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Phytolith pool in soils affected by different land use in southeastern pampean region, Argentina

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ABSTRACT

Phytoliths are important plant microfossils, but also relevant components of the clastic fraction of the soils. The phytolith pool present in soils not only depends on plant phytolith production but also on taphonomical soil processes. In the southeastern Pampean Plains, Argentina, where typical Argiudolls dominate, intense agricultural and livestock activities are carried on. These managements affect both plant diversity and soil properties, which in turn, may influence on the soil phytolith assemblages. The aim of this study was to describe and compare the phytolith assemblages of soils under different land uses and to compare them with the current phytolith production of plants. Three plots with different land uses were selected (pasture, cultivated field, and nature reserve). Phytoliths were extracted from plants and dung by calcination. Soil phytoliths were extracted using a centrifugation technique and the total soil phytolith content was determined. Phytolith production was higher in crops than in non-crop species. Differences in the distribution and content of phytoliths were found in soils under different land uses and no close relationship was observed between current vegetation and soil phytoliths. Soils in the nature reserve, where living plants are trace phytolith producers, had the highest phytolith content values. Cropland soils had the lowest phytolith content and the highest degradation state. The results showed that land use leads to differences in phytolith content in soils. Agricultural management modifies the typical pattern of phytolith distribution along profiles and reduces the total content of phytoliths, whereas nature plots with plant invasion modify the accumulation of organic debris in soils and promote a higher preservation of phytoliths. Finally, dung introduces both new and degraded phytoliths into soils.

Keywords: Taphonomy; phytolith; land uses; grasses; Argiudolls; terrestrials ecosystems

RESUMEN

Los fitolitos son importantes microfósiles vegetales con valor taxonómico pero también son componentes relevantes de la fracción clástica del suelo. El reservorio de fitolitos presentes en los suelos no solo depende de la producción de fitolitos por parte de la vegetación sino también de los procesos tafonómicos del suelo. En el sudeste de la llanura pampeana, Argentina, donde predominan los Arguidoles típicos, se llevan a cabo actividades agrícolas y ganaderas intensivas. Estas prácticas modifican la diversidad vegetal y las propiedades edáficas, las cuales, a su vez, pueden influir en las

asociaciones fitolíticas presentes en los suelos. El objetivo de este trabajo fue describir y comparar las asociaciones fitolíticas de los suelos con distintos usos productivos y compararlas con los fitolitos producidos por la vegetación actual. Se seleccionaron tres sitios con distintos usos del suelo (pastura, campo cultivado y reserva natural). Los fitolitos de las plantas y las bostas se extrajeron utilizando la técnica de calcinación. Los fitolitos del suelo se extrajeron mediante la técnica de centrifugación y se determinó su contenido total. La producción de fitolitos fue mayor en cultivos que en especies no cultivadas. Se encontraron diferencias en la distribución y el contenido de fitolitos en suelos con distinto uso, y no se observó una relación estrecha entre la vegetación actual y los fitolitos del suelo. Los suelos de la reserva natural, donde las plantas son productoras traza de fitolitos, presentan los valores más elevados de contenido de fitolitos. Los suelos cultivados registraron los contenidos de fitolitos más bajos y con un mayor estado de degradación. Los resultados muestran que el uso del suelo provoca diferencias en el contenido de fitolitos en los mismos. El manejo agrícola modifica el patrón típico de distribución de fitolitos en el perfil de suelo y reduce su contenido total. En áreas naturales, la invasión de plantas modifica la acumulación de residuos orgánicos en los suelos y promueve la preservación de fitolitos. Finalmente las bostas introducen fitolitos nuevos y/o degradados en los suelos.

Palabras clave: *tafonomía; fitolitos; usos de suelo; gramíneas; Arguidoles; ecosistemas terrestres*

INTRODUCTION

Phytoliths are crystalline or amorphous structures of varied chemical composition, generated by the metabolic activity of plants (Bertoldi de Pomar, 1975; Osterrieth, 2004; Piperno, 2006). Although phytoliths can have different compositions, the term "phytolith" in this paper will specifically refer to amorphous silica (SiO_2 x nH_2O) phytoliths. They are produced by almost all groups of embryophytes, from Bryophytes to Angiosperms (Hodson *et al*., 2005; Katz, 2015; Stromberg *et al*., 2016). Poaceae, the plant family that is the dominant component of grasslands and comprises a high number of crops, is a major producer of phytoliths (Hodson *et al*., 2005; Piperno, 2006; Tubana *et al*., 2016).

Upon the death and decay of plant organs, phytoliths become part of the clastic materials of soils and sediments, where, depending on environmental conditions, they can be preserved for thousands of years or be dissolved (Piperno, 2006). Due to their taxonomic value, these microfossils can be used as indicators of past plant communities in palaeoenvironmental, palaeobotanical, or archaeological studies (Piperno, 2006; Premathilake *et al*., 2022; Liu *et al*., 2023). On the other hand, depending on soil conditions, phytoliths may dissolve and release Si into the environment, providing an important source of this element for terrestrial and aquatic ecosystems (Borrelli *et al*., 2008; Fraysse *et al*., 2009; Sommer *et al*., 2006; 2013).

Phytolith accumulation in soils is closely related to the plant communities that grow or develop on the soil surface, whether natural or cultivated. Grasslands and most major crop species (maize, wheat, rice) produce abundant phytoliths and may contribute large amounts of amorphous silica to soils (Tubana *et al*., 2016; Benvenuto *et al*., 2025). However, agricultural practices (such as harvesting) may prevent the incorporation of dead plants into soils and, as a consequence, affect the amount of phytoliths that return to the soils (Desplanques *et al*., 2006; Keller *et al*., 2012; Vandevenne *et al*., 2012; Li *et al*., 2019).

In addition to the "in situ" accumulation of phytoliths due to local vegetation, wind action, surface and subsurface water movement, animal movement, and/or bioturbation in soils can mobilize and incorporate phytoliths produced by extra-local plants (Fernández Honaine *et al*., 2009; Osterrieth *et al*., 2009; Madella and Lancelotti 2012; Qader *et al*., 2023). Dung from herbivorous animals is another source of extra-local phytoliths in soils (Wallis, 2001; Paolicchi *et al*., 2021). Dung contains significant amounts of relatively degraded plant material, which includes phytoliths that will enter the soil after the degradation of organic matter (Paolicchi *et al*., 2021). Lastly, the soil parent material can also add phytoliths to the soil pool. For instance, the parent material of Argentinean Pampean soils is loess, where phytoliths represent between 2 % and 5 % of total mineralogy (Osterrieth *et al*., 2009).

Once incorporated into soils, phytoliths are subjected to weathering and taphonomic processes, including bioturbation, dissolution, and burial, which influence their preservation and distribution (Osterrieth *et al*., 2009, 2015; Cabanes *et al*., 2011; Premathilake *et al*., 2022). Anthropogenic activities, such as agricultural and livestock practices, can also modify these processes, affecting soil phytolith content and assemblage composition.

In the southeastern Pampean Plains, Argentina, typical Argiudolls predominate and, due to their fertility, are used for numerous agricultural and livestock production activities. Intensive agriculture can alter soil properties, which in turn may alter soil phytolith distribution and preservation, and modify the biogeochemical cycles of various chemical elements (Si, C, N) (Martínez *et al*., 2008; Allan *et al*., 2015; Haynes, 2017; Bardgett *et al*., 2021). Moreover, in fields used for livestock farming, cow traffic increases bulk density and compaction in the upper centimeters of soil (Yang *et al*., 2019; Bellora *et al*., 2023), affecting the translocation and distribution of phytoliths in soil profiles (Alvarez *et al*., 2012). Considering that phytoliths are an important taxonomic indicator of present and past plant communities, understanding how the use of land affects the phytolith pool in soils is crucial, especially in a region heavily affected by agricultural and livestock practices such as the Pampean region.

The aims of this study are (1) to describe and compare soil phytolith assemblages in three plots with different land uses (conservation, pasture (livestock), and agriculture) in typical Argiudolls from the Pampean region, Argentina; and (2) to relate these soil phytolith assemblages to the phytolith production of vegetation and land use. Taking into account that land use affects plant development and, consequently, plant phytolith input, as well as soil properties, it is expected that soil phytolith assemblages will differ both quantitatively and qualitatively between land uses. Specifically, in soils used for agricultural practices involving the harvest of crop plants that provide phytoliths, phytolith content is expected to be lower than in soils with other uses.

STUDY AREA

In South America, the Pampean Plains include several provinces of the central area of Argentina (INTA, 1989; Soriano *et al*., 1991). In the southeast of Pampean Plain, in Buenos Aires Province, four geomorphological units are described: the Ranges, the Perirange hills, the Fluvio-eolian Plain and the Coastal Plain (Martínez, 2001). The study area is located in Los Padres basin (37°56´ S and 57°45´ W, Figure 1) and it is part of the Perirange hills, which is a relief of morphologically complex hills originated from processes of primary eolian accumulation, later modified by superficial wash (Osterrieth and Martínez, 1993; Martínez, 2001). Three geological units are differentiated in the study area: a crystalline basement of metamorphic and pegmatitic rocks of pre-Cambrian age, a sedimentary layer of quartzites from Paleozoic age and a Quaternary loess layer. The predominant soils of the study area are generally deep, developed from this well-drained loessic parental material, with silty-loam texture. They are classified as Typical Argiudolls in the Mar del Plata Series (INTA, 1989). The climate is mesothermic and subhumid, with little or no water deficiency (Burgos and Vidal, 1951). The annual average temperature is 13.9 °C; while the annual average precipitation is 926.1 mm (Servicio Meteorológico Nacional, 2010).

The area belongs to the phytogeographic province of Southern Pampa, which has been dominated by grasslands since the Holocene (Soriano *et al*., 1991), especially in low lands. However, due to the fertility of the soils, the region has been subjected to intensive agricultural activities and most of the native grasslands have been replaced by crops or pastures.

MATERIAL AND METHODS

Plot selection

The plots included in this study belong to the Natural Reserve Laguna de Los Padres and some neighboring private fields (Los Padres Basin, Partido de Gral. Pueyrredon, Buenos Aires, Argentina) (Figure 1). In the middle of the last century, agricultural and livestock farming began in the area around this reserve; much of the original grassland has been replaced by croplands and horticulture areas, creating an important regional economic center (Manzoni, 2016).

To compare the effects of land use on soil phytolith content, three plots with similar topographical and pedological characteristics but with different land use were selected (Figure 1):

Nature reserve plot: The plot is included in the 90 ha Natural Reserve Laguna de Los Padres, where no agricultural or livestock practices have been applied, *i.e.* no machinery was used in the site. The only anthropic activity near this sector, that can also explain the invasion of exotic trees, was the plantation of *Acacia melanoxylon* in the 1980´s. Moreover, since at least the year 2000, another exotic species (*Rubus ulmifolius*) has invaded the area and replaced some of the native plants, including grasses and woody species such as *Celtis tala* and *Colletia paradoxa* (Fernández Honaine, 2001). The site has two distinct vegetation covers: a monospecific shrubland of *Rubus ulmifolius* (Rosaceae) (Figure 1d) and a monospecific forest of *Acacia melanoxylon* (Fabaceae) (Figure 1e).

Pasture plot: It includes a private area of 0.5 ha which has been grazed by cattle (8000 kg/ha) for at least 50 yr. The vegetation is composed of both exotic and native species, with a clear predominance

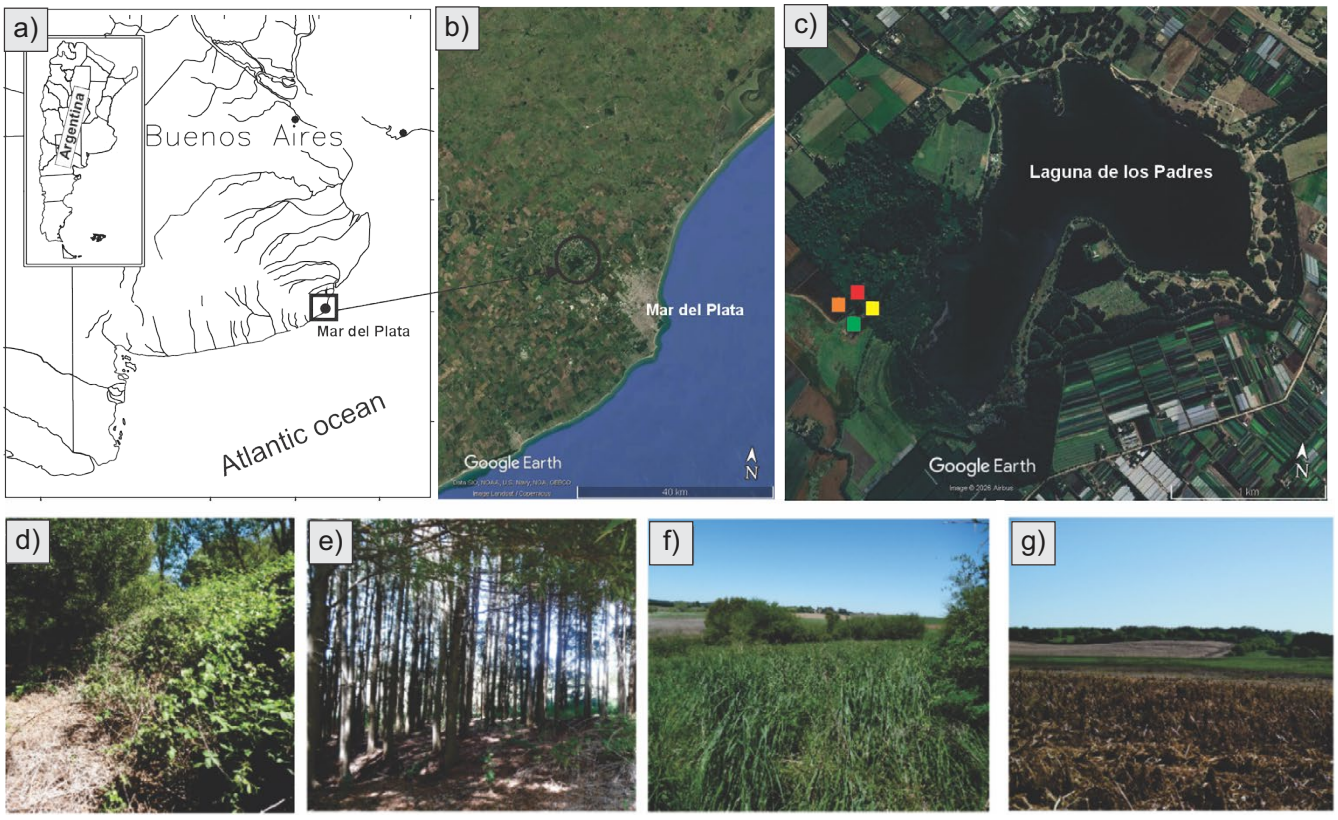


Figure1. Location of the study area and sampling plots. a) Location of the study area in Argentina. b) Southeastern Buenos Aires Province. The location of Laguna de los Padres is indicated by a black circle. c) Satellite image of Laguna de los Padres showing the sampling sites: pasture (green square), cultivated field (orange square), nature reserve with *Rubus ulmifolius* cover (red square), and nature reserve with *Acacia melanoxylon* cover (yellow square). d) Nature reserve with *Rubus ulmifolius* cover. e) Nature reserve with *Acacia melanoxylon* cover. f) Pasture. g) Cultivated field.

of *Phalaris arundinacea* (Poaceae) (70 %), as well as low percentages of other species such as *Hypochaeris grisebachii*, *Hypochaeris radicata*, *Cirsium vulgare* (Asteraceae), *Bromus catharticus* (Poaceae) and *Eryngium* sp. (Apiaceae) (Figure 1f) (Paolicchi, 2022). As a consequence of cattle, the presence of dung is common in the plot.

Cultivated field plot: it is included in a privately owned 6.5 ha site that has been subjected to conventional agricultural practices (intensive tillage, use of machinery, etc.) for the last 50 years with a crop rotation of *Triticum aestivum* (wheat) / *Glycine max* (soybean) / *Zea mays* (maize) (Figure 1g). At the time of sample collection, wheat seedlings and corn stover (stalks and leaves of corn, mainly) were present in the field.

Plants, soils and dung sampling

Information about the phytolith production in dominant species on nature reserve and cultivated field plots were obtained from previous publications (Borrelli *et al*., 2008; Benvenuto, 2017; 2025; De Rito *et al*., 2018). In the pasture plot, where no previous data about vegetation and/or phytoliths existed, a plant survey was carried out to identify the most abundant species (Paolicchi, 2022). For phytolith studies in pasture plot, a total of 6 species were selected and at least three specimens of each species were collected.

In each plot, composite soil samples (two subsamples from the same pedological level) were manually collected at two depths (0-10 cm and 10-20 cm), where differences in the current phytolith-producing vegetation and/or soil management are expected to be reflected (De Rito *et al*., 2018; Liu *et al*., 2021). Samples were also collected from the organic horizon (O) at each plot. In the pasture plot, where cow dung was common, the first 10 cm of the soil was collected in two sectors: a sector associated with dung and another not associated with dung. This specific sampling was done in order to analyze the transfer process of phytoliths from the dung to the soils. In parallel, five samples of dung present in pasture plot were collected with the purpose to evaluate their phytolith content.

Soil characterization

In order to characterized the soils studied in the three plots, routine techniques and descriptions were applied. The morphological description of soil samples (0-10 and 10-20 cm) was carried out according to the standards established by Soil Survey Staff (1996). Granulometry, pH and organic matter were determined in the laboratory. Textural analysis was carried out by sieving and pipetting (Galehouse, 1971; Ingram, 1971). Soil pH was measured in soil paste saturated with distilled water 1:1 (Orion Research digital pH meter, model 2010) and organic matter content was estimated by the Walkley and Black (1965) method.

Extraction of phytoliths

Phytoliths from plants, dung and organic horizon (O) were extracted by a calcination technique (Labouriau, 1983). Dung and organic horizon samples were air-dried before treatment and between 1 - 5 g were selected for phytolith extraction. For vegetal material, the samples were first placed in ultrasound for 15–20 min, washed with distilled water to remove mineral contaminants, dried at 60 °C for 24 h and weighed (initial weight). Plant, dung and organic horizon samples were charred at 200 °C for 2 h, boiled in 5 N HCl solution for 10 min, and finally ignited for 2–3 h at 700/800 °C. This technique destroys organic matter, dissolves calcium crystals and releases phytoliths. Only in the case of plant samples, ashes were weighed (final weight) and the percentage of phytoliths was calculated as following:

$$Si\ \% = \text{initial weight}/\text{final weight}*100$$

In the case of dung and organic horizon samples, the ashes may contain some mineral particles, and so the percentage of phytoliths couldn´t be calculated without an error.

Five grams from each composite soil samples were analyzed. Carbonates (with HCl 10 %), organic matter (with heat and H_2O_2 30 %), and clays (with Calgon 0.5 % and centrifugation at 1000 rpm for 3 min) were eliminated according to Álvarez *et al.* (2008). The samples after this treatment were analyzed for phytoliths, as it is described in the following paragraph.

Ashes from the plants, dung and organic horizon, and soil samples were mounted in immersion oil for optical microscope observation (Zeiss Axiostar Plus) at 400x. On each slide, at least 400 phytoliths were counted and morphologies were classified according to ICPN 2.0 (International Committee for Phytolith Taxonomy, 2019). In the specific case of the BILOBATE morphotype, it was differentiated into SIMPLE and PANICOID BILOBATE, based on the work of Fredlund and Tieszen (1994). This differentiation allowed a higher precision of phytolith plant origin. In soil samples, a minimum of 400 clastic particles were counted per sample, including phytoliths and other mineral particles and the total content of phytoliths was calculated in relation to total mineral content (Álvarez *et al*., 2008). In all the samples, the relative frequency of each morphotype was calculated in relation to total phytoliths.

In order to compare phytolith degradation in soil samples extracted from the different plots, the percentage of FRAGMENTED BILOBATE was calculated. BILOBATE is a very common morphotype in these soils and, due to its shape (two lobes joined by a central thin bar) is a labile phytolith that can be used as a soil disturbance indicator (Osterrieth *et al*., 2009).

Data analysis

Principal component analyses were performed to analyze the relationship between plots, considering the phytolith assemblages of the soils. Likewise, the relationship between the phytolith associations of the soils with those corresponding to the plant communities and dung was analyzed, in order to interpret the source of the phytolith pool. The relative frequencies of phytolith morphologies (ACUTE BULBOSUS, RONDEL, ELONGATE, CRENATE, BILOBATE, BLOCK, TRACHEARY, UNIDENTIFIED) were considered as variables. Prior to analysis, the phytolith relative abundance data were standardized using the scale function in R to ensure comparability across samples. Statistical analysis were performed using R-Studio software v. 4.3.3. (Rcore Team, 2024).

RESULTS

Phytolith content in plants and dung

Plants from the three plots differed in their phytolith content. As it was expected, plots where grasses dominate (cultivated field and pasture) produced higher contents of phytoliths: 10.5 – 13.8 % in the cultivated field, 2.3 – 5.2 % in the pasture and 0 – 0.6 % the nature reserve (Table 1).

The phytolith morphologies produced in the plants of each plot also differ, due to the different species composition. In the pasture plot, *Phalaris arundinaceae* (Poaceae: Pooideae) produced typical pooid morphologies (*e.g.* ACUTE BULBOSUS and CRENATE (Figure 2a and 2b)), and Asteraceae species (*Cirsium vulgare, Hypochaeris grisebachii, Hypochaeris radicata*) produced typical dicot morphologies such as POLYGONAL and TABULAR (Figure 2c-2d). The grass species present in the cultivated field belong to different subfamilies (*Triticum aestivum*: Pooideae (Figure 2f-2g); *Zea mays*: Panicoideae (Figure 2h)

Table 1. Mean ± s.d. of phytolith content (Si %) and main phytolith morphologies found in the plant species analyzed in the different plots.

Collection Site	Dominant species	Family	Si (%)	Main phytolith morphologies
Nature reserve	*Rubus ulmifolius Schott*	Rosaceae	0.6 ± 0.2*[1]	Tracheary, epidermal tissue, acute bulbosus*[1]
Nature reserve	*Acacia melanoxylon*	Fabaceae	Non producer*[2]	Non producer*[2]
Pasture	*Cirsium vulgare* (Savi) Ten.	Asteraceae	4.6 ± 0.4	Polygonal, elongate entire, acute bulbosus
Pasture	*Hypochaeris radicata* L.	Asteraceae	2.2 ± 1.0	Polygonal, tabular lobate, acute bulbosus
Pasture	*Hypochoeris grisebachii* Cabr.	Asteraceae	4.2 ± 0.6	Acute bulbosus, tabular lobate, polygonal
Pasture	*Phalaris arundinacea* L.	Poaceae	5.1 ± 0.7	Acute bulbosus, crenate, elongate entire
Cultivated field	*Triticum aestivum* L.	Poaceae	13.8 ± 1.4*[3]	Epidermal tissue, rondel, elongate entire, dendritic and crenate*[3]
Cultivated field	*Zea mays* L	Poaceae	10.5 ± 3.2*[3]	Elongate entire, dendritic and crenate, bilobate, blocky, cross*[3]

[1] Data taken from De Rito et al. (2018).[2] Data taken from Borrelli (2010). *[3] Data taken from Benvenuto *et al.* (2025).

and therefore produced different morphologies (Table 1). *Triticum aestivum* produced rondel and elongate entire, elongate dendritic and crenate, while *Zea mays* was characterized by crosses and bilobates. Both species produced elongate dendritic in the inflorescence. In the nature reserve plot, only *Rubus ulmifolius* produced scarce phytoliths derived from xylem silicification (Figure 2e) (Table 1).

In dung samples, a high percentage of unidentifiable phytoliths were recorded *i.e.* they were degraded or broken and could not be included in a specific category (46.1 ± 7.5 %) (Table S1 of the Supplementary Material; Figure 2x-2y). Within the identifiable morphologies, elongate (8.7 ± 2.5 %), rondel (7.3 ± 1.9 %), tabular (5.1 ± 1.1 %) and crenate (4.8 ± 1.4 %) (Figure 2aa) were the most abundant.

Soil characterization and phytolith content

Soils from the study sites were classified as Typical Argiudolls, and the analyzed samples corresponded to the A horizon. Specific soil characteristics are provided in the Table 2 and Figure S1, of the Supplementary Material. The three plots have similar granulometry and pH values. However, two aspects can be highlight. In the cultivated field, the presence of a plow layer at a depth of 19 cm is noteworthy, indicating the impact of conventional agricultural practices. On the other hand, in the nature reserve plot with *Rubus ulmifolius* cover, the organic matter content was significantly higher (9.2 – 13.5 %) compared to the other study sites, where it ranges from 5.1 % to 13 % (Table 2).

The content of phytoliths relative to the total mineral composition in the organic horizon ranged from 26 % to 42 %, with the highest values observed in the pasture (41.9 %) and the nature reserve plot with *Rubus ulmifolius* cover, where it reached 39.1 % (Table 3). The proportion of phytoliths in soil samples (0-10 and 10-20 cm) ranged from 25.3 % to 52.6 %. The highest phytolith content was found in the 0 – 10 cm soil sample from the nature reserve with *Rubus ulmifolius* cover (52.6 %), while the lowest was recorded in the cultivated field (25.3 %). In the top 10 cm of the pasture soils, the phytolith content was higher in the profile associated with dung (43.4 %) compared to the one without dung (40.3 %). Overall, the phytolith content was higher in the upper soil layers (0 – 10 cm) than in the lower layers (10 – 20 cm), except in the cultivated field, where the maximum phytolith content was observed at the level 10 – 20 cm.

In all the soil samples (including O) the predominant morphologies were elongates, crenate and rondel (Table 3, Figure 2n, 2o, 2q). Elongates are redundant morphologies that can be produced by a high diverse of plants, while crenate and rondel are typical of grasses. The abundance of the rest of morphologies found in all the soil samples showed little differences, except the ones detailed in the following lines. Most of these morphotypes clearly indicate the presence of grasses.

Nature reserve plots showed opposite patterns in rondel and crenate values in relation to depth, rondel decreased and crenate increased at 10 – 20 cm level respect to O horizon and 0 – 10 level (Table 3). In the particular case of *Rubus ulmifolius* profile, it is also important the increment of bilobates with depth. Also, simple bilobate was more abundant in *A. melanoxylon* profile than in *R. ulmifolius* profile. These patterns are probably showing some change in the grasses that may be present in the area before the *R. ulmifolius* and *A. melanoxylon* invasion. fragmented bilobate morphologies are more abundant in *R. ulmifolius* profile (1.5 – 6.1 %) than in *A. melanoxylon* profile (0.8 – 1.6 %), indicating some physical disturbance in the *Rubus* plot (Figure 2p). Finally, in both nature reserve sites, morphologies such as blocky, saddle and spheroid were observed in very low proportions (less than 3 %) and were therefore included in the category "others" (Table 3).

High values of acute bulbous were found in the O horizon (6.5 %) of the pasture, and along the profile (3.3 – 4.9 %), in comparison to the other plots (Table 3; Figure 2r). Another relevant pattern is the increment of rondel with depth, contrary to the pattern observed in the other plots. Also, in pasture plots, fragmented bilobate reached the highest abundances (2.5 – 7.4 %)(Figure 2l), indicating some physical disturbance, probably due to cattle traffic. Other morphotypes recorded in this plot included cross, simple bilobate and crenate phytoliths (Figure 2j, 2k and 2m). Although phytolith assemblages of 0 – 10 cm of soils associated and not-associated with dung are quite similar, some little differences can be highlighted. The top layer of pasture associated with dung can be distinguished by a higher abundance of fragmented bilobate morphologies (bilobates fractured at the junction of both lobes) (>5 %), rondel (12.5 %), and panicoid bilobate (1.9 %)(Figure 2i), compared to the samples without dung (Table 3).

Soils of the cultivated field contained substantial quantities of elongate dendritic (2.6 ± 0.8 %) (Figure 2u), as well as some cross (<2 %) (Figure 2t) and simple bilobate phytoliths (Figure 2s). The first two morphotypes are commonly associated with maize (Table 1).The plot of the cultivated field had higher concentrations of degraded phytoliths (Figure 2v) and lower total accumulated phytolith content, perhaps indicating more disturbance in the environment.

Relationship between plant communities, land use and the soil phytolith pool

The first two axes of the principal component analysis of the soil, plant and dung samples account for 71.73 % of the total variance (45.67 % for axis 1 and 26.06 % for axis 2) (Figure 3). In this analysis the

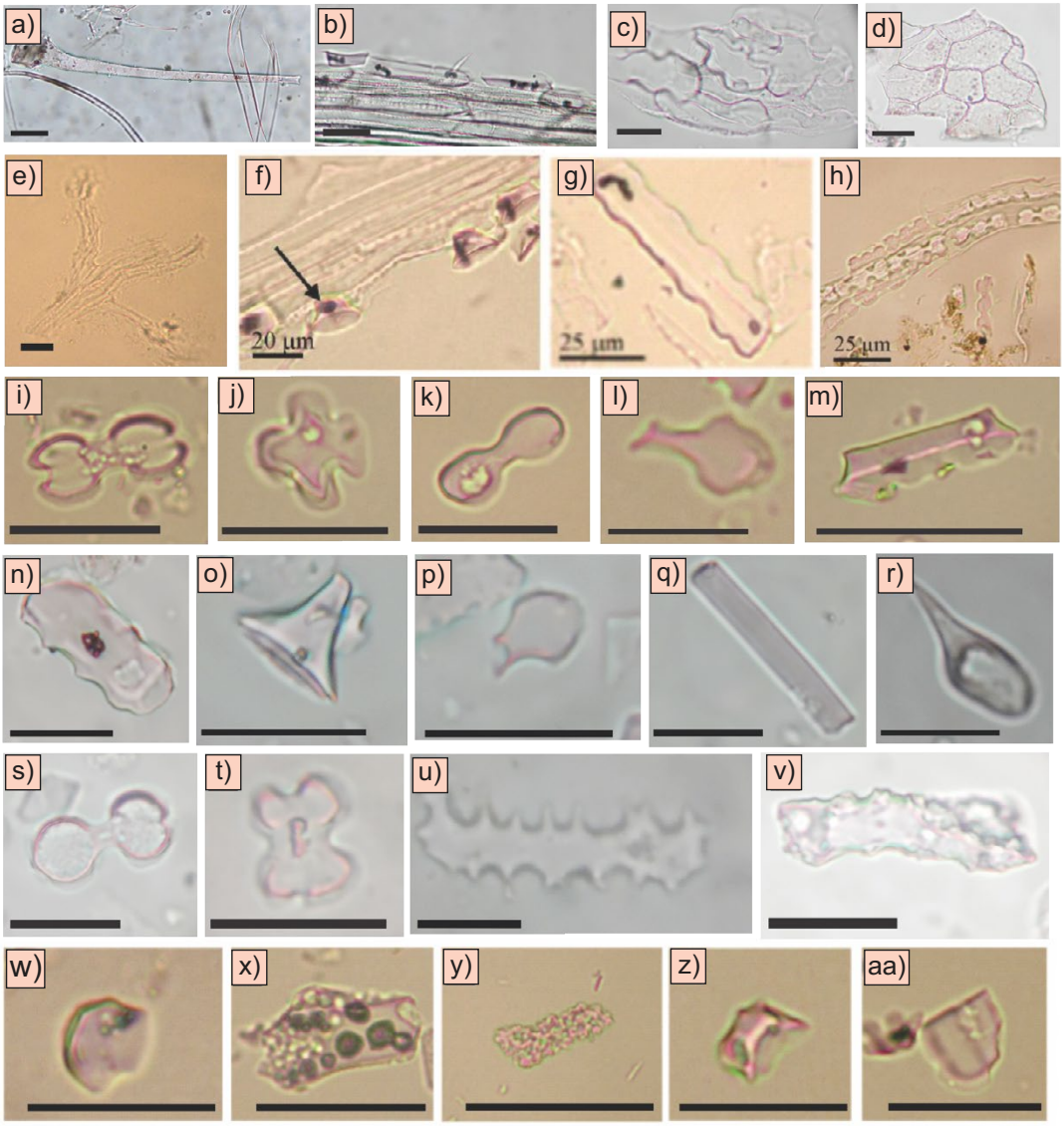


Figure 2. Representative phytolith morphologies identified in plant samples (a–h), soil samples (i–v), and dung samples (w–aa). Plant and soil phytoliths correspond to the following plots: pasture (a–d, i–m), nature reserve (e, n–r), and cultivated field (f–h, s–v). Acute bulbosus (a) and crenate (b) *of Phalaris arundinacea*, tabular lobate of *Hypochaeris grisebachii* Cabr (c), tabular polygonal of *Hypochaeris radicata* (d), tracheary of *Rubus ulmifolius* (e), rondel (f) and crenate (g) of *Triticum aestivum*, (h) bilobate articulated of *Zea Mays*, (i, s) panicoid bilobate, (j, t) cross, (k) simple bilobate, (l, p) fragmented bilobate, (m–n) crenate, (o) Rondel, (q) elongate, (r) acute bulbosus, (u) elongate dendritic, (v) degraded phytolith, (w–z) short cell, (x–y) not identified, (aa) fragmented crenate. Bar: 25 µm.

dung and plant samples from nature reserve and pasture are separated from soil samples and cultivated field plant sample. The first principal component (PC1) shows a positive correlation with the bilobate, elongate and rondel morphologies and a negative correlation with the acute bulbosus and tracheary morphologies. These last two morphologies are abundant in the plant samples from the natural reserve, which distinguishes them from the rest of the soil samples due to their poor preservation in the soil. The second principal component (PC2) has a positive correlation with elongate dendritic and unidentified morphologies, facilitating the separation of dung and the soil samples of the cultivated field from the remaining samples. The dung sample is isolated from the rest of the samples mainly due to an elevated proportion of unidentified morphologies which may indicate a high physical and/or chemical degradation of the phytoliths during the digestive process of the cow (Figure 3a). Only vegetation sample of cultivated field are in close proximity to the soil samples, probably due to a high content of elongate, rondel and low proportion of acute bulbosus compared with the rest of the plant samples. Within the soil samples, those from the cultivated field are mainly isolated from the rest, probably due to the high content of elongate dendritic.

In order to interpret if phytolith assemblages could differentiate soil samples, a second PCA was performed (Figure 4). The first three axes contribute to the 70.86 % of the variance (40.66 % for axis 1, 17.38 % for axis 2 and 12.82 % for axis 3). The variables that contribute most to axis 1 are elongate dendritic, unidentified and phytolith content. For axis 2, acute bulbosus, rondel and bilobate have the greatest effect. Contrary to expected, no clear groupings can be observed, nor between same plots, nor between same layers (*e.g.* between O horizons). Only two cases can be mention. Axis 1

Table 2. Pedological characteristics of the three plots analyzed in this study. Dominant vegetation, location and values of organic matter (OM), pH, soil moisture (Θ), bulk density (BD) and granulometry of the different soil samples are shown.

Plot	Vegetation	Location	Depth (cm)	OM (%)	pH (1:1)	Θ (%)	BD (g/cm³)	Granulometry		
								% sand	% silt	% clay
Reserve	Shrubland of *Rubus ulmifolius*	37° 56' 46.2" S 57° 45' 09.4" W	0 – 10	13.55	4.47	20.47	1.83	26.57	43.68	29.75
			10 – 20	9.23	5.47	-	-	31.19	32.73	36.09
	Forest of *Acacia melanoxylon*	37° 56' 46.2" S 57° 45' 09.4" W	0 – 10	11.32	4.52	18.65	1.82	35.24	39.94	34.82
			10 – 20	6.38	5.29	-	-	22.11	51.54	26.36
Pasture	Grasses	37° 56' 48.6" S	0 – 10 (associated with dung)	13.04	4.64	37.75	2.01	24.19	35.02	40.79
		57° 45' 07.3" W	0 – 10 (not associated with dung)	11.95	5.09	37.75	2.01	24.19	35.02	40.79
			10 – 20	9.77	5.56	-	-	35.14	31.21	33.65
Cultivated field	Crops	37° 56´ 47.42" S	0 – 10	9.73	4.64	23.65	2.40	21.12	54.91	23.97
		57° 45´ 0.9" W	10 – 20	5.13	5.88	-	-	20.66	65.34	14.00

allowed the separation of the cultivated field samples from the other soil samples, due to the presence of ELONGATE DENDRITIC and a low phytolith content. Axis 2 separated the sample from the O horizon of nature reserve from the rest of the samples due to the low abundance of ACUTE BULBOSUS.

DISCUSSION

The phytolith assemblage found in soils depends mainly on current and past vegetation as well as taphonomic processes (Borrelli *et al*., 2008; Osterrieth *et al*., 2009; Cabanes *et al*. 2011; Paolicchi *et al*., 2021). Because the three plots analyzed do not have topographic or climatic differences, and soil parent material is the same, the differences between the phytolith associations found in the different plot soils may result from soil management and/or changes in surface vegetation. Our data show that land use has influence on: plant phytolith production (because it modifies the plant community), and as a consequence plant phytolith input; and soil phytolith content and preservation (because it modifies some soil properties and this influences the content of soil phytoliths).

Plant and dung phytolith content

The plant species in the different plots produced different phytolith assemblages both in terms of quantities and morphologies, so the plant phytolith input also differed between plots. In the

Table 3. Relative frequency of phytolith morphologies and total phytolith content in soil samples from the three plots and the different levels analyzed. "Hz" is the horizon identifier. "Others" category represents morphologies with low frequencies in the counts (<3 %), such as blocky, saddle and spheroids. "Unidentified" corresponds to phytoliths that could not be assigned to any morphological category due to their high degree of weathering, fragmentation, or poor preservation.

Study site	Hz	Depth (cm)	Phytolith morphologies (%)										
			Acute bulbosus	Rondel	Trapezoid	Elongate	Simple bilobate	Panicoid bilobate	Fragmented bilobate	Elongate dendritic	Others	Unidentified	% total phytolith
Nature reserve (*Rubus ulmifolius* cover)	O		3.8	14.8	13.3	49.5	2.9	0.5	3.8	0.5	0.5	10.5	39.1
	A	0 – 10	4.2	11.3	14.7	51.5	4.8	0.7	6.1	0.2	0.3	6.2	52.6
		10 – 20	4.1	9.6	14.7	54.3	6.1	1.5	1.5	0.5	3.0	4.6	49.6
Nature reserve (*Acacia malanoxylon* cover)	O		0.7	15.0	11.8	49.0	9.8	1.3	1.3	0.0	0.0	9.8	34.9
	A	0 – 10	4.4	10.9	14.3	56.0	4.8	0.8	0.8	0.1	0.2	4.1	40.3
		10 – 20	3.6	9.4	17.7	46.9	5.7	1.6	1.6	0.0	0.0	9.9	39.4
Pasture	O		6.5	8.0	17.9	49.3	4.5	2.0	2.5	0.0	2.0	7.5	41.9
	A	0 – 10 (associated with dung)	3.3	12.5	19.0	46.2	3.3	1.9	4.8	0.5	0.7	8.0	43.5
		0 – 10 (not associated with dung)	3.9	9.4	20.6	47.6	4.4	1.1	3.2	0.2	1.3	8.2	40.3
		10 – 20	4.9	17.6	15.2	35.3	3.9	2.0	7.4	0.5	2.9	10.3	43.2
Cultivated field	O		5.8	18.0	10.8	43.2	3.6	0.7	3.6	1.4	2.9	10.1	26.2
	A	0 – 10	5.3	13.9	13.4	48.1	2.7	1.6	1.1	1.1	2.1	10.7	25.3
		10 – 20	1.6	8.8	18.1	52.8	6.7	1.6	2.1	2.6	0.5	5.2	34.3

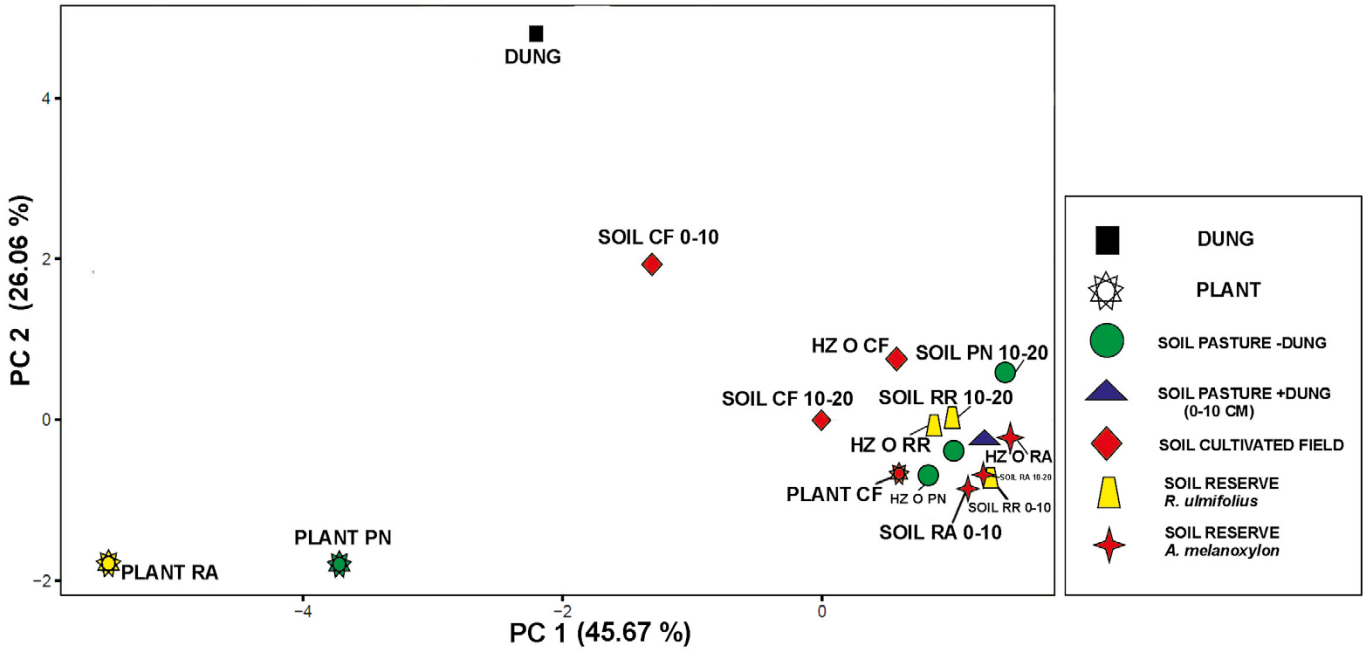


Figure 3. Score plots of PC1 versus PC2 for phytolith assemblages from vegetation, dung and the top 20 cm of soils from all studied plots. Abbreviations for samples are as follows: PN: pasture; RR: Nature reserve with *Rubus ulmifolius* cover. RA: Nature reserve with *Acacia melanoxylon* cover; CF: cultivated field. PLANT RA: vegetation of the nature reserve with *Rubus ulmifolius* cover. PLANT PN: vegetation of the pasture; PLANT CF: vegetation of the cultivated field. 'HZ O' refers to the organic horizon. –Dung indicates the soil sample not associated with dung; +dung indicates the soil sample associated to dung. 0 – 10 and 10 – 20 indicate the depth of the soil samples.

pasture, there was a clear predominance of *Phalaris arundinaceae* (Poaceae), whose silica content (5.18 %) is within the range reported by Gallego *et al.* (2004) and Fernández Honaine *et al.* (2008) (3 – 13 %) for other grasses in the Pampas region. The morphologies found in this species agree with those reported for Pooid grasses: CRENATE and ACUTE BULBOSUS. Asteraceae phytoliths were also observed in a low proportion. The morphologies found in these species are derived from epidermal tissue: TABULAR ENTIRE, TABULAR LOBATE and ACUTE BULBOSUS; the quantity and diversity of phytoliths in this family coincide with the antecedents in the family (Blinnikov, 2005; Fernández Honaine *et al.*, 2006; Piperno, 2006; Iriarte and Paz, 2009; Morris *et al.*, 2009; Borrelli *et al.*, 2011; De Rito *et al.*, 2018). Benvenuto (2017) studied the phytolith production of the species present in the cultivated field, *Triticum aestivum* (wheat) and *Zea mays* (maize). Silica content in these species were the highest (10.5 – 13.8 %) among all plants analyzed. These grass species belong to different subfamilies, and this was reflected on phytolith assemblage: morphologies found in wheat (subfamily Pooideae) are CRENATE and RONDEL, while in maize (subfamily Panicoideae) are BILOBATE and CROSS (Benvenuto, 2017) reflecting the taxonomic relevance of grass phytoliths (Pearsall *et al.*, 2003; Fahmy, 2008; Neumann *et al.*, 2017). Both species, as well as most grasses, produce ELONGATES DENDRITIC and PAPILLAE in their inflorescences (Piperno, 2006). Finally, in the nature Reserve plot, only *Rubus ulmifolius* showed phytolith production (De Rito *et al.*, 2018) with values similar to those found by Benvenuto *et al.* (2013) (0.5 %) for another species in the same genus (*Rubus geoides*), and morphologies derived from the silicification of TRACHEARY and epidermal cells. *Acacia melanoxylon*, like most legumes, does not produce phytoliths (Borrelli *et al.*, 2010).

The results obtained revealed that the dominant species in the three plots differ in the quantities of phytoliths and the morphologies they produce. Considering present vegetation, the highest input of phytoliths derive from cultivated field and the lowest from nature reserve. However, as it was shown in results section, no clear relation between plant and soil assemblages were observed.

Dung showed a high quantity of phytoliths (Table S1) and so constitute an important source of new phytolith morphologies to soils, many of them produced by plants in other sites where cows feed. They also contribute with a high percentage of degraded or broken phytoliths, *i.e.* in advance state of degradation, such as fragmented bilobates or unidentified phytoliths. This last aspect is relevant for biogeochemical Si cycle (Shahack-Gross, 2011; Paolicchi *et al.*, 2021).

Soil phytolith pool and its relation to land use and plant phytolith production

Soil phytolith contents described in this study (25.3 – 52.6 %) were similar than those observed previously for Typical Argiudolls of the Pampean region (Osterrieth 2006; Borrelli *et al.*, 2010; Osterrieth *et al.*, 2014; 2015; De Rito *et al.*, 2018). In three of the four plots analyzed, the phytolith content was higher in the upper soil samples (0 – 10 cm) compared to the lower ones (10-20 cm). Hart and Humphreys (2003) defined Phytolith Depth Functions (PDF), where they described the soils according to the distribution of phytoliths with depth. They considered three types of PDF. The decrease in the phytolith content from the surface towards the depth is classified as Type I PDF, and is usually considered as the "normal" distribution. This pattern was observed in all the profiles studied, except cultivated field. These results are consistent with previous studies in the region (Borrelli *et al.*, 2010; Osterrieth *et al.*, 2014, 2015; Benvenuto 2017; De Rito *et al.*, 2018). In the cultivated field, a different distribution was observed, with maximum soil phytolith content value at 10 – 20 cm (Table 3), coinciding with the plow floor. This pattern belongs to Type II PDF and shows a secondary zone of relative abundance of phytolith due to the impediment of vertical movement of these soils particles due to a change in texture or density (Hart and Humphreys 2003). The formation of a ploughed level causes changes in grain size distribution

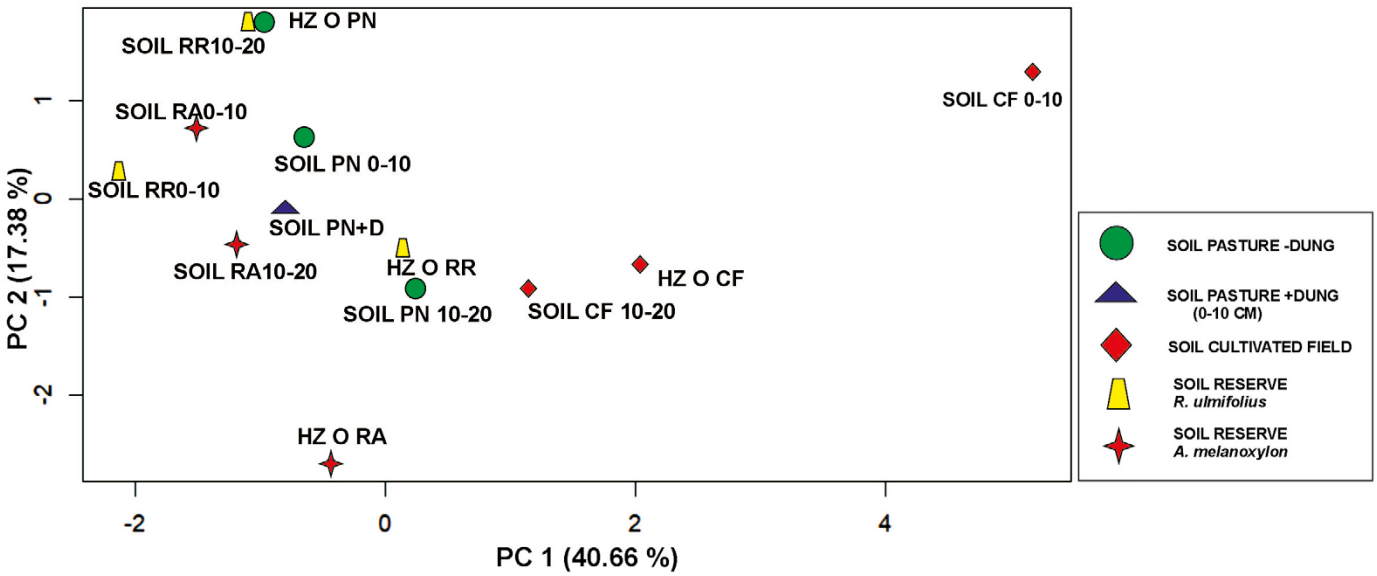


Figure 4. Score plots of PC1 versus PC2 for phytolith assemblages from top 20 cm soils from all studied plots. Abbreviations for samples are as follows: PN: pasture; RR: nature reserve with *Rubus ulmifolius* cover; RA: nature reserve with *Acacia melanoxylon* cover; CF: cultivated field. 'HZ O' refers to the organic horizon. –Dung indicates the soil sample not associated with dung; +dung indicates the soil sample associated to dung. 0 – 10 and 10 – 20 indicate the depth of the soil samples.

and increased compaction, which could restrict phytolith translocation and promote their accumulation in the soil layers immediately above this compacted layer (Nguyen *et al*., 2009; Benvenuto, 2017; Haynes, 2017). Nguyen *et al*. (2009) reported that the high clay content commonly associated with plow pans produces denser soil conditions that restrict phytolith movement toward deeper horizons, promoting their retention and accumulation in the overlying layers.

The plots in the nature reserve had the highest soil phytolith content (34.9 % – 52.6 %), contrary to expectations, as their main plant species (*Acacia melanoxylon* and *Rubus ulmifolius)* were null/trace phytolith producers (Borrelli *et al*., 2008; De Rito 2015; Wallis 2003; Piperno 2006). However, Borrelli *et al*. (2010) recorded similar results at a comparable site (23.1 % – 40.6 %). The relatively high content and preservation of phytoliths in this plot could be explained by: (1) phytoliths in the soil were originated from grasses, the natural vegetation before the *Acacia* and *Rubus* invasion; (2) the organic horizons in these plots protected the soil by reducing wind and water erosion, preserving the existing phytolith pool; and/or (3) the dense cover formed by *Rubus ulmifolius* may have contributed to reducing soil erosion and phytolith loss, while also trapping phytolith-rich organic residues from adjacent vegetation (grasses) within its stems (Mazzolari and Comparatore, 2014). Moreover, organic matter values were highest in the reserve plots (Table 2), supporting the idea of a greater organic accumulation at this site and, consequently, the buildup of plant material as a source of phytoliths.

The cultivated field showed the lowest soil phytolith content (26.2 – 34.3 %) compared to other plots, possibly because agricultural activities at this site include harvesting plant material (crops), a management that interrupts the recycling of the phytoliths produced by plants (Carey and Fulweiler, 2012; Keller *et al*., 2012; Vandevenne *et al*., 2012; Tubana *et al*., 2016; Haynes 2017). In addition, crops such as mays (*Zea mays*) and wheat (*Triticum aestivum*) are large accumulators of Si (10 mg Si g-1); they probably uptake large quantities of silicic acid from soils, but their harvest may cause a rapid depletion of soil phytolith pools (Keller *et al*., 2012; Vandevenne *et al*., 2012; Tubana *et al*., 2016; Li *et al*., 2019; Schaller *et al*., 2021). Lower phytolith content in these soils could also be due to higher degradation or fragmentation and dissolution due to agricultural practices. A high content of unidentified morphologies was observed in the top samples (< 10 %), as well as substantial percentages of FRAGMENTED BILOBATES (3.6 %), perhaps due to physical degradation caused by the passage of agricultural machinery (Keller *et al*., 2017; Nguyen *et al*., 2019). There are considerable edaphic alterations in the epipedon associated with conventional sowing, which may cause both physical and chemical degradation of soil phytoliths (Pan *et al*., 2017).

Pasture soils had intermediate values of phytolith content compared to the nature reserve and the cultivated field and they were slightly lower than those reported by Fernández Honaine (2007) for grasslands in highland areas of southeast Buenos Aires province, Argentina. Phytolith content was higher in the layer associated to dung (43.5 %) compared to the layer without dung (40.3 %). This suggests that dung may contribute to the incorporation of phytoliths into soils (Shahack-Gross, 2011; Paolicchi *et al*., 2021). However, a high proportion of the phytoliths recovered from dung samples were classified as unidentified due to their advanced state of degradation, which limited direct morphological comparisons between dung and soil assemblages. Therefore, although dung appears to be a potential source of phytolith input, additional studies including a larger number of dung and associated soil samples are required to better assess its contribution.

According to these quantitative results, land use may cause some differences in the phytolith content in the analyzed soils. Agricultural management modifies the typical pattern of phytoliths distribution along soil profiles and decrease the total content of phytoliths; on the other hand, nature plots (without anthropic management) but with plant invasion (*Rubus ulmifolius* and *Acacia melanoxylon*) modifies the natural accumulation of organic debris on soils which in turn promote a higher accumulation and preservation of phytoliths in the soils. Finally, the presence of dung, as a consequence of cattle farming, may influence in the input of more phytoliths (new and/or degraded) to soils (Vandevenne *et al*., 2013; Paolicchi *et al*., 2021). Also, considering the high content of degraded phytoliths, dung may represent a source of more labile biogenic silica than plant tissues (Paolicchi *et al*., 2021).

Principal component analysis (PCA) based on phytolith

assemblages shows that there is no close relationship between phytolith-producing plants and their associated soil, including O horizon. Many studies in the area and in other regions showed that soil phytolith assemblages differed from plant communities assemblages due to different taphonomic processes (*i.e.* Fredlund and Tiezsen, 1994; Fernández Honaine *et al*., 2009; Iriarte and Paz 2009; De Rito *et al*., 2018; Novello *et al*., 2018). Different agents affect phytolith input or phytolith conservation, such as water runoff, wind, animal movement, dung, fire, etc., and so are responsible for the non-match between plant and soil assemblages. Also, some specific morphologies, especially those produced in dicotyledons such as TRACHEARY or POLYGONAL, are very labile and are not easily preserved in soils (Thorn, 2004; Cabanes *et al*., 2011; De Rito *et al*., 2018). Another important factor that may be acting is time. It is probable that the modified vegetation actually present in the plots (invasion of *Acacia* and *Rubus*, crops) is too new to be totally reflected on soils. Moreover, previous natural vegetation (grasslands) of the area represents one of the main communities that accumulate phytoliths in their tissues, and it is known that they are sometimes overrepresented on soils (Thorn, 2004; Fernández Honaine *et al*., 2009; De Rito *et al*., 2018; Novello *et al*., 2018). This situation could explain the no-relation between phytolith assemblages of plants from nature plots and their soils, and the slightly association between the pasture and the nature reserve soil samples, where the morphologies found at both sites were originated from the grassy vegetation.

The effect of dung on soils showed a moderate increase in the amount of phytoliths bring into soils (see results and previous paragraphs). Also, some differences on phytolith morphologies could be observed between soils associated and not associated with dung. The first 0-10 cm of soil associated with dung had substantially higher content of RONDEL, PANICOID BILOBATE and FRAGMENTED BILOBATE compared to the profile not associated with dung. However, a large proportion of the phytoliths recovered from dung samples were classified as unidentified due to their advanced state of degradation. As a consequence, it was not possible to found a straight relation between dung and associated soils.

The only case where there was some slight relation between plant phytolith assemblage and soil phytolith assemblage was in the cultivated field plot, especially in top layers. The incorporation of morphologies characteristic of the crops was observed in both the O horizon and the top 10 cm of the soil. A substantial percentage of ELONGATE DENDRITIC, PANICOID BILOBATE, and CROSS phytoliths was recorded. These morphologies are commonly produced by grasses, including *Zea mays* and other Panicoideae taxa, and are consistent with the recent cultivation history of the plot. Finally, this plot shows a significant quantity of the unidentified phytoliths compared to the other plots analyzed. This group of phytoliths may indicate some extra physical degradation in this plot, probably due to the typical machinery of the agricultural management, which not only affect physical soil properties, but also some fragmentation of particles, including phytoliths (Alvarez *et al*., 2018; Duval *et al*., 2018; Mwiti *et al*., 2022).

CONCLUSION

The agricultural and livestock activities influence the phytolith pool present in soils, due to the modification of plant communities but also due to the promotion of some taphonomical processes, such as the physical fragmentation of phytoliths, alteration in depth distribution, and decrease in total phytolith content. The plots studied have different vegetation covers, which produce varying quantities and morphologies of phytoliths. Our results support the hypothesis proposed by several researchers that the phytolith association found in soils is composed of phytoliths produced not only by local vegetation, but also by extra-local and regional vegetation, gathered by different agents such as dung, wind and water (Fredlund and Tiezsen 1994; Fernández Honaine *et al*., 2009; Latorre *et al*., 2012; De Rito *et al*., 2018; Liu *et al*., 2021). It is important to consider the erosive processes enhanced by agricultural activity, as well as the contribution of extra-local plants and dung. Agricultural systems generate the most conspicuous changes in soil phytoliths, including their content, distribution, morphologies, and degradation state. Crop harvesting reduces soil phytolith content, by preventing their return to the soil, and increases the percentage of degraded phytoliths in the soil assemblage, due to the mechanical damage through machinery. The soil phytolith pool is affected by complex and diverse phytolith inputs, as well as by numerous taphonomic process, both anthropogenic and natural.

SUPPLEMENTARY MATERIAL

Supplemantary Table S1 and Figure s1 can be downloaded in teh abstract's preview page of this paper at www.rmcg.uam.mx

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Author contributions. M. Paolicchi: Conceptualization; methodology, data processing, analysis and interpretation, writing—original draft; writing—review & editing. M. Fernández Honaine: Conceptualization, analysis and interpretation, writing—original draft; writing—review & editing writing; funding acquisition. M. Osterrieth: Conceptualization; writing—review; funding acquisition. All authors discussed the results and contributed to the writing of the manuscript.

Data availability statement. The authors confirm that all data supporting the findings of this study are available in this article or its supplementary materials.

Declaration of competing interests. The authors declare that they are not aware of any financial conflicts of interest or personal relationships that could have influenced the work reported in this article.

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