



REVIEW

Paleoecology of Phytoliths: Evolutionary Links between Human-Environment Interaction and Plant Domestication

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Received: 01 July 2026; Accepted: 31 August 2026; Published: 19 October 2026

ABSTRACT: Long-term human–plant interactions have reshaped ecosystems and driven crop domestication, yet their reconstruction is often limited by poor preservation of organic remains in archaeological and sedimentary contexts. This review synthesizes current evidence on phytolith paleoecology to clarify evolutionary links among silica biomineralization, vegetation dynamics, human niche construction, and domestication processes. Beyond taxonomy, phytolith formation is presented as a biologically regulated, repeatedly evolved adaptive strategy in vascular plants, potentially conferring mechanical support, stress tolerance, and herbivory defense, implying that assemblages may reflect functional ecological responses as well as plant presence. In domestication research, diagnostic morphotypes and morphometrics improve detection of early cultivation and clarify dispersal pathways, as illustrated by rice domestication trajectories in the Lower Yangtze, including bulliform-based wild–domesticated distinctions and cautiously interpreted phytolith radiocarbon evidence, early broomcorn millet in second-millennium BCE Mesopotamia linked to irrigated summer multi-cropping, early Holocene maize cultivation in Mesoamerica distinguishable from teosinte, and size-based domestication signals in Cucurbita rind phytoliths from Ecuador. Key limitations include morphotype overlap among related taxa and taphonomic biases, reinforcing the need for multi-proxy integration (e.g., pollen, starch, macroremains, charcoal, micromorphology, geochemistry, ancient DNA). Overall, phytolith analysis is positioned as a methodological bridge connecting paleoecology, evolutionary biology, and archaeobotany to reconstruct coevolutionary feedbacks underlying agricultural origins and long-term landscape transformation.

KEYWORDS: Archaeobotany; coevolution; crop domestication; human–plant interactions; niche construction theory; paleoecology; phytoliths; plant evolution; silica biomineralization

1 Introduction

For thousands of years, interactions between humans and plants have influenced both the natural ecosystems and the evolution of cultivated species. These processes have left botanical evidence that remains preserved in archaeological and paleoecological records, providing valuable insights into past environments and human activities [1–3]. Since prehistoric times, plants have played a central role in human societies, serving as core economic resources and drivers of cultural modification. Consequently, deciphering these deep-time human–plant dynamics is central to modern archaeobotanical inquiry [4,5]. Understanding these long-term interactions depends on the identification and interpretation of botanical remains preserved in archaeological contexts. Plant macroremains, pollen, starch grains, charcoal, and phytoliths provide complementary lines of evidence for reconstructing past environments, subsistence strategies, agricultural

practices, and patterns of plant use [4,6,7]. Fossilized plant remains preserved *in situ* provide a visual example of the types of botanical evidence that may occur in geological contexts (Fig. 1). More broadly, the preservation of plant remains in archaeological and sedimentary contexts provides valuable evidence for reconstructing past vegetation, agricultural practices, and long-term human–environment interactions [5,8]. Among the various types of botanical evidence, phytoliths occupy a distinctive position because they often remain preserved in archaeological and sedimentary contexts where other plant remains have deteriorated. Phytoliths are microscopic silica bodies precipitated within or between plant cells that can persist long after the original plant tissues have decomposed. Their durability in archaeological and sedimentary deposits makes them one of the most informative botanical microremains for reconstructing past vegetation, plant use, and environmental conditions [9,10]. Because they are frequently preserved where other botanical remains are absent or poorly represented, phytoliths provide a reliable source of evidence for investigating long-term environmental change and human–plant interactions [6,8]. In archaeobotanical research, phytoliths contribute to the investigation of crop domestication, the emergence and spread of agriculture, crop-processing activities, land-use practices and the multiple ways in which plants were managed and exploited by past societies [5,6]. Their interpretative potential increases when phytolith data are considered alongside other archaeobotanical and geoarchaeological evidence, including pollen, starch grains, plant macroremains, charcoal, micromorphology, geochemical analyses and ancient DNA [6–8]. The late 1980s marked an important period in the expansion of phytolith analysis in archaeological research [11], followed by its increasingly widespread application in archaeobotanical, paleoecological, and evolutionary studies [6,8,12].



Figure 1: Fossilized plant remains in situ, Toplița, Romania, July–August 2023, including woody plant remains and visible impressions of needle-like leaves. Photographs by Mădălina B.

From an ecological and evolutionary perspective, silica accumulation in plants can contribute to several functional responses, particularly in grasses. Experimental studies have shown that silica deposited in plant tissues can increase resistance to herbivory by increasing leaf abrasiveness and reducing herbivore feeding and performance [13]. Phytolith characteristics may also respond to environmental conditions,

including water availability, supporting their use as indicators of past growing conditions [14]. These findings highlight the functional and ecological significance of plant silicification, although this biological role should be distinguished from the use of preserved phytoliths as archaeological indicators of past human–plant interactions.

In archaeological contexts, phytoliths provide a different but complementary form of evidence. Their preservation in sediments can document plant use, cultivation, crop domestication and dispersal, as well as vegetation changes associated with human landscape management [15–20]. When integrated with archaeological and environmental evidence, phytolith assemblages can therefore contribute to examining long-term changes in human–plant–environment relationships.

Understanding plant domestication requires an evolutionary perspective in which organisms are not viewed simply as passive recipients of environmental pressures. Through their activities, organisms can modify the biotic and abiotic conditions of their surroundings, altering resource availability, ecological interactions, and, in some cases, the selective pressures experienced by themselves and other species. When these environmental modifications persist across generations, they can contribute to ecological inheritance and influence subsequent evolutionary processes [21]. Humans represent a particularly influential form of niche construction because activities such as vegetation clearance, cultivation, burning, and water management can produce lasting changes in local environments [1,2]. From this perspective, plant domestication can be understood as a dynamic and reciprocal process involving human management, environmental modification, plant adaptive responses, and the transmission of cultural knowledge across generations [2,3]. Beyond their taxonomic value, phytoliths can contribute to tracing these long-term interactions between people, plants and environments by documenting changes in vegetation, plant use, and the development of agricultural landscapes through time [3,5,7].

This review first outlines the historical and methodological development of phytolith research, followed by its applications to vegetation reconstruction and major centers of plant domestication. It then examines how phytolith evidence can contribute to understanding human landscape modification, niche construction, and long-term human–plant–environment interactions, while highlighting current methodological limitations and future research directions.

2 History of Phytolith Research

2.1 Evolution of Phytolith Research

The development of phytolith research reflects a gradual shift from the description and identification of plant silica bodies to their use in archaeological and paleoecological research. Phytolith analysis is now used to investigate past vegetation, ecological change, agricultural practices and long-term human–environment interactions [6,22].

Early phytolith research relied largely on optical microscopy for the description and taxonomic comparison of silica bodies. With the development of digital imaging and computer-assisted analysis, phytolith research increasingly incorporated quantitative morphometric approaches, allowing size and shape variation to be quantified and improving taxonomic discrimination [23,24]. Scanning electron microscopy (SEM) has provided complementary high-resolution visualization of phytolith morphology and surface features, while standardized morphometric protocols and image-analysis software have further strengthened quantitative approaches [25]. More recently, automated image analysis and deep-learning methods have opened new possibilities for phytolith detection and taxonomic classification [26]. These methodological developments expanded the range of questions addressed through phytolith analysis, including whether

morphometric variation can be used to distinguish closely related plant taxa or domesticated crops from their wild relatives.

The International Meetings for Phytolith Research (IMPR) have also contributed to the development of the field by providing an international forum for discussing methodological advances, taxonomic challenges and new analytical approaches, and by encouraging collaboration among botanists, archaeologists, palaeoecologists and geoarchaeologists [8].

The growing application of phytolith analysis has also broadened its role in archaeobotanical research. Phytolith assemblages are now used to investigate environmental change, landscape history, plant domestication and human modification of vegetation. In this way, phytolith evidence contributes not only to identifying past plants but also to examining how plant communities changed in relation to human activities and environmental conditions [6,8,22].

Today, phytolith analysis is an established component of archaeobotanical and paleoecological research. Methodological improvements, together with the expansion of reference collections and standardized analytical protocols, have increased the consistency and scope of phytolith studies, including in regions where the preservation of macrobotanical remains is limited [8,12].

2.2 Expanding Applications of Phytolith Analysis

Continuous methodological advances have greatly broadened the scope of phytolith research beyond its original taxonomic applications. Improvements in extraction procedures, reference collections and morphotype characterization have enhanced the reliability of phytolith identification, allowing researchers to address increasingly complex questions related to archaeology, paleoecology and plant evolution [5,8]. The principal research fields in which phytolith analysis currently contributes are summarized in Table 1.

Table 1: Major applications of phytolith analysis in evolutionary and archaeobotanical research.

Research Field	Main Contribution of Phytolith Analysis	References
Paleoecology	Reconstruction of vegetation dynamics, paleoclimate and ecosystem evolution	[5,6]
Plant evolution	Understanding silica accumulation, phytolith evolution and plant adaptive responses	[9]
Plant domestication	Identification of early cultivation, domestication processes and crop dispersal	[3,5]
Human–environment interactions	Reconstruction of landscape modification, vegetation management and ecological feedbacks	[1–3]
Archaeobotany	Investigation of crop processing, land use and archaeological plant exploitation	[5,7]
Outlook	Multi-proxy integration, standardized methodologies and open-access reference collections	[8,10,12]

Advances in phytolith identification have expanded their application to the study of early agriculture. Diagnostic morphotypes can help distinguish cultivated plants from their wild relatives and provide evidence of cultivation practices, crop processing and the spread of agricultural systems across different regions [5]. The information provided by phytoliths extends well beyond crop identification. Phytolith assemblages recovered from archaeological sediments, combustion features, occupation surfaces and artifacts offer valuable insights into fuel use, plant processing, resource management and everyday activities, contributing to a more comprehensive understanding of past human lifeways [5,6].

Integrating phytoliths with pollen, starch grains, plant macroremains, charcoal, micromorphology, and sedimentological evidence can further strengthen interpretations of past environments and human activities by bringing together complementary lines of evidence [3,6,7].

2.3 Standardization of Phytolith Research

As phytolith research expanded across different regions and scientific disciplines, the need for greater methodological consistency became increasingly evident. Differences in extraction procedures, morphotype descriptions and taxonomic classifications often made it difficult to compare results among studies, limiting the broader interpretation of phytolith datasets [10,12].

An important step toward overcoming these challenges was the development of the International Code for Phytolith Nomenclature (ICPN), which established a common framework for describing and naming phytolith morphotypes. The revised ICPN 2.0 introduced standardized terminology for morphology, ornamentation and anatomical origin, reducing inconsistencies that had previously complicated comparisons among research groups [10].

The adoption of standardized nomenclature has greatly improved the reproducibility of phytolith analyses while facilitating comparisons between modern reference collections and archaeological assemblages. It has also strengthened communication among researchers working in archaeobotany, paleoecology, plant systematics and related disciplines, promoting greater consistency in data interpretation [5,10]. At the same time, methodological progress has extended far beyond nomenclature. The continuous expansion of modern reference collections, together with advances in morphometric analyses, digital imaging and analytical workflows, has improved the taxonomic resolution of phytolith identification and increased confidence in phytolith-based interpretations across a wide variety of archaeological and environmental contexts [5,8].

Despite these advances, several challenges remain. Differences in reporting standards, incomplete descriptions of analytical procedures and the limited availability of reusable datasets continue to hinder reproducibility and large-scale comparative studies [12].

For this reason, recent international initiatives increasingly promote methodological transparency, standardized analytical workflows and the adoption of FAIR (Findable, Accessible, Interoperable and Reusable) data principles. These recommendations seek to improve data accessibility, encourage international collaboration and facilitate the integration of phytolith datasets into broader archaeological and paleoecological syntheses [8,12].

The ongoing standardization of phytolith research has provided a robust methodological foundation for the discipline. By improving the comparability and reproducibility of phytolith datasets, it has strengthened their contribution to studies of plant evolution, domestication, paleoecology and the long-term interactions between humans and their environments [5,8,10].

2.4 From Descriptive Analyses to an Evolutionary Perspective

The continued development of phytolith research has broadened the scope of questions that can be addressed using phytolith evidence. Whereas early studies focused mainly on plant identification and vegetation reconstruction, current research increasingly uses phytolith assemblages to investigate ecological dynamics, evolutionary processes and the interactions between humans and their environments [8,9].

This change reflects a wider evolution within archaeobotany, where botanical microremains are no longer viewed simply as indicators of plant presence. Instead, they are increasingly interpreted as long-term

records of the interactions linking vegetation, environmental change and human activities, providing a more integrated perspective on past ecosystems [6,8].

At the same time, research into phytolith formation has revealed that these silica bodies are more than passive products of silicon accumulation. Growing evidence indicates that silicification represents an adaptive process that has evolved repeatedly across vascular plant lineages under different ecological and environmental conditions, highlighting its biological significance in plant evolution [9].

A similar shift has taken place in archaeobotanical studies of agriculture. Rather than documenting only the appearance of cultivated plants, researchers increasingly seek to understand the evolutionary processes that shaped domestication, recognizing it as a dynamic outcome of continuous interactions among environmental conditions, human management practices and plant adaptive responses [1,2].

Within this broader evolutionary perspective, phytolith assemblages provide evidence that extends well beyond species identification. They help reconstruct changes in vegetation, agricultural practices and landscape management while also revealing how human activities influenced plant evolution and how environmental change, in turn, affected human subsistence strategies [3,5].

Together, these developments have positioned phytolith research at the intersection of evolutionary biology, archaeobotany and paleoecology. Rather than documenting isolated botanical events, phytolith assemblages now contribute to a more comprehensive understanding of the long-term relationships among plants, environments and human societies, providing valuable insights into the coevolutionary processes that shaped past landscapes [2,8,9].

3 Phytoliths in Paleoecology and Plant Evolution

3.1 *Paleoecology and Vegetation Evolution: An Insight into Phytoliths*

Paleoecological reconstruction benefits from integrating complementary proxies that operate at different temporal and biological scales. Dendrochronology can provide high-resolution chronological and environmental records, while molecular biomarkers offer information on past vegetation and environmental conditions. Phytolith assemblages complement these approaches by documenting changes in plant communities and vegetation structure, particularly where other botanical remains are poorly preserved. When considered together, these independent lines of evidence can strengthen paleoenvironmental interpretations and help distinguish local vegetation changes from broader environmental trends [27]. On the other hand, macrobotanical and microbotanical remains such as phytoliths, pollen traces, and starch can provide evidence of human-plant interaction [28,29]. The morphotypes of phytoliths, which vary in size, define the plant taxa from which they originate, helping to map the evolution of vegetation throughout history and understanding how man has contributed to the introduction, domestication, and cultivation of certain plant species [30]. Phytoliths are an important proxy for reconstructing past human activities and human-induced landscape modification [5], the exploitation of plant resources [31,32], and long-term climatic and environmental change [33]. Phytoliths have been extensively studied for the paleoecological data they provide, beginning in Germany [34] and continuing in Europe [30], Australia [34,35], and Africa [36]. Currently, phytolith analysis is performed using technology, which improves the accuracy of taxonomic determinations and accelerates phytolith research [26]. Interdisciplinary approaches that include the deepening of continuous phytolith research help to characterize plant evolution throughout the geological era and contribute significantly to the determination of the paleoclimate in which they have adapted to form the succession of today's vegetation, as well as the expansion of plants cultivated in various climates around the world.

3.2 Evolutionary Significance of Phytolith Formation

Interpreting phytolith records also requires an understanding of how silica accumulation evolved in plants. Phytolith formation is influenced by plant physiology, environmental conditions and evolutionary history, and therefore cannot be regarded simply as a passive consequence of silicon uptake from the soil [9].

Comparative studies show considerable phylogenetic variation in silica accumulation across vascular plants. High silicon concentrations occur in several distinct lineages and are particularly common in groups such as Poales and Arecales [9,37]. This pattern suggests that high levels of silica accumulation evolved more than once during plant evolution and that its significance may differ among plant groups.

Several selective pressures may have contributed to the evolution and maintenance of silicification. Herbivory has received particular attention, especially in silica-rich grasses, although palaeontological and phylogenetic evidence does not support a simple evolutionary “arms race” between grasses and herbivores. Other factors, including mechanical support, resource economy and environmental stress, may also have played a role, with their importance differing among taxa and environments [9].

These evolutionary differences are relevant when phytolith assemblages are used in paleoecological reconstruction. Variation in phytolith production depends not only on which plants are present, but also on their evolutionary history and growing conditions. These factors need to be considered when phytolith assemblages are used to interpret past vegetation and environmental change [9,37]. Studies of modern plants also show that phytolith production can vary considerably among species and between different plant tissues. Differences in phytolith occurrence and morphology reflect both plant anatomy and growing conditions, showing that silicification is not uniform even among closely related plants. This variability is important for paleoecological interpretation, as phytolith assemblages may reflect not only the plants present in a given environment but also differences in their biological and ecological responses [38].

3.3 Functional Roles of Phytoliths in Vascular Plants

Silica deposition in plants has been associated with several functions, including mechanical support, reduced structural costs, defense against herbivores and responses to environmental stress. The importance of these functions, however, varies among plant groups and growing conditions [9].

One of the best-documented functions of phytoliths is the mechanical reinforcement of plant tissues. Silica deposited within epidermal and supporting cells increases tissue rigidity, helping leaves maintain their structure while reducing the need for carbon-intensive compounds such as lignin [9]. From an evolutionary perspective, this substitution may provide a metabolic advantage because silica can contribute to structural support at a substantially lower energetic cost than carbon-based structural compounds such as lignin and cellulose [39]. Experiments with the model grass *Brachypodium distachyon* (L.) P. Beauv. found higher foliar silicon accumulation under low atmospheric CO₂, suggesting a relationship between carbon availability and silicon accumulation [40].

Silica also plays a role in plant defense against herbivores. Experiments in grasses have shown that higher silica levels can increase leaf abrasiveness, reduce feeding and negatively affect the growth and digestion of folivorous insects [13]. Similar effects have been reported for mammalian herbivores, with increased silica reducing foliage digestibility and growth rates in voles [41]. These effects are not identical across herbivores, however, and appear to depend partly on feeding strategy and plant species [9,13].

Silicon accumulation is also affected by water availability. Experimental studies have reported changes in plant silicon concentrations under drought, waterlogging and flooding, although the responses differ among species and functional groups [42]. The relationship between silicification and water

stress is therefore not uniform and needs to be considered in relation to the species and environmental conditions involved.

3.4 Phytolith Evidence for Vegetation Dynamics

Phytolith assemblages preserve a long-term record of vegetation because they often remain intact long after organic plant tissues have disappeared. Their resistance to physical and chemical degradation allows vegetation history to be reconstructed across a wide range of climatic settings and archaeological contexts, including environments where other botanical remains are poorly preserved [5,6].

Changes in phytolith assemblages can reflect shifts in vegetation through time, making it possible to recognize changes in dominant plant communities associated with climatic fluctuations, environmental disturbance, and different forms of land use [5,15]. Recent field-based evidence has shown that phytolith assemblages can distinguish managed landscapes, abandoned fields, and relatively undisturbed forests, demonstrating their potential for reconstructing both human land use and subsequent vegetation recovery [15].

Because many phytolith morphotypes are characteristic of particular plant groups or ecological communities, their distribution can be used to reconstruct former habitats and landscape structure [5,43]. Such reconstructions have greatly improved our understanding of the development of forests, grasslands, wetlands and cultivated landscapes throughout the Holocene, revealing how vegetation responded to environmental change over time [3,5]. Recent regional reference studies have further demonstrated the value of modern phytolith assemblages for paleoecological reconstruction. Research in extremely arid environments, such as the Atacama Desert, shows that detailed knowledge of phytolith production across local plant taxa can strengthen the interpretation of past vegetation, particularly where other botanical proxies are poorly preserved [44].

Phytolith evidence has also contributed substantially to the study of agricultural landscapes. Variations in phytolith assemblages document changes in vegetation cover, crop cultivation and land management, providing direct evidence of the ways in which human activities progressively transformed natural ecosystems during the expansion of agriculture [3,5,7].

The interpretation of phytolith records becomes even more robust when they are considered alongside other archaeobotanical and geoarchaeological evidence. Integrating phytoliths with pollen, starch grains, plant macroremains, charcoal, sedimentological analyses and micromorphology allows a more comprehensive reconstruction of past environments while reducing the uncertainties associated with individual datasets [6–8].

Increasingly, phytolith research adopts a multi-proxy perspective in which phytolith assemblages are interpreted as part of broader environmental systems rather than as isolated botanical indicators. This approach has strengthened the role of phytolith analysis in paleoecological research by revealing the long-term interactions among vegetation, climate and human societies that shaped past landscapes [6,8].

Quantitative interpretations of phytolith assemblages should nevertheless consider the influence of both silicification and preservation. Because phytolith formation can vary with environmental conditions, differences in morphotype abundance or ratios may reflect changes in silicification as well as changes in plant or tissue abundance. In sedimentary sequences, differential preservation may further modify the original assemblage. These factors should therefore be considered when phytolith assemblages are used to reconstruct changes in past vegetation and environmental conditions.

3.5 Integrating Paleoecology with Evolutionary Processes

Interpreting phytolith assemblages requires more than the reconstruction of past vegetation. Their full paleoecological significance becomes apparent when phytolith evidence is considered alongside the evolutionary processes that regulate silica accumulation and the biological history of the plants that produced them. Integrating these perspectives provides a broader understanding of how vegetation responded to environmental change over long periods of time [8,9].

Viewed in this way, phytolith assemblages offer information that extends beyond taxonomic composition. They preserve evidence of changes in plant communities while also recording the ecological processes that influenced vegetation dynamics under changing climatic and environmental conditions. As a result, phytolith analysis contributes not only to the reconstruction of ancient ecosystems but also to understanding how plant populations adapted to long-term environmental change [5,9].

The integration of evolutionary concepts has also strengthened the interpretation of human-driven environmental change. As cultivation expanded and landscapes were increasingly modified through agriculture, vegetation management and resource use, human activities altered the ecological conditions under which plant populations evolved. Phytolith assemblages can preserve evidence of changes in vegetation associated with human land use and landscape modification. Differences between cultivated, previously managed, and relatively undisturbed environments demonstrate their potential for tracing long-term ecological responses to human activities [15]. When combined with archaeological and other environmental evidence, these records can contribute to understanding the broader interactions among human activities, vegetation change, and plant management.

Recent interdisciplinary research increasingly combines phytolith evidence with ecological, archaeological and evolutionary approaches to investigate long-term feedbacks between human societies and their environments. Such integrative studies make it easier to distinguish natural vegetation dynamics from anthropogenic transformations while providing a more complete understanding of the processes that shaped plant domestication and agricultural development [3,5,8].

Together, these developments have broadened the role of phytolith research far beyond the reconstruction of past vegetation. By linking paleoecology with evolutionary biology and archaeobotany, phytolith analysis now provides an integrated perspective on the long-term relationships among plants, environments and human societies. This broader framework naturally leads to the following section, where phytolith evidence is examined in the context of plant domestication and the origins of agriculture [2,5,9].

Importantly, phytolith assemblages can provide evidence for both sides of this interaction. Changes in morphotype composition and abundance can reflect shifts in vegetation and plant communities, while the occurrence of crop-specific phytoliths and changes associated with cultivation can document increasing human influence on those environments. Interpreted within their archaeological and environmental context, these records therefore offer a means of examining how human modification of landscapes and changes in plant communities developed together through time.

4 Phytoliths as Evidence for Plant Domestication

4.1 Plant Domestication: An Evolutionary Process

Plant domestication is increasingly understood as a gradual process shaped by interactions among human management, environmental change, and plant responses rather than as the result of deliberate selection alone. Within a niche-construction framework, practices such as cultivation, harvesting, and landscape management altered local ecological conditions and created new selective environments for plant

populations. Domestication can therefore be viewed as a long-term process in which cultural practices, environmental modification, and plant adaptation developed together [1,2].

This perspective provides a useful context for interpreting archaeobotanical evidence. Phytolith assemblages can document changes associated with early cultivation, vegetation management, and landscape transformation, contributing to the reconstruction of long-term interactions between human activities, plant communities, and changing environments [3,5].

4.2 Phytoliths as Indicators of Early Cultivation and Domestication

Identifying the earliest stages of plant domestication remains one of the central challenges in archaeobotanical research. During the initial phases of cultivation, morphological differences between wild progenitors and early domesticated plants are often subtle, making them difficult to detect when interpretation relies solely on macrobotanical remains [5].

Phytolith analysis offers an important advantage in this context because silica bodies frequently remain preserved even when seeds, fruits and other plant tissues have decomposed. As a result, phytolith assemblages extend the archaeobotanical record and provide valuable evidence for investigating the timing, intensity and nature of early cultivation practices [5,6].

Progress in phytolith morphology, together with the expansion of modern reference collections, has made it possible to identify diagnostic morphotypes for several economically important crops. These advances have improved the distinction between wild and cultivated plant populations and have increased confidence in the interpretation of archaeological assemblages associated with the origins of agriculture [5].

Phytolith evidence also highlights that domestication was not a single event but a gradual process of ecological and cultural transformation. Changes in phytolith assemblages can reflect shifts in vegetation management and patterns of plant use associated with the transition toward food production [3,5], as illustrated by crop-specific case studies discussed below.

Archaeobotanical records based on phytoliths further suggest that the emergence of agriculture involved long periods of experimentation and adaptation. As human communities progressively modified local environments through cultivation and resource management, they also influenced the evolutionary trajectories of the plants they exploited. In this way, phytolith assemblages document the close relationships among cultivation practices, environmental change and plant domestication [1–3].

Dental calculus represents an additional archaeological archive for plant microfossils, complementing evidence recovered from sediments, artifacts, and other archaeological contexts. Phytoliths and starch grains preserved in mineralized dental plaque can provide direct evidence of plants introduced into the oral cavity and offer valuable insights into plant use, food processing, and dietary practices [45]. More recent multi-proxy studies have shown that dental calculus may also preserve phytoliths, starch, pollen, spores, and other plant-derived microparticles, providing complementary information on plant exploitation and the local environmental and ecological settings in which past populations lived [46,47]. However, the interpretation of such microremains requires consideration of multiple pathways of incorporation into dental calculus, including deliberate and accidental ingestion, inhalation, and exposure during plant-processing and other plant-related activities [48].

The interpretation of these early agricultural systems becomes even more robust when phytolith evidence is integrated with pollen, starch grains, plant macroremains and geoarchaeological data. Such multi-proxy approaches help distinguish natural vegetation change from anthropogenic landscape modification and provide a more complete understanding of the environmental and cultural contexts in which domestication unfolded [5–7].

4.3 Phytolith Evidence from Major Centers of Plant Domestication

Plant domestication and the emergence of agriculture, dating around 11,000–10,000 years ago, marked a major turning point in human and environmental history [49]. Reconstructing the origins of agriculture relies on the accurate identification of domesticated plants and their wild progenitors [5]. Over the last few decades, phytolith analysis has become an essential component of archaeobotanical research, complementing evidence obtained from pollen, macrobotanical remains, and starch grains [5,50–52].

Modern studies increasingly incorporate comparative analyses of wild taxa closely related to domesticated crops and the development of regional reference collections, thereby enhancing reconstructions of the origins and dispersal of agriculture [5].

As a result, phytolith analysis has become an important tool for investigating the origins and spread of early agriculture. The following sections review phytolith evidence from the world's major centers of plant domestication, highlighting its contribution to reconstructing the domestication history of key crop species (Fig. 2).

The origins and spread of agriculture have long been central topics in archaeobotanical research. Among the different lines of botanical evidence, phytoliths have proven particularly valuable because they are often preserved in regions where seeds, fruits and other plant remains are scarce or absent. Their durability, together with the taxonomic information they retain, has made phytolith analysis an important approach for investigating the emergence and dispersal of cultivated plants across diverse environmental settings [5].

Progress in phytolith morphology and the continuous expansion of modern reference collections have greatly improved the recognition of diagnostic morphotypes for economically important crops. These advances have strengthened the reconstruction of independent centers of domestication and provided new insights into the movement of cultivated plants and agricultural traditions across different parts of the world [5].

Studies from East Asia illustrate the contribution of phytolith analysis to understanding the origins of rice agriculture. Diagnostic phytolith morphotypes have helped distinguish cultivated rice from its wild relatives and have refined the chronological reconstruction of the transition from wild plant exploitation to managed agricultural systems [5].

Comparable evidence from the Near East has improved our understanding of the early cultivation of cereals by documenting changes in vegetation associated with the establishment of farming communities and the gradual conversion of natural landscapes into agricultural ecosystems [3,5].

In Africa and the Americas, phytolith assemblages have provided valuable evidence for reconstructing regional pathways of domestication, particularly for crops that are poorly represented in the macrobotanical record. These studies demonstrate the broad applicability of phytolith analysis across different environments and agricultural traditions, emphasizing its importance for understanding the diversity of domestication processes worldwide [5]. Recent research from the Horn of Africa has provided further evidence for the importance of plant microremains in tracing early plant exploitation. The combined analysis of phytoliths and starch grains has revealed the use of C₄ plants before the widespread establishment of agriculture, suggesting that intensive exploitation of local plant resources formed part of the longer transition toward food production [53].

Phytolith evidence also extends beyond identifying where cultivated plants were grown. Changes in phytolith assemblages reveal patterns of crop management, plant processing and land-use practices associated with the spread of farming communities, offering insights into the ecological consequences of agricultural expansion and the progressive transformation of natural vegetation under increasing human

influence [3,5,7]. Representative examples of domesticated crops investigated through phytolith analysis and their archaeobotanical significance are summarized in Table 2.

Table 2: Selected case studies of plant domestication and crop dispersal discussed in this review.

Crop	Center of Domestication	Main Contribution of Phytolith Analysis
Rice (<i>Oryza sativa</i> L.)	East Asia	Early cultivation, domestication and wetland agriculture
Wheat (<i>Triticum</i> spp.)	Fertile Crescent	Early cereal cultivation and agricultural expansion
Barley (<i>Hordeum vulgare</i> L.)	Fertile Crescent	Crop management and early farming systems
Millets (<i>Setaria</i> spp.; <i>Panicum</i> spp.)	East Asia	Dryland agriculture and crop dispersal
Maize (<i>Zea mays</i> L.)	Mesoamerica	Domestication pathways and agricultural dispersal
Squash (<i>Cucurbita</i> spp.)	South America	Early horticulture and domestication

Source: Adapted and synthesized from [3,5].

4.3.1 East Asia—Rice (*Oryza sativa* L.)

The Yangtze basin is widely regarded as one of the earliest centers of rice domestication, with cultivated rice obtained from its wild form *Oryza rufipogon* Griff. [18,54–56] (Fig. 2). Diagnostic rice phytoliths, particularly bulliform, double-peaked husk, and parallel bilobate morphotypes, provide reliable evidence for identifying *Oryza* in archaeological contexts, even where macrobotanical remains are poorly preserved [55,56].

Beyond taxonomic identification, phytolith analyses have been used to reconstruct harvesting practices and distinguish wild from domesticated rice through bulliform morphology [54–56]. Radiocarbon dating of phytolith-occluded carbon has also been applied to chronological questions concerning early rice domestication [54]; however, the reliability of this approach remains debated because potential contributions of older carbon, as well as extraction and contamination effects, may influence apparent phytolith ages. Phytolith-derived radiocarbon dates should therefore be interpreted cautiously and, where possible, evaluated alongside other chronological evidence [57].

Phytolith evidence indicates that rice domestication was a gradual and regionally heterogeneous process rather than a single domestication event. Comparative analyses of rice bulliform phytoliths from numerous Lower Yangtze sites demonstrate that the Jinqu Basin, Ningshao Plain, and Taihu Plain followed different domestication trajectories, with varying rates and patterns of morphological change [56,58].

Evidence from the Qugou site in the middle–lower Huai River further illustrates the regional complexity of early crop cultivation in eastern China. Phytolith assemblages indicate that rice was cultivated as a staple crop from at least 8.8 ka BP, while broomcorn and foxtail millet were introduced later as supplementary crops. Morphological evidence from rice phytoliths also points to the presence of domesticated Japonica, whereas broomcorn millet appears to have been undergoing a continuing process of domestication [59].

Together with archaeological evidence for harvesting strategies and paddy-field cultivation, phytolith data indicate that domesticated traits accumulated progressively throughout the Neolithic, while the Taihu Plain played a key role in the development of intensive rice farming systems [56].

4.3.2 Southwest Asia (Fertile Crescent)—Wheat (*Triticum* spp.) and Barley (*Hordeum vulgare* L.) Domestication

Southwest Asia was one of the major centers of early plant domestication, with wheat and barley forming key components of emerging Neolithic agricultural systems. Archaeobotanical evidence indicates that cereal domestication was a geographically variable and protracted process, involving the cultivation of morphologically wild populations followed by the gradual appearance and increasing frequency of

domestication traits, particularly non-shattering rachises [60,61]. Einkorn and emmer wheat (*Triticum* spp.) and barley (*Hordeum vulgare* L.) became major components of early agricultural economies across the Fertile Crescent, although the timing and trajectories of domestication varied among regions [60,61]. Phytolith analysis can complement macrobotanical evidence in cereal archaeobotany. Morphometric analysis of inflorescence phytoliths has demonstrated the potential to distinguish wheat (*Triticum* spp.) and barley (*Hordeum* spp.), including discrimination among selected taxa [23]. More recently, three-dimensional morphometric analysis of elongate dendritic phytoliths has further explored their potential for cereal identification and the detection of morphological variation associated with domestication, while also highlighting limitations in their taxonomic and domestication-related discrimination [62]. More broadly, phytolith assemblages can provide complementary evidence for investigating crop-processing activities, particularly where macrobotanical remains or specific plant parts are poorly preserved [63].

4.3.3 Southwest Asia (Mesopotamia)—Crop Dispersal and Integration of Broomcorn Millet (*Panicum miliaceum* L.)

At Khani Masi (northeastern Mesopotamia) (Fig. 2), morphometric analysis of inflorescence phytoliths enabled secure identification of broomcorn millet using multiple diagnostic criteria, distinguishing it from wild panicoid grasses, showing that phytolith morphometrics are a reliable tool for species-level identification in contexts where macrobotanical remains are limited or ambiguous [20,64].

Broomcorn millet (*Panicum miliaceum* L.) was domesticated in northern China, with archaeobotanical evidence indicating a domestication process likely occurring between 7000 and 3300 BC, potentially preceded by a prolonged period of harvesting and small-scale management [65]. Following its domestication, the crop dispersed westward across Eurasia and was eventually introduced into Southwest Asia [64,65]. Broomcorn millet phytoliths from Khani Masi provide the earliest secure microbotanical evidence for this crop in Mesopotamia during the second millennium BCE [64]. The assemblages indicate irrigated summer cultivation and seasonal multi-cropping, pointing to earlier-than-expected agricultural diversification and the introduction of summer cereals in Bronze Age Mesopotamia, and highlighting the value of phytolith analysis for reconstructing crop dispersal and irrigation-based farming systems in Southwest Asia [64].

4.3.4 Mesoamerica—Maize (*Zea mays* L.)

Analyses from Mesoamerican archaeological contexts show that silica bodies preserved in plant tissues can reliably identify domesticated maize (*Zea mays* L.) and distinguish it from wild teosinte, overcoming the limitations of pollen analysis where strong morphological overlap prevents secure separation [19,66,67].

Unlike pollen, which cannot consistently differentiate wild and cultivated *Zea*, phytoliths from maize cob glumes, cupules, and leaves produce diagnostic morphotypes that allow secure identification of domestication and processing [66,67]. At sites such as Xihuatoxtla in the Balsas region (Fig. 2), these maize-specific phytoliths occur in direct association with stone tool residues and stratified sediments, while diagnostic teosinte phytoliths are absent, indicating cultivation and processing of domesticated maize during early Holocene occupations [67].

Phytolith evidence from Mesoamerican archaeological sites provides important evidence for the presence and processing of domesticated maize during the early Holocene. Diagnostic phytolith morphotypes can help distinguish maize from wild teosinte, particularly where other botanical remains provide limited taxonomic resolution [66,67]. The occurrence of maize-type phytoliths in stratified sediments and tool residues, together with the absence of diagnostic teosinte phytoliths, supports the early cultivation and processing of maize [66,67]. In such contexts, phytolith analysis can provide a valuable complementary line of evidence for investigating maize domestication and early agricultural practices.

4.3.5 South America—Squash (*Cucurbita* spp.)

Phytoliths from *Cucurbita* are diagnostic scalloped silica bodies formed in the fruit rind and genetically linked to rind lignification, present in both wild and domesticated forms but varying in size and morphology under human selection [16,17]. Because they preserve well in tropical contexts (Fig. 2), they allow identification and tracking of *Cucurbita* even without macroremains, as shown in Ecuadorian archaeological sequences spanning late Pleistocene to early Holocene deposits [16,17].

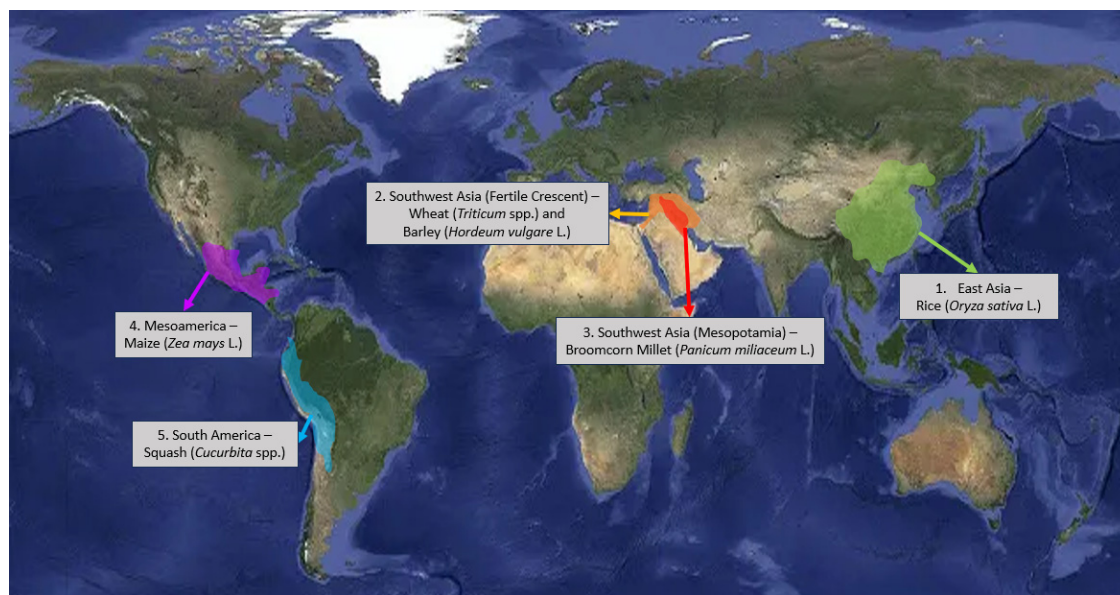


Figure 2: World's major centers of plant domestication (Original by Alexandru C.).

Evidence indicates early use of wild *Cucurbita* followed by phytolith size increase consistent with domestication in coastal South America, marking an early shift toward cultivation and possible independent agricultural development, with morphological changes reflecting selective pressures targeting reduced rind lignification, thereby establishing phytolith morphometrics as a diagnostic proxy for early management in organic-poor depositional environments [16,17].

Taken together, these findings show that phytoliths do more than identify centers of plant domestication. They document the ecological and cultural processes that accompanied the spread of agriculture, helping to reconstruct changes in vegetation, cultivation practices and landscape management across both space and time [5,6].

When considered together with archaeological and environmental evidence, these changes provide a record of how human practices progressively altered plant communities and landscapes, while creating new ecological settings in which cultivated plants were selected, managed, and dispersed. Phytolith evidence can therefore contribute to understanding domestication as part of a longer process of human–environment interaction rather than simply marking the appearance of domesticated taxa.

4.4 Strengths and Limitations of Phytolith Evidence in Domestication Studies

Phytolith analysis has become an essential component of archaeobotanical research on plant domestication, yet its interpretation requires an awareness of both the strengths and the limitations of the evidence it provides. Like any archaeobotanical proxy, phytoliths capture only part of the complex sequence of ecological, evolutionary and cultural processes that accompanied the emergence of agriculture [5,6].

One of the greatest strengths of phytoliths lies in their exceptional preservation. Because silica bodies frequently survive where seeds, pollen and other botanical remains have deteriorated, they extend the archaeobotanical record across regions and time periods in which organic preservation is limited, particularly in tropical and semi-arid environments [5].

Progress in phytolith morphology, together with the continuous expansion of modern reference collections, has considerably improved the taxonomic resolution of phytolith analysis. These developments have increased confidence in the identification of cultivated taxa and strengthened the reconstruction of early agricultural systems [5,10].

At the same time, several challenges continue to influence the interpretation of phytolith assemblages. A major limitation is phytolith redundancy and multiplicity: similar morphotypes may be produced by several plant taxa (redundancy), while a single taxon may produce multiple morphotypes (multiplicity). These patterns can reduce taxonomic specificity and lead to ambiguous identifications when individual phytolith forms are considered in isolation. Reliable interpretation therefore depends on well-developed reference collections, standardized nomenclature, assemblage-based approaches and careful contextual analysis [5,10,68].

Taphonomic processes add a further level of complexity. Phytolith production, deposition, preservation and post-depositional movement can all influence the composition of archaeological assemblages. Differential dissolution is particularly important, as some phytolith morphotypes may be preferentially dissolved or altered under unfavorable soil conditions, including alkaline environments, thereby modifying the original assemblage composition. These preservation biases make it essential to consider soil chemistry and site formation processes before drawing archaeobotanical or paleoecological conclusions [5,6,69].

Heat exposure represents another factor that can affect phytolith preservation in archaeological contexts. Experimental studies on common and foxtail millet have shown that prolonged heating can alter the morphology of diagnostic husk phytoliths, with different levels of damage observed between the two crops. Such changes may affect their identification and quantification and can lead to an underrepresentation of particular taxa in archaeological assemblages. These effects should therefore be considered when interpreting phytoliths recovered from hearths, burned deposits, or other contexts exposed to high temperatures [70].

For this reason, phytolith analysis is increasingly integrated with other archaeobotanical and geoarchaeological evidence. Combining phytoliths with pollen, starch grains, plant macroremains, charcoal, sedimentological analyses and micromorphology provides a more reliable basis for reconstructing domestication, agricultural practices and environmental change than any single line of evidence alone [3,6,7].

Recent international initiatives have also emphasized the importance of methodological transparency, standardized analytical procedures and open-access reference datasets. The implementation of ICPN 2.0 together with the adoption of FAIR data principles is expected to improve reproducibility, facilitate international collaboration and support large-scale comparative studies of plant domestication [8,10,12].

Taken together, these developments highlight that the future of phytolith research depends not only on methodological innovation but also on the integration of complementary sources of evidence. Within this interdisciplinary framework, phytoliths provide a powerful record of the interactions among plants, environments and human societies, offering new opportunities to investigate the evolutionary and ecological processes that accompanied the emergence and spread of agriculture [5,6,8].

5 Human–Environment Interactions Shaping Plant Domestication and Evolution

5.1 Human Landscape Modification: Evidence from Phytolith Records

For thousands of years, human societies have reshaped natural environments through cultivation, vegetation clearance, water management and the use of plant resources. These activities transformed landscapes in ways that created new ecological conditions, influencing not only the distribution of plant communities but also the evolutionary pathways of many species [1,2].

As environments changed under continuous human influence, plant populations were exposed to new selective pressures. The evolution of many wild and managed species was therefore shaped not only by climate and other natural factors but also by the cumulative ecological effects of human activities carried out over successive generations [1].

Within evolutionary ecology, humans are increasingly viewed as ecosystem engineers because they actively modify the physical and biological characteristics of the environments they inhabit. Through these modifications, they alter resource availability, species composition and ecological interactions, creating environmental legacies that persist long after the original activities have ceased [1].

This perspective differs from traditional evolutionary models, which largely emphasized adaptation to pre-existing environments. Niche Construction Theory instead highlights the reciprocal relationship between organisms and their surroundings, recognizing that humans continuously reshape the environments in which natural selection operates while simultaneously responding to the ecological conditions they create [1,2].

Viewing humans as ecosystem engineers also provides an important framework for interpreting archaeobotanical evidence. Phytolith assemblages can reflect vegetation changes associated with cultivation and landscape management, providing evidence of the ecological effects of past human activities. Recent field-based research has shown that phytolith assemblages can distinguish managed landscapes, abandoned cultivation areas, and relatively undisturbed forests, highlighting their potential for tracing human-induced vegetation change and subsequent ecological recovery [15].

5.2 Niche Construction and Reciprocal Evolution

Niche Construction Theory provides a useful framework for understanding plant domestication as a reciprocal process in which organisms modify their environments and, in doing so, alter the selective conditions experienced by themselves and other species [1]. Humans became particularly influential niche-constructors through practices such as vegetation clearance, controlled burning, cultivation, irrigation and resource management. When maintained over generations, these modifications created persistent anthropogenic environments and forms of ecological inheritance that influenced both plant populations and subsequent human practices [1,2]. Domestication can therefore be viewed as a long-term interaction among cultural practices, environmental modification, and plant responses rather than as the outcome of human selection alone [1,2].

Phytolith records offer a way to examine some of these interactions over archaeological timescales. Repeated cultivation, vegetation clearance, burning, irrigation, and other forms of landscape management can alter the composition and distribution of plant communities, producing changes that may be reflected in phytolith assemblages [15,71]. Shifts in the abundance of crop-related phytoliths may also document the introduction, persistence, or increasing importance of cultivated plants within these modified landscapes [5]. When such changes occur alongside evidence of disturbance, altered vegetation structure, or changing

water conditions, they can contribute to reconstructing how human activities progressively reshaped local environments.

These patterns should not be interpreted as direct evidence of niche construction in isolation. Their significance lies in their integration with archaeological context and other environmental evidence, which can reveal whether changes in plant communities coincided with sustained human activities [71]. In this way, phytoliths can help connect ecological change with human practices and provide a long-term perspective on the reciprocal relationships among landscape modification, plant use, and the development of agricultural systems.

5.3 Human-Induced Environmental Change and Plant Responses

For millennia, human societies have continuously reshaped landscapes through cultivation, vegetation clearance, controlled burning and the management of water and soil resources. These activities transformed natural habitats and created new ecological conditions that differed markedly from the surrounding environments, influencing both vegetation structure and ecosystem functioning [1,3].

As landscapes changed, plant communities also changed. Human-driven modifications altered species composition, ecological interactions and the availability of resources, leading plant populations to adjust their distribution, abundance and adaptive strategies. Over time, these processes produced vegetation assemblages that differed substantially from those maintained under natural ecological conditions [2,3].

Phytolith assemblages can preserve evidence of long-term environmental transformations associated with human land use. Variations in phytolith abundance and morphotype composition can distinguish cultivated and previously managed landscapes from relatively undisturbed vegetation, providing a means of tracing human-induced vegetation change and subsequent ecological recovery [15]. Multi-proxy archaeobotanical studies also show that long-term plant management can be detected beyond the simple presence of domesticated crops. At Monte Castelo in southwestern Amazonia, the combined analysis of phytoliths, starch grains, and carbonized plant remains revealed persistent and diversified plant-management practices associated with long-term landscape use [72]. Such evidence illustrates how phytoliths, when integrated with complementary proxies, can contribute to reconstructing the relationships among plant management, environmental change, and cultural niche construction. Human landscape management can also affect vegetation structure, disturbance regimes, and water availability, leaving signals that may be detected in phytolith records. Experimental studies have shown, for example, that phytolith production in cereals responds to different water regimes, providing a potential proxy for past water availability and agricultural water management [14]. Other studies have demonstrated that phytolith assemblages can reflect vegetation and disturbance changes associated with human land use [15]. Together, these records provide complementary evidence for investigating how human activities progressively modified the ecological settings in which plant management and agriculture developed. Specific phytolith morphotypes can provide more direct evidence for investigating human modification of plant-growing environments. Experimental studies on wheat and barley have demonstrated that the relative abundance of water-sensitive and fixed phytolith forms varies under different water regimes, providing a proxy for past water availability and potentially for agricultural water management [14]. Archaeological applications to early rice cultivation have similarly used changes in phytolith assemblages, including water-sensitive forms and rice bulliform phytoliths, to investigate shifts from cultivation under largely natural water availability toward more controlled wetland management [73]. Such indicators should not be interpreted as direct evidence of irrigation in isolation, but rather alongside archaeological and paleoenvironmental evidence.

Viewed from this perspective, phytolith assemblages record much more than the presence of cultivated plants. They preserve evidence of the ecological processes through which human activities reshaped landscapes, modified selective environments and influenced vegetation over time. This broader interpretation highlights the value of phytoliths as archives of long-term human–environment interactions and their role in understanding the coevolution of plants, environments and human societies [3,5,8].

5.4 Phytoliths and the Coevolution of Humans, Plants and Environments

The relationship between humans, plants, and environments is characterized by long-term reciprocal interactions involving plant management, environmental modification, and ecological responses. Within this context, phytolith assemblages provide a durable record that can contribute to tracing changes in vegetation, cultivated plant presence, and land-use practices through time. Rather than documenting these processes independently, phytolith evidence becomes particularly informative when interpreted within its archaeological context and alongside complementary environmental proxies [1,2,5].

The value of phytoliths within a coevolutionary framework lies in their potential to connect evidence of plant use and cultivation with broader changes in vegetation and landscape management. Archaeological studies have shown that phytolith assemblages can contribute to distinguishing managed from less-disturbed environments and to reconstructing long-term changes associated with human land use [15]. Other applications have explicitly incorporated phytolith evidence within niche-construction approaches to investigate changing relationships among human communities, vegetation, and resource management [71]. Importantly, changes in phytolith assemblages should not be interpreted as direct evidence of niche construction or plant evolutionary change in isolation. Similar assemblage changes may result from climatic variation, natural disturbance, taphonomic processes, or human activities. A niche-construction interpretation therefore requires independent archaeological and environmental evidence linking vegetation change to specific human practices. In this context, phytoliths are most informative as one component of a multi-proxy approach rather than as a stand-alone indicator of human-driven evolutionary processes [1,2].

For this reason, integrating phytolith analysis with other archaeobotanical and environmental proxies is essential for evaluating long-term human–plant interactions. Pollen, charcoal, starch grains, plant macroremains, sedimentological evidence, and archaeological features can provide complementary information needed to distinguish climatic and ecological change from human-driven landscape modification [3,7,8].

Viewed in this way, phytoliths are more than taxonomic indicators of past plant presence. Their broader contribution lies in providing evidence that can connect changes in plant communities, cultivation, crop dispersal, and landscape management across long timescales. When interpreted within a niche-construction framework and supported by complementary archaeological and environmental evidence, phytolith records can therefore contribute to reconstructing how human activities and plant communities influenced one another during the development of agricultural landscapes [1,2,5,8].

6 Future Research Perspectives and Conclusions

Phytolith research has considerable potential to provide a more detailed understanding of past human–plant relationships, but several questions still need closer attention. One important direction is to better establish how particular phytolith signals relate to specific agricultural practices. Experimental studies, together with well-documented archaeological case studies, are especially needed to assess indicators of cultivation, water management, crop processing and other forms of landscape modification.

At the same time, phytolith evidence needs to be interpreted with greater attention to archaeological context and preservation. Problems such as taxonomic redundancy and multiplicity, dissolution and other

taphonomic processes can influence the composition of phytolith assemblages and, consequently, their interpretation. Combining phytoliths with plant macroremains, pollen, starch grains, charcoal, sedimentological evidence and other proxies remains important for distinguishing changes related to human activity from those resulting from environmental or post-depositional processes.

Future work would also benefit from broader reference collections, greater methodological consistency and more accessible datasets. Quantitative approaches and automated identification methods offer promising possibilities, but their usefulness will depend on the quality and comparability of the data on which they are based. Ultimately, phytoliths are most valuable not as isolated indicators, but as part of a wider body of evidence for tracing how plant use, agricultural practices and environments changed through time. This is also where phytolith research can make a meaningful contribution to discussions of plant domestication and human niche construction.

Acknowledgement: Not applicable.

Funding Statement: The authors received no specific funding for this study.

Author Contributions: The authors confirm contribution to the paper as follows: Conceptualization, Mădălina A. Borcă, Andreea D. Ona; methodology, Ioana V. Berindean, Leon Muntean; investigation, Alexandru D. Costin, Mihai C. Popa; data curation, Alexandru D. Costin; writing—original draft preparation, Mădălina A. Borcă, Andreea D. Ona, Alexandru D. Costin; writing—review and editing, Ioana V. Berindean, Mihai C. Popa, Leon Muntean; visualization, Mădălina A. Borcă, Andreea D. Ona, Alexandru D. Costin; supervision, Ioana V. Berindean, Mihai C. Popa, Leon Muntean; project administration, Andreea D. Ona. All authors reviewed and approved the final version of the manuscript.

Availability of Data and Materials: Not applicable.

Ethics Approval: Not applicable.

Conflicts of Interest: Given his/her role as Guest Editor/Editorial Board Members of this journal, Andreea D. Ona, Ioana V. Berindean and Leon Muntean had no involvement in the peer review of this article and had no access to information regarding its peer review. Full responsibility for the editorial process for this article was delegated to another journal editor. The authors declare no other conflicts of interest.

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