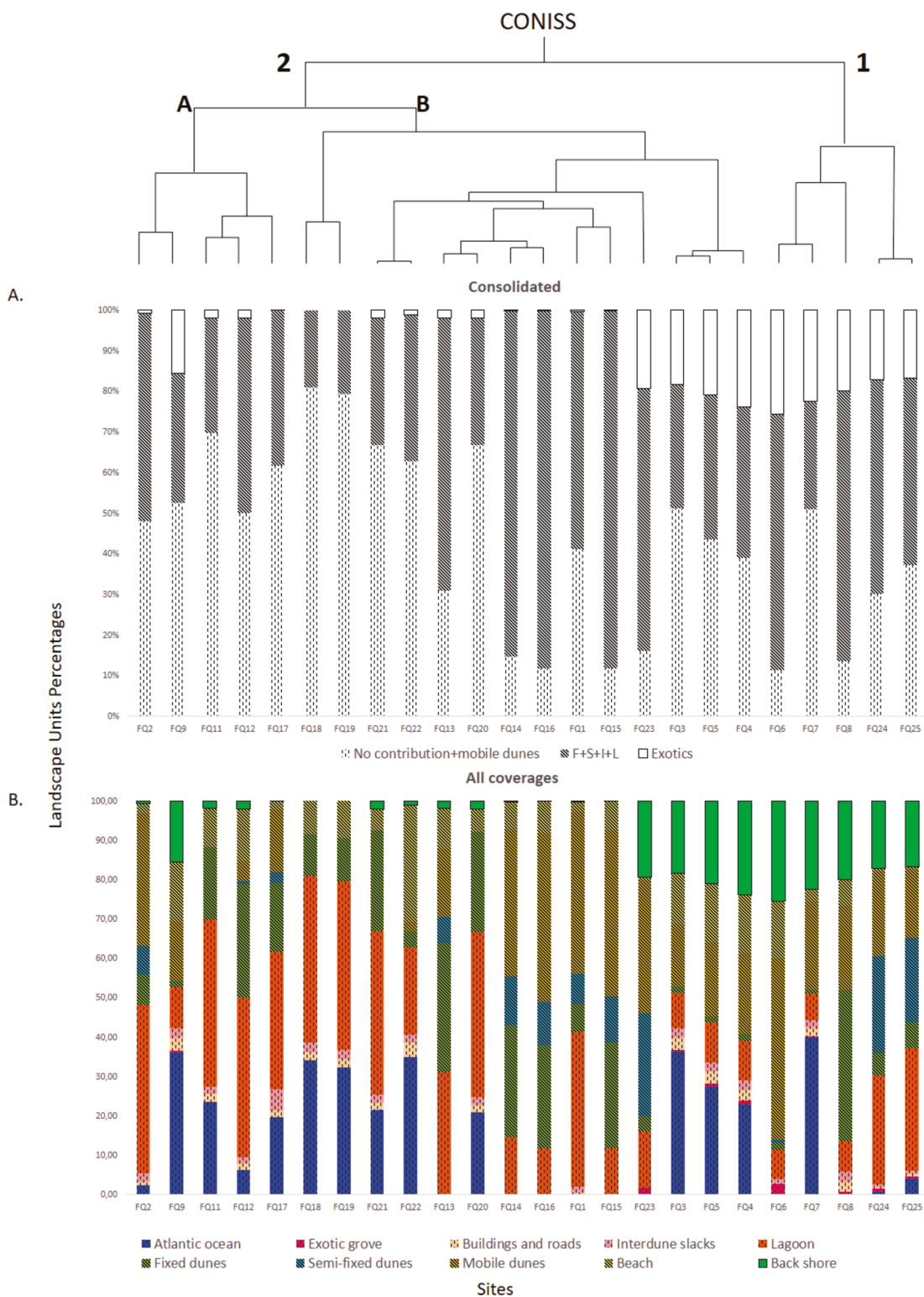


Fig. 4. Stacked columns graph of landscape units cover (%) at 2000 m radius, ordered according to CONISS analysis. 4B. Low or no vegetation cover units (<30%); moderate to high vegetation cover units (>30%).

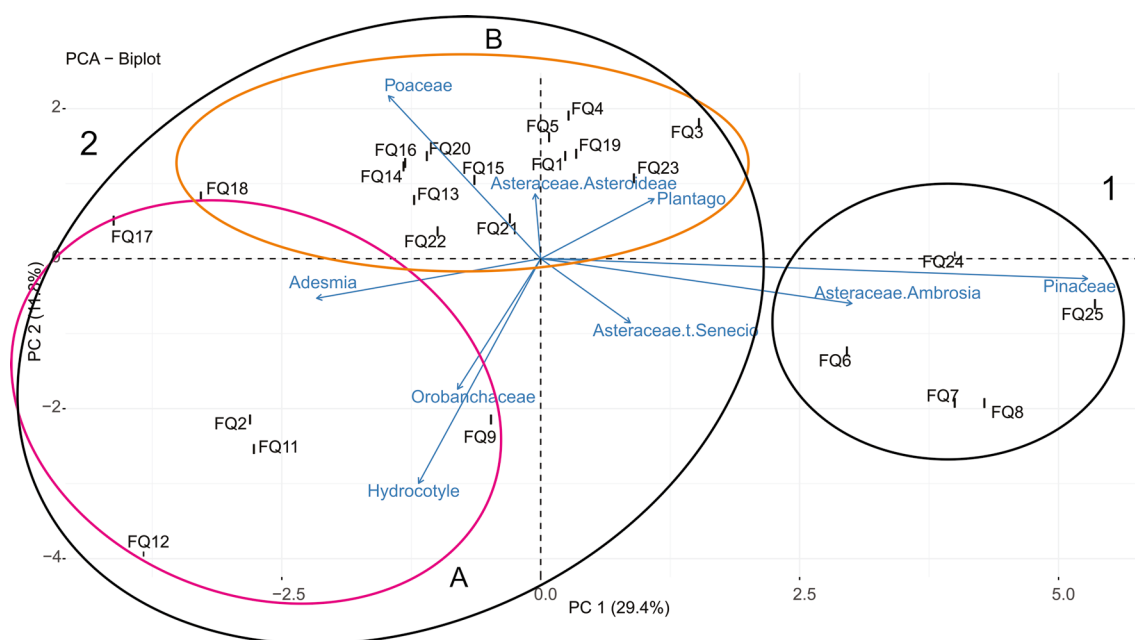


Fig. 5. Principal Component Analysis biplot, with squared transformation, for the different sampling sites according to the pollen types, and the loadings (eigenvectors), on the first two principal component axes. The main groups separated by CONISS (Fig. 4) are delimited in black circles (1 and 2), and the subgroups 2A and 2B are delimited in pink and orange respectively. Orobanchaceae = Orobanchaceae (Agalinis/ Castilleja). For visual purposes, we only show the 10 variables that contribute the most (>3%) to PC1 or PC2.

Table 2. Linear regression results between PSRPT, and LPRI vs. Pollen richness. Abbreviations= PSRPT: plant species richness transformed into pollen types; LPRI: landscape plant richness Index. *Significance 0.05.

Variables evaluated	Scale of analysis – Pollen source area scale	Adjusted R-squared	p-value
PSRPT vs. Pollen richness	5 m - Local	-0,04	0,8
	10 m - Local	-0,03	0,54
	20 m - Local	0,16	0,03*
PSRPT vs. Pollen richness Entomophilous	5 m - Local	-0,01	0,42
	10 m - Local	-0,04	0,78
	20 m - Local	-0,008	0,37
PSRPT vs. Pollen richness Anemophilous	5 m - Local	-0,02	0,52
	10 m - Local	0,01	0,28
	20 m - Local	0,39	0,002*
LPRI vs. Pollen richness	1000 m (landscape)	0,27	0,006*
LPRI vs. Pollen richness Entomophilous	- extra-local	0,07	0,11
LPRI vs. Pollen richness Anemophilous		0,18	0,02*
LPRI vs. Pollen richness		0,28	0,005*
LPRI vs. Pollen richness Entomophilous	2000 m (landscape)	0,04	0,17
LPRI vs. Pollen richness Anemophilous	- extra-local	0,14	0,04*

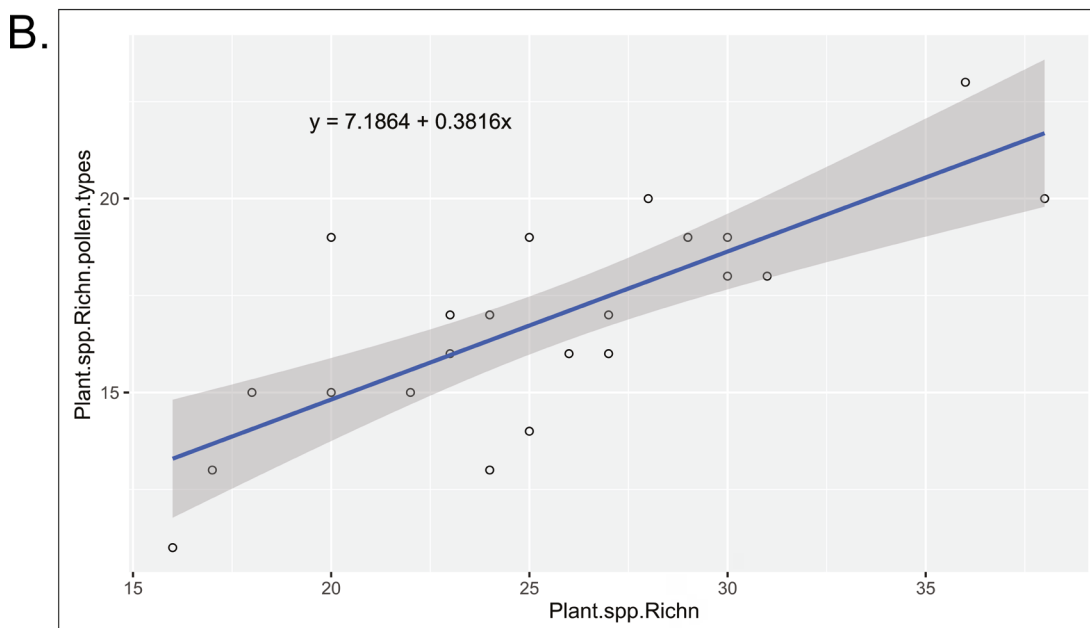
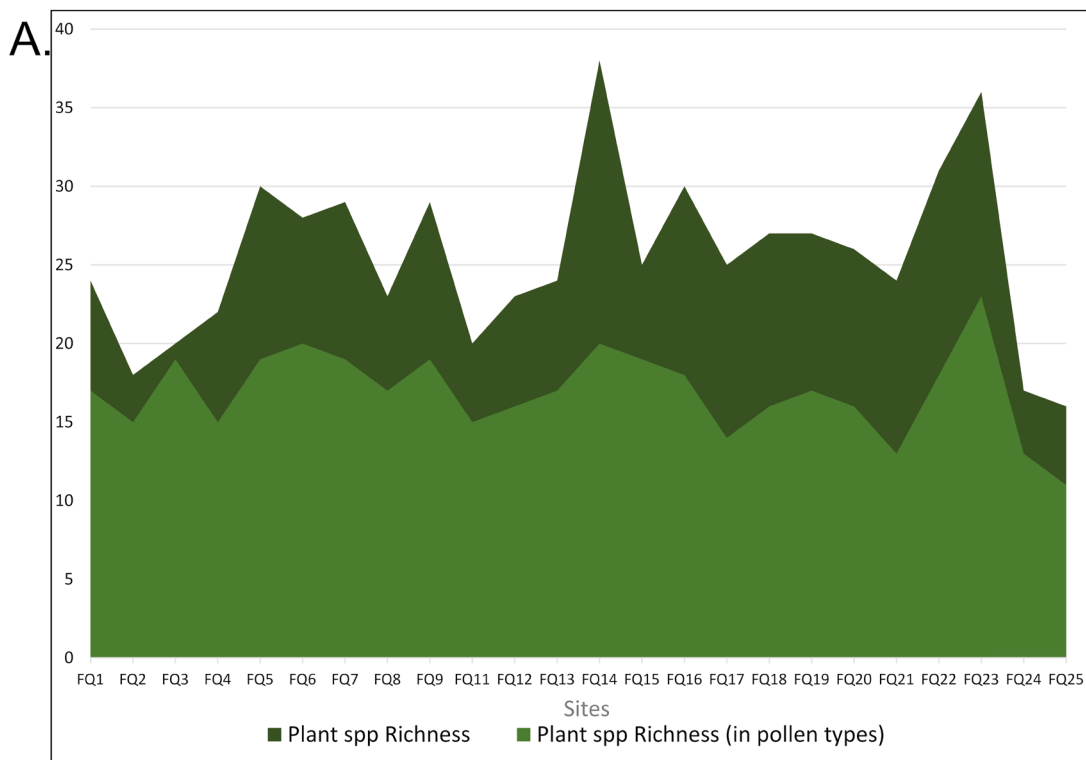


Fig. 6. The loss of plant species richness due to taxonomic smoothing to plant genus or family levels and pollen types equivalents. A. Area graph that shows the magnitude of the differences according to Plant spp. richness vs. Plant spp. richness (in pollen types-PSRPT) categories for each pollen sample. B. Linear regression graph between Plant spp. richness vs. PSRPT. β estimate is shown at the modelled regression equation.

positive and significant adjusted r^2 values at the 20 m and extra-local scales.

Comparison between pollen richness values and different pollen assemblages suggested that sites with the presence of exotic forest (those with high values of Pinaceae and Asteroideae *Ambrosia* type pollen percentages) within a 2000 m radius

presented higher pollen richness values than pure native environments (those with high values of *Adesmia* and Poaceae pollen percentages), see Fig. 5 and Table 3. Indeed, the average pollen richness of the sites in Group 1 (Fig. 5) was 33.4, while for those in the middle zone (subgroup 2B) it was 29 and for those on the right (subgroup 2A) it was 28.

Table 3. Linear regression results between PC1 Axis vs. Pollen richness and the pollen variables that most contribute to PC1, with squared transformation. * Significance 0.05.

Variables evaluated	Adjusted R-squared	Adjusted R-squared p-value	b	b p-value
PC1 Axis vs. Pollen richness	0.07	0.11	0.59	0.11
PC1 Axis vs. % Pinaceae	0.8	1.643e-09*	0.71	1.64e-09*
PC1 Axis vs. % Ambrosia	0.6	5.057e-06*	0.4	5.06e-06*
PC1 Axis vs. % Adesmia	0.34	0.001*	-0.29	0.001*
PC1 Axis vs. % Poaceae	0.18	0.02*	-0.2	0.02*

DISCUSSION

Pollen - Vegetation relationships analysis

Do surface sediment pollen assemblages reflect landscape heterogeneity at the CDS?: The challenge of this study was to assess whether pollen assemblages reflect the heterogeneity of plant communities within the Coastal Dune Systems (CDS) area. We found that pollen assemblages were strongly influenced by landscape unit cover, beyond the local scale, and reflected landscape heterogeneity. This is mainly reflected in the pollen composition of sampling sites with predominantly exotic forest, mobile dunes or mixed landscape units.

Several studies carried out in coastal dunes ecosystems in Argentina, Uruguay and in small lake in the northeastern United States, have also found correspondence between plant communities and environments, and confirmed that pollen spectra reflect the spatial heterogeneity of different plant communities (Stutz & Prieto, 2003; Fontana, 2005a; Marcos & Mancini, 2012; Montserrat *et al.*, 2012; Masciadri *et al.*, 2013; Liu *et al.*, 2022). All these studies have evaluated pollen and

vegetation relationships at a local scale or compared qualitatively different vegetation units. This study presents the first quantitative analysis of pollen and vegetation relationship in terms of spatial heterogeneity at an extra-local scale (2000 m radius from a sampling site). The pollen-vegetation model presented here shows that pollen assemblages may discern between forested and non-forested landscapes. Furthermore, mobile dunes vs. fixed dunes+semi-fixed dunes+interdune slacks could be separated as well. These results about the attributes of the pollen record may be compared with other coastal dune systems to evaluate the effect of different vegetation compositions on pollen representation.

We found that pollen assemblages from sites of the CDS surrounded by exotic forests showed high values of Pinaceae and Asteroideae *Ambrosia* type (e.g. Group 1: FQ6-FQ8, Fig. 3 and Fig. 4). The relevant values of Pinaceae reported in this study had already been highlighted in previous steppe environments (Li *et al.*, 2022), considering also that e.g. *Pinus* spp. has a good pollen dispersal and is usually over-represented in pollen assemblages (Felde *et al.*, 2015). Also, the large amount of

Pinaceae may be related to a) higher pollen productivity than native herbs and shrubs of the CDS and b) the regional pollen source area is composed mainly of landscape units with low or no vegetation cover. Likewise, it has been possible to evidence that afforestation with exotic species reduces the area of psammophytic grassland (Yezzi *et al.*, 2018) which implies less participation of other pollen types.

Sites FQ3 to FQ5 with intermediate percentages of exotic forest landscape unit (in a 2000 m radius) registered intermediate values of Pinaceae, but they also recorded high values of Poaceae, both pollen types with anemophilous dispersal. As already stated, the composition of pollen spectra is influenced by dominant wind patterns (Fontana, 2005a) since high wind speed could carry more pollen grains (van der Sande *et al.*, 2021). In these sites, landscape units with moderate to high vegetation cover dominate south/southwestward (to sampling sites). As Faro Querandí Municipal Nature Reserve (FQNR) presented a south/southwest dominant wind direction, this factor would counteract the over-representation of Pinaceae and favored the contribution of Poaceae and other taxa. On the contrary, in Group 1, the highest exotic forest cover was located north/northwestward, which favored the over-representation of Pinaceae.

We found a strong Asteroideae *Ambrosia* type association with sites located in patchy grassland-forested areas. This was consistent with post disturbance colonization of *Ambrosia* associated with pine forest (Yezzi *et al.*, 2018). These high values of *Ambrosia* pollen type in the CDS have already been reported in previous studies such as that of Stutz & Prieto (2003) and Fontana (2005a), although these authors did not investigate the association of *Ambrosia* pollen type with pine forests.

We also found that sampling sites surrounded up to 40% of landscape units with low vegetation cover (e.g. Mobile dunes, Group 2A) had a strong influence of psammophytic species pollen types, like *Adesmia*, *Hydrocotyle*, and Orobanchaceae (*Agalinis communis* (Cham. & Schltld.) D'Arcy and *Castilleja arvensis* Schltld. & Cham.), genera and species which have entomophilous pollen dispersal. *Adesmia incana*, a psammophytic species abundant in sandy dunes, can be affected by indirect anthropogenic action, being substituted

by various adventitious species (Cabrera, 1941). This could explain the lower values of *Adesmia* in Group 1, both at the pollen record and plant cover. *Hydrocotyle bonariensis* is a frequent hydrophytic species in sandy and humid soils that adapts easily to sandy soils, as do *Agalinis communis* and *Castilleja arvensis*, adapted to coastal dunes (Cabrera, 1941). The other sites -Group 2B- showed the highest values of Poaceae and Asteraceae.

The major vegetation taxa belong to Poaceae, Cyperaceae, and Asteraceae in this study coinciding with those results reported by Fontana (2005a) in the southern CDS. The higher values of Poaceae could be because this family includes several species and had representatives in all landscape units. Likewise, they have a high pollen production, with an anemophilous and easily dispersed pollen grain, that favors their good representation in the pollen spectra (Fernández & Grill, 2016). Stutz & Prieto (2003) also highlighted that Poaceae, Cyperaceae, and psammophytic types (like *Adesmia incana*, *Calycera crassifolia*, *Senega cyparissias* (A. St.-Hil. & Moq.) J.F.B. Pastore & Agust. Martinez (*Polygala* type), Apiaceae -including *Hydrocotyle* - and Asteraceae which grow on sandy soils), conformed the pollen assemblages of the coastal dune barrier in the area of the Mar Chiquita coastal lagoon, adjacent to the FQNR. Also, Fontana (2005a) pointed out that pollen assemblages differed considerably from the composition of surrounding local vegetation. These results are coherent with those reported in this study as pollen assemblages from surface samples reflect not only local vegetation, but indeed they reflect a wider pollen source area and sense landscape heterogeneity.

Group 2B recorded a greater variety of psammophytic pollen types in addition to Poaceae and Asteraceae (like Apiaceae, Caryophyllaceae, and *Calycera*). These sites also had a mix of landscape units, mainly fixed/semi-fixed dunes and interdune slacks. This situation was similar to that reported by Montserrat *et al.* (2012), who found that the sectors located on these landscape units were characterized by diverse plant associations, and the species composition was highly diverse. This great vegetation heterogeneity and the effect of taxonomic smoothing, would trigger the pollen assemblages of these landscape unit overlap. It is not possible to separate at the genus or species

level of Poaceae and Asteraceae, pollen types that could be indicative of each type of environment. These difficulties have been previously reported in southern CDS (Fontana, 2005a) and dune deserts in north China (Li *et al.*, 2022).

Pollen, plant and, landscape richness analysis

The relationship between plant richness and pollen richness is driven both by taxonomic smoothing, pollen production, and taphonomic constraints (pollen dispersal and preservation). The effect of taxonomic smoothing is likely due to the abundance of plant species producing pollen grains often only identifiable to genus, and sometimes to family, like Poaceae, Asteraceae and Cyperaceae. In this study, *Panicum racemosum*, *Poa lanuginosa*, and *Polypogon monspeliensis* (L.) Desf. were registered in the vegetation surveys, but at the pollen level they could only be identified as Poaceae. Also, *Eleocharis maculosa* (Vahl) Roem. & Schult., *Isolepis* spp., and *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller were recorded in the vegetation but their pollen grains could only be determined at the family level: Cyperaceae. The fidelity of pollen richness relative to plant richness may be affected by taxonomic smoothing since the taxonomy in the plant dataset is not equivalent to pollen taxonomy, but this effect may be recoverable (Goring *et al.*, 2013). Thus, taxonomic smoothing of CDS plant richness could be overcome by the use of the statistical models presented in this paper and adding different paleobotany proxies to the classic vegetation-palynological based reconstruction when studying Holocene records.

As we discussed in the previous section (“Pollen-Vegetation relationships analysis”) that pollen assemblages reflect landscape heterogeneity, the Relevant Pollen Richness Source Area (RPRSA) for small lagoons of the CDS correlate with extra-local scale vegetation heterogeneity. Even though the regression models between plant and pollen richness were significant at the local scale (20 m, Table 2), the goodness of fit of these models increase and stabilize up to the extra-local scale (1000 and 2000 m, Table 2). Recent studies have shown that modern pollen assemblages can reflect plant richness at different scales (Birks *et al.*, 2016), however, the relationship is not direct as pollen richness reflects pollen evenness, productivity, and dispersal across the landscape (Prentice, 1985;

Sugita, 1994; Odgaard, 2018). The relation between local and extra-local plant and pollen richness reported in our study may reflect vegetation structure and diversity at these scales, rather than at the regional level, as previously published by Goring *et al.* (2013), Matthias and Giesecke (2014) and Matthias *et al.* (2015). Odgaard (2018) highlighted that modern pollen assemblages can better reflect α , γ , or ε -diversity according to the size of the lakes or basin where they have been deposited. Sugita (2007a) indicates small lakes (up to 350 m radius, like those of this study) are more suitable to capture local vegetation spatial heterogeneity (ca. 700 m) by the 30-45% of the total pollen loading deposited in the basin. However, pollen richness calculation is based on the pollen counts of the complete pollen loading deposited in a basin. That includes those pollen types from the local scale (the Relevant Pollen Source Area- RPSA- *sensu* Sugita, 2007a) and those beyond the RPSA from extra-local. Thus, firstly, the fact that our models present significant adjusted-r² values for local scales pollen-plant richness relationship coincides with those results previously published by Sugita (2007a). Secondly, our results suggest that the RPRSA fits with extra-local scale pollen-plant richness relationships. This inference coincides with previously published semiquantitative-qualitative pollen-vegetation relationships studies for the CDS (e.g. Stutz & Prieto, 2003; Latorre *et al.*, 2010). The wider RPRSA than expected RPSA may be related to extra-local pollen inputs linked to a) anemophilous species (e.g. Poaceae and Amaranthaceae/Chenopodiaceae species) growing in open landscapes as semifixed and mobile dunes (Latorre *et al.*, 2010; Felde *et al.*, 2015; Adeleye *et al.*, 2020) and b) species with high pollen productivity (Latorre, 1999; Odgaard, 1999; Weng *et al.*, 2006) growing in forest patches (e.g. *Ambrosia tenuifolia*, *Pinus* spp.) of the CDS. Weng *et al.* (2006) and Goring *et al.* (2013) have also highlighted that anemophilous pollen types are usually the main component of pollen assemblages and drive pollen richness patterns. Some entomophilous and hydrophytic-anemophilous species are also important local scale components of pollen richness. Between entomophilous species we found Asteraceae (*Tessaria* type, *Baccharis* type, *Senecio* type, and other Asteroideae), *Hydrocotyle* spp., and *Adesmia incana* which pollen grains can be transported over

a few meters (Wang *et al.*, 2022), they usually produce low quantity of pollen grains (Väli *et al.*, 2022) and are under-represented in pollen assemblages (Mourelle *et al.*, 2017). Hydrophytic-anemophilous species growing at interdune slacks (Cyperaceae species and *Typha* spp.) produce high quantities of pollen which are highly dispersed (Xu *et al.*, 2012; Frazer *et al.*, 2020). This fact explains the high values of these pollen types reported in most sites of the CDS even though these species may be absent in some interdune slacks.

Pollen richness is also a function of landscape structure, openness and plant diversity within the Relevant Pollen Source Area (RPSA), pollination syndromes and dispersal, and other taphonomic processes (Birks *et al.*, 2016). Within these taphonomic processes, we found that pollen preservation could be different between taxa and could be a source of uncertainty (Goring *et al.*, 2013; Grindean *et al.*, 2019; Li *et al.*, 2022; Wang *et al.*, 2022). Regarding taphonomic processes triggering pollen-vegetation representation, we found that Juncaceae and Juncaginaceae pollen types as those with minor preservation potential in the CDS. As noted in the results section, in the vegetation surveys, species of these families were recorded although they were absent from the pollen record in the first case, or with low representation in the second. These and other taxa of hydrophilic pollen present very thin exines that hinders their preservation, and also tends to disintegrate during acetolysis (Moore *et al.*, 1991), therefore, causes their low representation in the pollen records (Fontana, 2005a; Erdtman, 1952; Chenlo, 2014).

The higher pollen richness values recorded at sampling sites with high values of exotic forest (up to 20% coverage within a 2000 m radius) is one of the most outstanding results we reported for the CDS. All these sites presented a forest matrix mixed with open grasslands areas with diverse herbaceous and shrub species, which were characterized by more stable substrate and sheltered from wind desiccation effects. These factors favor higher organic matter content accumulation and less frequency of disturbances related to burial effects produced by sand over vegetation, which may also favor greater species richness (Montserrat *et al.*, 2012). The increase in pollen richness associated to the development of forest patches with open steppe environments was also reported by Sottile

et al. (2020) for Patagonian forest-steppe ecotone and for Central Europe by Abraham *et al.* (2020). Birks & Line (1992) and Matthias *et al.* (2015) have discussed the relationship between disturbance frequency and pollen richness. They state that a disturbed environment is related to higher pollen richness than a stable environment. Disturbances promote the availability of new niches and thus the establishment of new species. If disturbance frequency is high (low), vegetation communities are expected to be dominated by r-strategy plants (k-strategy plants). Intermediate disturbance frequencies favor the coexistence of both r and k-strategy plants, thus showing the highest species richness values (“intermediate disturbance hypothesis”, Wittaker *et al.*, 2001). The higher pollen richness values linked to sampling sites with values of exotic forest up to 20% may be associated with coastal dune environments characterized by intermediate disturbance frequencies regime. The establishment of small patches of forest communities may diminish the frequency of vegetation burial because of they partially prevent dune movements and provides a mosaic of heliophilous and shade-tolerant environments. Also, anthropogenic fires, vegetation clearings linked to off-road tourism, and horse sheltering usually increase near forested areas, and thus these types of disturbance frequency. Conversely, sites with the lowest pollen richness were found in more pristine areas with a high presence of landscape units with low or no vegetation cover, mainly mobile dunes, and with a low presence of the exotic forest. This low plant richness (and consequently low pollen richness) may be due to the strong stress conditions that occur in active dunes, such as high wind intensity, substrate instability, saline spray, and low organic matter content, among others, which cause that few species can adapt to these conditions (Kumler, 1997; Fontana, 2005a; Montserrat *et al.*, 2012).

CONCLUSIONS

Landscape heterogeneity (in terms of vegetation type cover, patchiness, and location with respect to dominant wind direction), pollen production, taphonomic constraints and taxonomic smoothing determined pollen assemblages from small lagoons

in Pampean CDS. Pollen assemblages are good proxy records to reconstruct past landscape heterogeneity at an extra-local scale (ca. 2000 m) of coastal grasslands of southern South America. As other grassland ecosystems (dominated by Poaceae, Asteraceae and Cyperaceae), pollen richness represents less than 50% of real plant richness. However, we reported a significant relation between plant and pollen richness as a promising proxy record encouraging future landscape scale paleoecological reconstructions. Our results suggest that anemophilous pollen types play a major role in driving pollen richness, and that a landscape composed of coastal dunes and small forest patches provides higher values of pollen richness than pristine coastal dune patches. Even though we detected few entomophilous species that frequently contribute to pollen richness, we encourage the consideration of the presence of all pollen types (those produced by anemophilous or entomophilous) to draw a better picture of the paleoenvironmental changes. Future studies may explore other techniques that avoid the use of strong acid-base solutions that may affect the preservation of vulnerable pollen grain walls such as Juncaceae or Juncaginaceae. We presented the first work in South America that shows that pollen assemblages and pollen richness patterns in coastal dune ecosystems reflect landscape (1000-2000 m) variability. These findings encourage paleoecologist to model quantitatively pollen-vegetation representation and perform pollen-based-quantitative vegetation reconstruction during different time windows of the last millennia to understand vegetation dynamics from a long-term perspective.

AUTHORS' CONTRIBUTION

All authors have jointly and equally carried out the data collection, interpretation, and writing of the manuscript.

ACKNOWLEDGEMENTS

This research was supported by the Neotropical Grassland Conservancy (NGC) [Student Grant Program, 2020], CV; Universidad Nacional de Mar del Plata (EXA1105/22), SS; CONICET, PIP (PIP

2021 -11220200100204CO), SS. We also thank to the park rangers of the Faro Querandí Municipal Nature Reserve, for their help during the field work and two anonymous reviewers whose comments contributed improving a previous version of this manuscript.

PRIMARY DATA AVAILABILITY

All plant species recorded in this work are available at <https://www.gbif.org/es/dataset/36fc65f3-ba8d-4c06-917e-6ffe62b63577> and pollen information is deposited in Repositorio Institucional CONICET (<https://ri.conicet.gov.ar/>).

BIBLIOGRAPHY

- ABRAHAM, V., J. ROLEČEK, O. VILD, E. JAMRICOVÁ ... & P. KUNEŠ. 2020. Spatial scaling of pollen-based alpha and beta diversity within forest and open landscapes of Central Europe. *bioRxiv*: 2020.08.18.255737. <https://doi.org/10.1101/2020.08.18.255737>
- ADELEYE, M. A., M., MARIANI, S. CONNOR, S. HABERLE ... & J. STEVENSON. 2020. Long-term drivers of vegetation turnover in Southern Hemisphere temperate ecosystems. *Global Ecol Biogeogr.* 30: 557-571.
- ALBERIO, C. 2010. *Patrones de invasión de especies vegetales leñosas en Mar Azul, Buenos Aires*. Tesis de Grado, Universidad Nacional de Mar del Plata, Argentina.
- ALBERIO, C. & V. COMPARATORE. 2014. Patterns of woody plant invasion in an Argentinean coastal grassland. *Acta Oecol.* 54: 65-71. <https://doi.org/10.1016/j.actao.2013.09.003>
- ANDERSEN, S. T. 1995. History of vegetation and agriculture at Hassing Huse Mose, Thy, Northwest Denmark since the Ice Age. *J. Danish Archaeol* 11: 57-79. <https://doi.org/10.1080/0108464X.1993.10590072>
- BARRIOS, Y. & N. RAMÍREZ. 2020. Biología floral y solapamiento fenológico de las angiospermas de un bosque inundable, cuenca del lago de Maracaibo, Venezuela. *Acta Bot. Mex.* 127: e1704. <https://doi.org/10.21829/abm127.2020.1704>
- BENNETT, K. & K. J. WILLIS. 2001. Pollen. En: SMOL, J. P., H. J. B. BIRKS, W. M. LAST, R. S. BRADLEY

- & K. ALVERSON (eds.), *Tracking Environmental Change Using Lake Sediments*. Developments in Paleoenvironmental Research, vol. 3: 5-32, Springer, Dordrecht. https://doi.org/10.1007/0-306-47668-1_2
- BENNETT, K. D., S. BOREHAM, M. J. SHARP & V. R. SWITSUR. 1992. Holocene history of environment, vegetation and human settlement on Catta Ness, Lunnasting, Shetland. *J. Ecol* 80: 241-273. <https://doi.org/10.2307/2261010>
- BENSENY, G. C. 2011. *La zona costera como escenario turístico: Transformaciones territoriales en la costa Atlántica Bonaerense Villa Gesell (Argentina)*. Tesis de Doctor en Geografía. Universidad Nacional Del Sur, Argentina.
- BÉRTOLA, G. R., M. FARENGA, L. CORTIZO & F. I. ISLA. 1999. Dinámica morfológica de las playas de Villa Gesell (1994-1996), provincia de Buenos Aires. *Rev. Asoc. Geol. Argent.* 54: 23-35.
- BÉRTOLA, G. R., F. I. ISLA, L. CORTIZO & H. A. ORELLANO. 2002. Modelo sedimentario de la barrera medanosa al norte de Villa Gesell (provincia de Buenos Aires) – de aplicación hidrogeológica. *Lat. Am. J. of Sedimentol. Basin. Anal.* 9: 109-126.
- BIRKS, H. J. B. & J. M. LINE. 1992. The use of Rarefaction Analysis for estimating palynological richness from Quaternary Pollen-Analytical Data. *Holocene* 2: 1-10. <https://doi.org/10.1177/095968369200200101>
- BIRKS, H. J. B., V. A. FELDE, A. E. BJUNE, J. GRYTNES ... & T. GIESECKE. 2016. Does pollen-assembly richness reflect floristic richness? A review of recent developments and future challenges. *Rev. Palaeobot. Palynol.* 228: 1-25. <https://doi.org/10.1016/j.revpalbo.2015.12.011>
- BUNTING, M. J. 1994. Vegetation history of Orkney, Scotland; pollen records from two small basins in west Mainland. *New Phytol.* 128: 771-792. <https://doi.org/10.1111/j.1469-8137.1994.tb04039.x>
- BUNTING, M. J. & D. MIDDLETON. 2005. Modelling pollen dispersal and deposition using HUMPOL software, including simulating windroses and irregular lakes. *Rev. Palaeobot. Palynol.* 134: 185-196. <https://doi.org/10.1016/j.revpalbo.2004.12.009>
- BUNTING, M. J. & R. MIDDLETON. 2009. Equifinality and uncertainty in the interpretation of pollen data: the Multiple Scenario Approach to reconstruction of past vegetation mosaics. *Holocene* 19: 799-803. <https://doi.org/10.1177/0959683609105304>
- BUNTING, M. J., M. FARRELL, A. BROSTRÖM, K. L. HJELLE ... & C. L. TWIDDLE. 2013. Palynological perspectives on vegetation survey: a critical step for model-based reconstruction of Quaternary land cover. *Quat. Sci. Rev.* 82: 41-55. <https://doi.org/10.1016/j.quascirev.2013.10.006>
- BURRY, L. S., M. E. TRIVI DE MANDRI, P. I. PALACIO & M. C. LOMBARDO. 2001. Relaciones polen-vegetación de algunas taxas de la estepa patagónica (Argentina). *Rev. Chil. Hist. Nat.* 2: 419-427. <https://dx.doi.org/10.4067/S0716-078X2001000200016>
- CABRAL, E. L. & C. PASSICOT. 2010. *Asterideas: Diversidad vegetal, biotaxonomía de spermatofitos*. Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Argentina.
- CABRERA, A. L. 1941. Las comunidades vegetales de las dunas costaneras de la Provincia de Buenos Aires. D.A.G.I. *Publicaciones técnicas* 1: 5-44.
- CABRERA, A. L. & E. M. ZARDINI. 1953. *Manual de la flora de los alrededores de Buenos Aires*. Editorial Acme, Buenos Aires.
- CHENLO, U. 2014. *Palinoteca de plantas vasculares acuáticas para el análisis polínico en paleolimnología*. Tesis de Grado, Universidade da Coruña, España.
- CELSI, C. E. 2016. La vegetación de las dunas costeras pampeanas. En: ATHOR, J. & C. E. CELSI (eds.), *La costa atlántica de Buenos Aires: naturaleza y patrimonio cultural*. pp. 116-138. Fundación de Historia Natural Félix de Azara, Buenos Aires.
- CODIGNOTTO, J. O., F. I. ISLA & A. L. MONTSERRAT. 2012. Manejo del Sistema Playa-Dunas en las Costas en la Provincia de Buenos Aires (Argentina). En: RODRÍGUEZ-PEREA, A., G. X. PONS, X. ROIG-MUNAR, Á. MARTÍN-PRIETO... & A. CABRERA (eds.), *La gestión integrada de playas y dunas: experiencias en Latinoamérica y Europa. Monografies de la Societat d'Història Natural de les Balears*, vol 19: 271-287. Societat d'Història Natural de les Balears, Palma de Mallorca.
- DEL VITTO, L. A. & E. M. PETENATTI. 2015. Asteráceas de importancia económica y ambiental: Segunda parte: Otras plantas útiles y nocivas. *Multequina* 24: 47-74.
- ERDTMAN, G. 1952. *Pollen Morphology and Plant Taxonomy—Angiosperms*. Almqvist and Wiksell, Stockholm.
- FAYE, P. F., A. M. PLANCHUELO & M. L. MOLINELLI. 2002. Relevamiento de la flora apícola e identificación de cargas de polen en el sureste de la provincia de Córdoba, Argentina. *Agriscientia* 19: 19-30. <https://doi.org/10.31047/1668.298x.v19.n0.2649>

- FELDE, V. A., S. M. PEGLAR, A. E. BJUNE, J. A. GRYTNES & H. J. B. BIRKS. 2015. Modern pollen–plant richness and diversity relationships exist along a vegetational gradient in southern Norway. *Holocene* 26: 163–175.
<https://doi.org/10.1177/0959683615596843>
- FERNÁNDEZ, A. L. & S. C. GRILL. 2016. Análisis de la vegetación y del polen actual en la cuenca inferior del río Colorado, sudoeste de la provincia de Buenos Aires, Argentina. *Rev. Bras. Paleontol.* 19: 111-126.
<https://doi.org/10.4072/rbp.2016.1.09>
- FONTANA, S. L. 2003. Pollen deposition in coastal dunes, south Buenos Aires Province, Argentina. *Rev. Palaeobot. Palynol.* 126: 17-37.
[https://doi.org/10.1016/S0034-6667\(03\)00034-4](https://doi.org/10.1016/S0034-6667(03)00034-4)
- FONTANA, S. L. 2004. *Present and past coastal dune environments of southwest Buenos Aires Province, Argentina*. Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology, vol. 940. Acta Universitatis Upsaliensis, Upsala.
- FONTANA, S. L. 2005a. Coastal Dune Vegetation and Pollen Representation in South Buenos Aires Province, Argentina. *J. Biogeogr.* 32: 719-735.
<https://doi.org/10.1111/j.1365-2699.2004.01221.x>
- FONTANA, S. L. 2005b. Holocene vegetation history and palaeoenvironmental conditions on the temperate Atlantic coast of Argentina, as inferred from multiproxy lacustrine records. *J. Paleolimnol.* 34: 445-469. <https://doi.org/10.1007/s10933-005-5792-8>
- FRAZER, H., A. R. PRIETO & J. C. CARBONELLA, 2020. Modern pollen source and spatial distribution from surface lake sediments in the southwestern Pampa grasslands, Argentina: Implications to interpret Holocene pollen records. *Rev. Palaeobot. Palynol.* 277: 104207.
- GIESECKE, T., S. WOLTERS, S. JAHNS & A. BRANDE. 2012. Exploring Holocene changes in palynological richness in northern Europe – did postglacial immigration matters? *PLoS ONE* 7: 1-12.
<https://doi.org/10.1371/journal.pone.0051624>
- GORING, S., T. LACOURSE, M. PELLATT & R. MATHEWES. 2013. Pollen assemblage richness does not reflect regional plant species richness: a cautionary tale. *J. Ecol.* 101: 1137-1145.
<https://doi.org/10.1111/1365-2745.12135>
- GOSLING, W. D., A. C. M. JULIER, S. ADU-BREDU, G. D. DJAGBLETEY ... & S. MOORE. 2018. Pollen-vegetation richness and diversity relationships in the tropics. *Veg Hist Archaeobot.* 27: 411-418.
<https://doi.org/10.1007/s00334-017-0642-y>
- GRIMM, E. 2020. *TILIA* 2.6.1 [Software]. Illinois State Museum, Illinois.
- GRINDEAN, R., A. B. NIELSEN, I. TANȚĂU & A. FEURDEAN. 2019. Relative pollen productivity estimates in the forest steppe landscape of southeastern Romania. *Rev. Palaeobot. Palynol.* 264: 54-63.
<https://doi.org/10.1016/j.revpalbo.2019.02.007>
- INSTITUTO DE BOTÁNICA DARWINION. 2020. Catálogo de las Plantas Vasculares del Conosur. Buenos Aires, Argentina: Instituto de Botánica Darwinion. Available in: <http://www.darwin.edu.ar/Proyectos/FloraArgentina/BuscarEspecies.asp>.
- ISLA, F. I., L. C. CORTIZO & E. J. SCHNACK. 1996. Pleistocene and Holocene beaches and estuaries along the Southern Barrier of Buenos Aires, Argentina”. *Quat. Sci. Rev.* 15: 833-841.
[https://doi.org/10.1016/S0277-3791\(96\)00065-0](https://doi.org/10.1016/S0277-3791(96)00065-0)
- ISLA, F. I., L. C. CORTIZO & H. A. TURNO ORELLANO. 2001. Dinámica y Evolución de las Barreras Medanosas, Provincia de Buenos Aires, Argentina. *Rev. Bras. Geomorfol.* 2: 73-83.
<https://doi.org/10.20502/rbg.v2i1.9>
- KUMLER, M. L. 1997. Critical environmental factors in dry coastal ecosystems. En: VAN DER MAAREL, E. (ed.), *Dry Coastal Ecosystems, Part C. Ecosystems of the World, 2C*. pp. 387–409. Elsevier, Amsterdam.
- LATORRE, F. 1999. El polen atmosférico como indicador de la vegetación y de su fenología floral. Tesis Doctoral. Universidad de Buenos Aires, Argentina.
- LATORRE, F., C. PÉREZ, S. STUTZ & S. PASTORINO. 2010. Pollen deposition in Tauber traps and surface soil samples in the Mar Chiquita Coastal Lagoon Area, Pampa Grasslands (Argentina). *Bol. Soc. Argent. Bot.* 45: 321-332.
- LEGENDRE, P. & H. BIRKS. 2012. From classical to canonical ordination. En: BIRKS, H., A. LOTTER, S. JUGGINS & J. SMOL (eds), *Tracking environmental change using lake sediments*. Developments in paleoenvironmental research, vol 5: 201–248. Springer, Dordrecht.
https://doi.org/10.1007/978-94-007-2745-8_8
- LI, B., W. WANG, H. WANG, Y. ZHANG ... & Y. MA. 2022. Pollen–vegetation relationship based on lake surface sediments of arid and semi-arid northern China; considerations and limitations. *Rev. Palaeobot. Palynol.* 303: 104694.
<https://doi.org/10.1016/j.revpalbo.2022.104694>

- LIU, Y. K. OGLE, J. LICHSTEIN & S. JACKSON. 2022. Estimation of pollen productivity and dispersal: How pollen assemblages in small lakes represent vegetation. *Ecol. Monogr.* 92: e1513. <https://doi.org/10.1002/ecm.1513>
- MADANES, N. & C. A. FERNÁNDEZ. 2018. Pollen dispersal and deposition in an agroecosystem at Province of Buenos Aires, Argentina. *Darwiniana*, n. s. 6: 35-46. <https://dx.doi.org/10.14522/darwiniana.2018.61.785>
- MARCOMINI, S., R. LÓPEZ, P. PICCA, N. MADANES & L. BERTOLÍN. 2017. Natural Coastal Dune-Field Landforms, Plant Communities, and Human Intervention along Buenos Aires Northern Aeolian Barrier. *J. Coast. Res.* 33: 1051-1064. <https://doi.org/10.2112/JCOASTRES-D-15-00219.1>
- MARCOS, M. A. & M. V. MANCINI. 2012. Modern pollen and vegetation relationships in northeastern Patagonia (Golfo San Matías, Río Negro). *Rev. Palaeobot. Palynol.* 171: 19-26. <https://doi.org/10.1016/j.revpalbo.2011.11.007>
- MASCIADRI, S., S. STUTZ & F. GARCÍA-RODRÍGUEZ. 2013. Modern pollen-vegetation relationship of plant communities in the Uruguayan Atlantic coast. *Braz. J. Bot.* 36: 31-44. <https://doi.org/10.1007/s40415-013-0006-5>
- MATTHIAS, I. & T. GIESECKE. 2014. Insights into pollen source area, transport and deposition from modern pollen accumulation rates in lake sediments. *Quat. Sci. Rev.* 87: 12-23.
- MATTHIAS, I., M. SWEN SEMMLER & T. GIESECKE. 2015. Pollen diversity captures landscape structure and diversity. *J. Ecol.* 103: 880-890. <https://doi.org/10.1111/1365-2745.12404>
- MEDINA, R. (ed). 2018. *Flora del valle de Tehuacán-Cuicatlán: Lemnaceae*. Instituto de Biología, Universidad Nacional Autónoma de México, México.
- MELTSOV, V., A. POSKA, B.V. ODGAARD, M. SAMMUL & T. KULL. 2011. Palynological richness and pollen sample evenness in relation to local floristic diversity in southern Estonia. *Rev. Palaeobot. Palynol.* 166: 344-351.
- MONSERRAT, A. L., C. E. CELSI & S. L. FONTANA. 2012. Coastal dune vegetation of the Southern Pampas (Buenos Aires, Argentina) and its value for conservation. *J. Coast. Res.* 28: 23-35. <https://doi.org/10.2112/JCOASTRES-D-10-00061.1>
- MOORE, P. D., J. A. WEBB & M. E. COLLINSON. 1991. *Pollen analysis*. 2nd ed. Blackwell, Oxford.
- MOURELLE, D. & A. PRIETO. 2016. Pollen and spores from surface samples in the campos region of Uruguay and their paleoecological implications. *Acta Bot. Bras.* 30: 351-370. <https://doi.org/10.1590/0102-33062016abb0117>
- MOURELLE, D., A. PRIETO & F. GARCÍA-RODRÍGUEZ. 2017. Riparian woody vegetation history in the campos region, southeastern South America, during two time windows: late Pleistocene and late Holocene. *Quat. Sci. Rev.* 167: 14-29. <https://doi.org/10.1016/j.quascirev.2017.04.024>
- NAVARRO, C., J. S. CARRIÓN, M. MUNUERA & A. R. PRIETO. 2001. Sedimentación y distribución superficial de palinomorfos en cuevas del SE Ibérico. Implicaciones en paleoecología. *An. biol.* 23: 103-132.
- ODGAARD, B. V. 1999. Fossil pollen as a record of past biodiversity. *J. Biogeogr.* 26: 7-17.
- ODGAARD, B. V. 2018. Reconstructing past biodiversity development. En: ELIAS, S. A. (ed.), *Reference module in earth systems and environmental sciences*. Elsevier, Amsterdam. <https://doi.org/10.1016/B978-0-12-409548-9.11644-6>
- OKSANEN, J., G. L. SIMPSON, G. BLANCHET, R. KINDT ... & J. WEEDON. 2017. *Vegan: Community Ecology Package*. R package Version 2.4-3. Available in: <https://CRAN.R-project.org/package=vegan>
- OYARZABAL, M., J. CLAVIJO, L. OAKLEY, F. BIGANZOLI ... & R. J. C. LEON. 2018. Vegetation units of Argentina. *Ecol. Austral* 28: 40-63.
- PAPADOPOULOU, M., I. TSIRIPIDIS, S. PANAJIOTIDIS, G. FOTIADIS... & T. GIESECKE. 2022. Testing the potential of pollen assemblages to capture composition, diversity and ecological gradients of surrounding vegetation in two biogeographical regions of southeastern Europe. *Veg. Hist. Archaeobotany* 31: 1-15. <https://doi.org/10.1007/s00334-021-00831-4>
- PRENTICE, I. C. 1985. Pollen representation, source area, and basin size: toward a unified theory of pollen analysis. *Quat. Res.* 23: 76-86.
- PROVENDOLA, J. I. 2013. Villa Gesell. La baliza que invento un lugar: Al principio, fue el faro. <https://www.pagina12.com.ar/diario/suplementos/turismo/9-2558-2013-05-05.html>. [Access: May 9 2023].
- R DEVELOPMENT CORE TEAM. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available in: <https://www.R-project.org/>.

- REITALU, T., A. E. BJUNE, A. BLAUS, T. GIESECKE ... & J. B. BIRKS. 2019. Patterns of modern pollen and plant richness across northern Europe. *J. Ecol.* 107: 1662-1677. <https://doi.org/10.1111/1365-2745.13134>
- SANZ, M., D. SÁNCHEZ & S. VESPERINAS. 2004. *Atlas de las Plantas Alóctonas Invasoras en España*. Dirección General para la Biodiversidad, Madrid.
- SÁNCHEZ, A. C. & L. C. LUPO. 2011. Origen botánico y geográfico de las mieles de El Fuerte, Departamento de Santa Bárbara, Jujuy, Argentina. *Bol. Soc. Argent. Bot.* 46: 105-111.
- SENN, C., W. TINNER, V. FELDE, E. GOBET ... & C. MORALES-MOLINO. 2022. Modern pollen – vegetation – plant diversity relationships across large environmental gradients in northern Greece. *Holocene* 32: 159–173. <https://doi.org/10.1177/09596836211060494>
- SOTTILE, G. D., M. E. ECHEVERRÍA, M. S. TONELLO, M. A. MARCOS... & M. V. MANCINI. 2020. Dinámica de la vegetación andina del lago Argentino (50° S, 72° O) desde el retiro de los glaciares (ca. 12.000 años cal AP). *Andean Geol.* 47: 599-627. <http://dx.doi.org/10.5027/andgeoV47n3-3303>
- STUTZ, S. 2000. *Historia de la vegetación del litoral bonaerense durante el último ciclo transgresivo – regresivo del Holoceno*. Tesis Doctoral. Universidad Nacional de Mar del Plata, Argentina.
- STUTZ, S. 2001. Vegetación del área de la laguna Mar Chiquita. En: IRIBARNE, O. (Ed), *Reserva de Biosfera Mar Chiquita: Características físicas, biológicas y ecológicas*, pp. 75-78. Editorial Martín, Mar del Plata.
- STUTZ, S. & A. R. PRIETO. 2003. Modern pollen and vegetation relationships in Mar Chiquita coastal lagoon area, southeastern Pampa grasslands, Argentina. *Rev. Palaeobot. Palynol.* 126: 183-195. [https://doi.org/10.1016/S0034-6667\(03\)00084-8](https://doi.org/10.1016/S0034-6667(03)00084-8)
- SUGITA, S. 1994. Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *J. Ecol.* 82: 881-897. <https://doi.org/10.2307/2261452>
- SUGITA, S. 2007a. Theory of quantitative reconstruction of vegetation I: pollen from large sites REVEALS regional vegetation composition. *Holocene* 17: 229-241. <https://doi.org/10.1177/0959683607075837>
- SUGITA, S. 2007b. Theory of quantitative reconstruction of vegetation II: all you need is LOVE. *Holocene* 17: 243-257. <https://doi.org/10.1177/0959683607075838>
- VÄLI, V., B. V. ODGAARD, Ü. VÄLI & A. POSKA. 2022. Pollen richness: a reflection of vegetation diversity or pollen-specific parameters? *Veg. Hist. Archaeobot.* 31: 611-622. <https://doi.org/10.1007/s00334-022-00879-w>
- VAN DER SANDE, M. T., M. B. BUSH, D. H. URREGO, M. SILMAN ... & GOSLING W. 2021. Modern pollen rain predicts shifts in plant trait composition but not plant diversity along the Andes–Amazon elevational gradient. *J. Veg. Sci.* 32: e12925. <https://doi.org/10.1111/jvs.12925>
- VÁSQUEZ, C., G. SOTTILE, S. STUTZ, G. SÁNCHEZ-VUICHARD & V. MERINO-CAMPOS. 2023. Reconstrucción paleoambiental en el Sistema de Dunas Costeras del SE bonaerense. In: *Libro de Resúmenes XXX Reunión Argentina de Ecología*. INIBIOMA/IFAB CONICET-ASAE, Bariloche.
- VELÁZQUEZ, N. J. & BURRY, L. S. 2019. Análisis palinológico de superficie de hojas y tallos de ítems dietarios de Lama guanicoe (Fam. Camelidae) en Patagonia (Argentina): implicancias en la identificación del origen del polen en coprolitos. *Bol. Soc. Argent. Bot.* 54: 67-78.
- WANG, Q., J. LI, K. LU, G. XIE ... & Y. WANG. 2022. Pollen R-values in arid central Asia for quantitative palaeo-vegetation reconstruction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 596: 110993. <https://doi.org/10.1016/j.palaeo.2022.110993>
- WENG, C., H. HOOGHIEMSTRA & J. F. DUIVENVOORDEN. 2006. Challenges in estimating past plant diversity from fossil pollen data: statistical assessment, problems and possible solutions. *Divers. Distrib.* 12: 310-318.
- WIEMER, A. P., A. N. SÉRSIC & A. O. SIMÕES. 2009. Biología floral de *Oxypetalum solanoides* (Apocynaceae). *Bol. Soc. Argent. Bot.* 44 (Supl), p. 177. Huerta Grande, Argentina.
- WITTAKER, R. J., K. J. WILLIS, R. FIELD. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *J. Biogeogr.* 28: 453-470.
- XU, Q., F. TIAN, M. J. BUNTING, Y. LI... & Z. HE. 2012. Pollen source areas of lakes with inflowing rivers: modern pollen influx data from Lake Baiyangdian, China. *Quat. Sci. Rev.* 37: 81-91.
- YEZZI, A. L., A. J. NEBBIA & S. M. ZALBA. 2018. Fragmentación de pastizales psamófilos por plantaciones de pinos: efectos sobre la riqueza y la composición vegetal. *Ecol. Austral* 28: 133-144. <https://doi.org/10.25260/EA.18.28.1.0.640>
- ZULOAGA, F., M. BELGRANO & C. ZANOTTI. 2019. Actualización del Catálogo de las Plantas Vasculares del Cono Sur. *Darwiniana*, n. s.7: 208-278.

