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Review / Revisión

Understanding perspectives of current palynology: using science with practical discourse

Comprensión de las perspectivas en la palinología actual: utilizando la ciencia con un discurso práctico

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Abstract
Background: Palynological studies have contributed with topics closely linked to sustainability. However, there are still few scientific reviews that have discussed the relevance of practical applications in current palynology and its perspectives as a theoretical framework for the study of integrated landscape management. This review shows palynological contributions within agricultural model diversities in both natural and novel ecosystems.
Questions: What are the current perspectives and concerns of the mature phase in palynology? What are the approaches of pollen analysis on landscape management and biodiversity conservation?
Studied species: Pollen analysis and palynomorphs.
Study site and dates: Global literature from current palynology.
Methods: Global scientific literature using keywords, theoretical frameworks, and original articles.
Results: We identified palynological perspectives for the study of sustainability based on global scientific literature: 1) ecological-evolutionary and 2) interdisciplinary research. In addition, we discussed some synergies and trade-offs between ecosystem services that were recognized through current palynology in different farming landscapes: biodiversity-based farming systems and chemical input-based farming systems. While pollen morphology and descriptive palynology can provide the basis for crop improvement, biological invasions, and the effect of deforestation on native species, more analytical approaches such as land-use indicators are necessary for sustainable management. In addition, we have included some biocultural aspects to conservation, due to a lack of practical discourse in current palynology.
Conclusions: Innovative influences from current palynology are powerful approaches to integrated landscape management.
Keywords: biodiversity conservation, descriptive palynology, pollen analysis.

Resumen
Antecedentes: Los estudios palinológicos han contribuído con temas relacionados a la sostenibilidad. Sin embargo, existen pocas revisiones científicas que discutan la relevancia de dichas aplicaciones y sus perspectivas como marco teórico para la gestión integrada del paisaje. En la presente revisión, se muestran algunas contribuciones palinológicas en modelos agrícolas, tanto de ecosistemas naturales como novedosos.
Preguntas: ¿Cuáles son las perspectivas y preocupaciones actuales de la fase madura palinológica? ¿Cuáles son los enfoques del análisis polínico en el manejo del paisaje y la conservación biológica?
Especies de estudio: Análisis polínico y palinomorfos.
Sitio y años de estudio: Literatura global y actualizada.
Métodos: Literatura científica utilizando palabras clave, marcos teóricos y artículos científicos originales.
Resultados: Identificamos dos perspectivas palinológicas para el estudio de la sostenibilidad: 1) una ecológica-evolutiva y 2) la investigación interdisciplinaria. Además, discutimos algunas sinergias y compromisos entre servicios ecosistémicos, a través de la palinología en diversos paisajes: sistemas agrícolas basados en la biodiversidad y en insumos químicos. Si bien la palinología descriptiva y la morfología polínica pueden proveer la base para el mejoramiento de los cultivos, las invasiones biológicas y el efecto de la deforestación sobre especies nativas, los enfoques analíticos con indicadores de uso de suelo son necesarios para una gestión sostenible. Además, incluimos algunos aspectos bioculturales para la conservación, debido a la falta de un discurso práctico y palinológico.
Conclusiones: Las influencias innovadoras de la palinología son un enfoque poderoso en la gestión integrada del paisaje.
Palabras clave: análisis polínico, conservación biológica, palinología descriptiva.

Lennart von Post, Gustaf Lagerhaim, and Gunnar Erdtman have influenced the development of palynology since 1916. They also contributed to the birth of the discipline by resolving the tension created by the geology-botany dichotomy (pollen analysis and systematics) (Birks & Berglund 2018, Edwards 2018). Whereas some palynologists continued as pollen analysts (palaeoecology), Erdtman moved in 1931 to pollen morphology and systematics (Birks & Berglund 2018). This fact allowed for the emergence of taxonomic approaches in areas related to ecology (pollination systems) and evolution (pollen wall development) (Blackmore *et al*. 2007, Halbritter *et al*. 2018). In this context, historical aspects have led to the formation of an evolutionary and ecological approach, while palaeoecology has switched to an interdisciplinary perspective.

In the beginning, Erdtman's acetolysis technique was the most popular geological procedure for extracting palynomorphs (pollen and spores) from sediments and sedimentary rocks. In the paleontological context, paleopalynology did the groundwork for an understanding of Earth's geological history, according to the evolution of fossil palynomorphs covered by sporopollenin and chitin as the result of geological and taxonomic approaches (Traverse 2007). Furthermore, in the second half of the twentieth century, scanning and transmission electron microscopy unraveled a biological process known as microsporogenesis and its implications for pollen wall development, especially in embryophytes (Pacini 1990). After decades of research, the scientific community regards palynology as the discipline that encompasses the study of pollen grains from gymnosperms and flowering plants, in addition to spores from mosses, liverworts, ferns, lycophytes, streptophyte algae, and fungi from an evolutionary ecological perspective (Dafni & Firmage 2000, Stephen 2014).

In the last 25 years, quaternary palaeoecologists and pre-quaternary palaeobiologists have urged conservationists to consider palaeoecological studies in their management plans to include a historical perspective on diversity changes, ecosystems dynamics, and biotic responses to environmental change (Birks 2019). According to Birks (2019), this conceptual framework has emerged in the last 30 years under specific approaches such as ecosystem services, ecosystem functions, and even the study of socio-ecological systems from an interdisciplinary perspective. Mace (2014) elegantly shows this in her scientific paper titled: Whose conservation? changing views of nature and conservation over the past 50 years. The article highlights the importance, for example, of a change in emphasis from species to ecosystems, also known as "people and nature" (Mace 2014). As claimed by Mace (2014), this "people and nature" thinking stresses the importance of cultural structures and institutions for developing sustainable and resilient interactions between human societies and the natural environment.

Although palaeoecology has widely been applied to solve current concerns of palynology, some limitations remain in explaining past vegetation dynamics. For example, a) plants produce different amounts of pollen (differential production), b) plants produce entomophilous pollen (it is always underrepresented) and anemophilous pollen grains in large quantities (differential dispersal), c) pollen wall can be degraded by both physical and chemical attack (differential preservation and anaerobic conditions), and d) in some cases there are morphological differences of pollen production on the same plant (Bennet & Willis 2001, Mourelle *et al*. 2016). For these reasons, the inclusion of pollen morphology deals with methodological issues not achieved only by the palaeoecological approach. Furthermore, current studies have recognized that certain morphological variations among tree populations can be a barrier to calculating biomass over time (Seppä *et al*. 2009). Thus, palynological perspectives and geological methods have been linked for those research purposes (Martínez-Hernández *et al*. 1980).

A scientific paper published in 2011 by Vegas-Vilarrúbia *et al*. (2011) showed that Quaternary palaeoecology and nature conservation had been strongly related through some organisms such as The International Geosphere-Biosphere Program (IGBP) to understand the Earth's environmental past to make predictions for the future under scenarios of global change. Vegas-Vilarrúbia and collaborators (2011) also recognized the frontier research of some palynologists, particularly John Birks and Katherine J. Willis. They have made significant contributions to the utility of palaeoecology to conservation (Birks 1996, Willis *et al*. 2007). Some of these works have included the role of palaeoecology in assessing ecosystem processes and services (Jeffers *et al*. 2015), ecological restoration (Jackson & Hobbs 2009), resilience and synergistic effects between native forests and agriculture (Bhagwat *et al*. 2012) as well as current and historical perspectives on socio-ecological systems (Hanley *et al*. 2008, Davies 2011).

Some aspects recognized by palaeoecology to conservation are: 1) land cover change represents one of the significant threats to global biodiversity (Hanley *et al*. 2008, Mensing *et al*. 2018), *2*) the ecosystem processes such as biomass, soil formation, and nutrient cycling are critical for managing ecosystems through palynological and geochemical data (Jeffers *et al*. 2015), 3) positive and negative cultural legacies are crucial to developing effective management as well as restoration (Davies 2011), and 4) resilience depends on natural and cultural disturbances (soil erosion, fire, the variation in monsoon rainfall, and taxonomic richness) because they can determine some positive effects on ecosystems (Bhagwat *et al*. 2012, Nogué *et al*. 2018, Adolf *et al*. 2020). Thus, the interaction of palaeoecology, palynology, and ecology can be relevant in topics such as soil quality in sustainable development for adaptive land use and management, especially in long-term approaches where uncertainty is the main obstacle to sustainability as far as actor and stakeholder involvement is concerned (Bünemann *et al*. 2018).

Our manuscript represents a review of current palynology inside the limits of the mature phase (Birks & Berglund 2018). During 100 years of palynological research, paradigm shifts have occurred much more frequently, such as some innovative aspects within descriptive and analytical approaches (Birks & Berglund 2018). Consequently, palynology has involved ideas for use in hypothesis-testing and meta-analyses around environmental science and cultural history (Edwards 2018), with such topics as climate change, archaeology, ecosystem-level models, conservation biology, and landscape management (Birks & Berglund 2018, Edwards 2018). Edwards (2018) recognized that palynology and incremental science development could inform current concerns and provide the necessary data for use in present-day studies and modeling activities. This approach is being adopted in some regions of Mesoamerica (Caballero *et al*. 2006, Lozano-García *et al*. 2007, Domínguez-Vázquez & Islebe 2008, Figueroa-Rangel *et al*. 2008, Correa-Metrio *et al*. 2014, Islebe *et al*. 2018, Ramírez-Arriaga *et al*. 2018). For these reasons, our framework shows the involvement of palynology in sustainable development. It stresses the term "using science with practical discourse" to suggest multiple expressions between theory and practice in urgent topics from current palynology.

This manuscript draws innovative and significant information from some analytical, morphological, and descriptive approaches to palynology in practical applications and discusses promising opportunities for future research. Here, we will only summarize each perspective considering food security because it may include an interplay between ecosystem functioning and human well-being through current palynology. Thus, our objectives were to 1) delimit current palynological perspectives and applications to preserve agrobiodiversity and native species, and 2) evaluate whether palynology is crucial to understanding synergies and trade-offs with ecosystem services enhancing landscape management as a framework for sustainable development.

Materials and methods

To understand the perspectives and concerns of current palynology, we identified peer-reviewed scientific papers from two theoretical principles in Quaternary botany: a) species respond in an individualistic way to environmental changes (Gleasonian aspects), and b) pollen assemblages to explain stochastic processes such as disturbance and historical legacies (Clementsian ideas) (Vegas-Vilarrúbia *et al*. 2011, Birks 2019).

In this context, pollen assemblages refer to a landscape mosaic of different communities or vegetation types (Birks 2019). As mentioned by Jackson & Blois (2015), a spatial mosaic of communities is determined by random processes such as seed dispersal or patch dynamics in the composition of Holocene forest communities rather than environment assembly (physiological and demographic responses to the physical environment) as the only possible explanation. This idea has brought with it that the concept of "community" in Quaternary palaeoecology must consider aspects such as pollen production, dispersal, and taphonomy to avoid mismatches between data and applications (Kidwell & Flessa 1995, Jackson & Blois 2015). Although the Gleasonian approach has mostly considered climatic factors (at the species level) rather than historical contingencies and cross-scale interactions (at a community level), both perspectives have shared ideas. However, it was ignored mainly among pioneers of Quaternary botany (Birks 2019).

We revised scientific literature and consulted the Web of Science and Scopus databases (Zhu & Liu 2020) to recognize some innovative applications. We searched with the keyword filters: pollen viability/quality, palynological techniques, cryopreservation, melissopalynology, historical ecology, ecosystems services, and food security or agrobiodiversity that should be featured in topics and titles methods, keywords, and abstracts during the last 30 years at least. This period coincided with soil quality definitions, including biological productivity, environmental quality, and plant, animal, and human health, whereas definitions before 1990 only considered productivity and suitability for crop growth (Bünemann *et al*. 2018). In addition, the scientific manuscripts need to accomplish some requirements, such as rural development projects, biological corridors, adaptive management, multifunctional landscapes, and forest restoration.

Results

We obtained palynological perspectives from the scientific literature review done: evolutionary-ecological and interdisciplinary research (Table 1). We delimited the first perspective with practical and exclusive applications of botany in globalized agriculture systems, such as the cryopreservation of pollen grains for the balance of "*ex situ*" and "*in situ*" conservation, pollinator monitoring, and the role of fossil pollen databases for "*inter situ*" restoration. We observed that most of these scientific papers had been applied within taxonomic categories like genus, species, or populations (e.g., code/accession, germplasm, population genetics, population ecology, landrace, cytological experiments). Therefore, we have also considered the above applications as part of the ecological and evolutionary perspective.

Some palynological applications have incorporated studies such as agrobiodiversity conservation and preservation of native species in the Anthropocene into ecological and evolutionary perspectives (Mourelle *et al*. 2016, Silva *et al*. 2018). This research has shown that biodiversity conservation can provide ecosystem services to agriculture. At the same time, integrated management encompasses the nexus of food, non-food, and natural resources to develop local and regional sustainable agriculture (Therond *et al*. 2017, Zimmerer *et al*. 2019). The relevance of this evolutionary and ecological perspective is mainly focused on the transition from global to sustainable agricultural systems, including plant breeding programs and the cooperation between companies and government institutions (Padureanu & Patras 2018, Silva *et al*. 2018). On the other hand, avian palynology studies suggest that commercial and garden flowering trees are an essential resource for migrating warblers based on foraging preferences by palynological techniques (Wood *et al*. 2014). Similar studies emphasize the importance of pollinators in the conservation of native forests for multiple ecosystem services such as crops (Borgella *et al*. 2001, Matias *et al*. 2019). In other words, current palynology has embraced approaches from species to communities (Vegas-Vilarrúbia *et al*. 2011, Birks 2019).

Moreover, we found that specific palynological studies included socio-ecological approaches and historical ecology studies for sustainability. 1) The conservation of agrobiodiversity using melissopalynology and its relevance to the alternative food systems in Palawan, Philippines (Matias *et al*. 2019), 2) the legacy of agroforestry of Western Ghats, India (Nogué *et al*. 2018), and 3) the landscape transformation of central Italy during the Roman period based on archaeological evidence and its biogeographical implications (Figure 1) (Mensing *et al*. 2018). Therefore, from an interdisciplinary perspective, we mentioned that those palynological scientific papers had interconnected with other disciplines (*e.g*., geochemistry, paleoclimatology, biogeography, archaeology, socio-ecological research).

In this context, novel landscapes, including native and non-native ecosystems, have had an essential role in biodiversity conservation. According to the Food and Agriculture Organization of the United Nations (FAO) and the World Food Summit (FAO 1996), food security, which can be identified as the availability and access of food, dietary needs, and stability as a synonym of sustainability, has experienced four-dimensional evolution over the last three decades. Food security has evolved by the inclusion of some international programs such as The Millennium Ecosystem Assessment (2005). This framework underpins food demand and availability in response to biodiversity loss, land cover change, and future climate scenarios (Jeffers *et al*. 2015). In this sense, food systems have emerged to underscore the importance of sustainable agriculture to climate change because this relationship facilitates actions in favor of integrated landscape management (Scherr *et al*. 2012). The components of agricultural landscape management may include protecting natural areas, restoring hydrographic basins, climate-friendly livestock systems,

Table 1. Palynological perspectives based on the Web of Science and Scopus.

Urgent Topics	**Evolutionary and ecological perspective (Pollen morphology and descriptive palynology)**			
	Conservation & Restoration	**Deforestation**	**Crops**	**Biological invasions**
Borgella *et al*. 2001	✸	✸		
Burney & Piggot 2007	✸	✸		
Ferrauto *et al*. 2015	✸			
Froyd & Willis 2008	✸			✸
van Leeuwen *et al*. 2008	✸			✸
Mourelle *et al*. 2016	✸	✸		
Padureanu & Patras 2018	✸		✸	
Rodríguez-Riaño *et al*. 1999	✸			
Silva *et al*. 2018	✸		✸	
Stewart & Dudash 2017	✸			
Syamsuardi *et al*. 2018	✸			✸
Wood *et al*. 2014	✸	✸	✸	
	Interdisciplinary research (Quaternary botany and melissopalynology)			
	Conservation & Restoration	**Ecosystems services (Biomass & soil formation)**	**Landscape ecology & climate change**	
Bhagwat *et al*. 2012	✸		✸	
Bush & Silman 2007	✸	✸	✸	
Davies 2011	✸		✸	
Divisek *et al*. 2020	✸		✸	
Jeffers *et al*. 2015	✸	✸		
Matias *et al*. 2019	✸		✸	
Mensing *et al*. 2018	✸		✸	
Nogué *et al*. 2018	✸	✸		
Ponnuchamy *et al*. 2014	✸		✸	
Ramírez-Arriaga *et al*. 2018	✸			
Seppä *et al*. 2009		✸		

and others (Scherr *et al*. 2012). Consequently, several authors have emphasized the importance of crucial landscape components on different scales to achieve social, economic, and ecological impacts for multi-stakeholder planning (Scherr *et al*. 2012, Therond *et al*. 2017, Zimmerer *et al*. 2019).

The essential palynological perspectives and applications come from different farming systems. They incorporate a wide variety of short- and long-term measurements, including palynological descriptions to decrease chemical inputs in monocultures, melissopalynological studies for landscape management using mobile-agent-based ecosystem services (MABES), and historical ecology approaches to identify agricultural landscapes that transform but maintain biodiversity, such as agroforestry techniques (Nogué *et al*. 2018, Padureanu & Patras 2018, Matias *et al*. 2019).

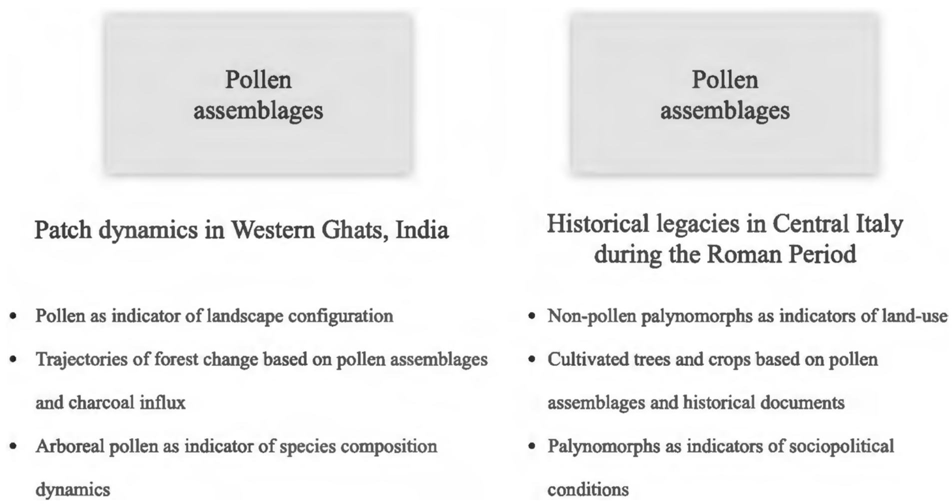

Figure 1. Historical legacies and patch dynamics by using pollen analysis.

These practical studies are frequently done in certain regions in Asia-Pacific, Europe, and North and South America, such as strategies for mitigation and adaptation to climate change.

We obtained examples of palynological applications in two models of agriculture: chemical input-based farming systems and biodiversity-based farming systems (Figure 2). We identified some benefits between ecosystem services in monocultures, such as germplasm programs for livestock and control of soil erosion. In addition, we also recognized trade-offs between ecosystem services (*e.g.*, the relevance of aquatic systems in the restoration of temperate forests) through indicators of soil quality using palynomorphs and historical ecology. These palynological applications are part of projects that may be important for transitions between agricultural systems for sustainable development as well as for the management of non-timber resources such as honey. On the other hand, as discussed below, we present the perspectives and development of palynology towards sustainability.

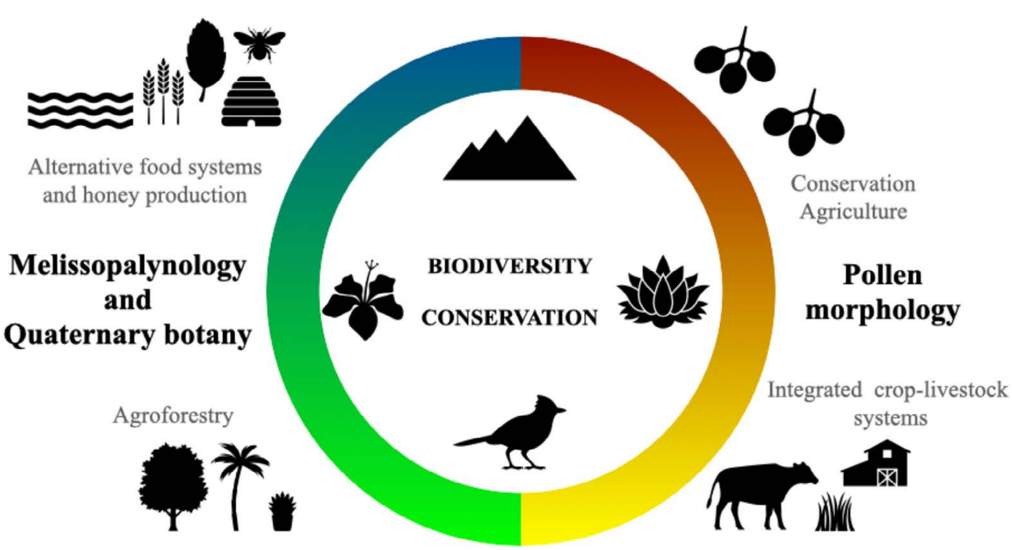

Figure 2. Palynological applications in current plant breeding (pollen morphology) and landscape management (melissopalynology and Quaternary botany).

Discussion

Palynology: an evolutionary and ecological perspective. Although the fundamental principles of pollination have probably existed since Assyrian times (the earliest Neolithic sites date from c. 9000 to c. 7000 years B.P.), the significant breakthroughs in the evolution and ontogeny of pollen grains began in the middle of the last century with innovations in SEM, TEM, and LM microscopy (Halbritter *et al*. 2018, Chen *et al*. 2019). Subsequently, a critical age of palynology began with describing the process of microsporogenesis through the *Tapetum* (Blackmore *et al*. 2007) and its relationship with the detection of germplasm resources in both natural habitats and agrobiodiversity systems (Souza *et al*. 2017, Silva *et al*. 2018).

The cytological and palynological characteristics that can be studied through the formation of the microspores are morphology, viability, and pollen production. The morphology of the pollen wall is essential, among other things, to correlate the type of ornamentation with reproductive strategies, as in some invasive plants (Syamsuardi *et al*. 2018). For instance, Kolczyk *et al*. (2015) demonstrated that some cytological features, such as the regular and proper course of meiosis and high viability of pollen grains, lead to the formation of aggressive weedy races that can colonize highly disturbed ecological habitats. In Quaternary botany, palynological records provide a reliable approach to determining the native or introduced status of a species in a particular region (Birks 2019). Such an approach has found that some doubtfully invasive species are, in fact, native to the Galapagos archipelago and possibly in other regions in the Pacific (van Leeuwen *et al*. 2008). This information would result in relevant strategies for conserving and restoring natural ecosystems related to biological invasions (Froyd & Willis 2008, Birks 2019).

Moreover, the comparative pollen morphology and seed germination studies in *Retama raetam* ssp. *gussonei* (Fabaceae) discriminate the relevance of palynology in practical conservation actions for dune stabilization and renaturation of desert areas (Ferrauto *et al*. 2015). Similar approaches can be applied in vulnerable endemic populations such as epiphytic angiosperms (Bromeliaceae), which are commonly threatened by loss of pollinators, poaching and habitat isolation (Palma-Silva *et al*. 2008). In fragmented ecosystems, Aizen & Feinsinger (1994) showed that there was a reduction in number of pollen tubes that are responsible for fertilization in some tree species due to geographic isolation. In contrast, Mourelle *et al*. (2016) found that two native South American *Butia* palms (Arecaceae) produce two pollen grain types, which has been considered a derivation. Despite habitat fragmentation, pollen viability was high enough to ensure pollination; therefore, viability is not the limiting factor for conservation of pollen grains, but intra-or inter-specific morphological differences in populations and habitat fragmentation should be considered to ensure effective pollination (Mourelle *et al*. 2016).

The palynological applications also provide economic and ecological value mainly in the Poaceae family due to their use as forage for animal feeding and erosion protection (Silva *et al*. 2018). The accessions comparisons among species of the genus *Cynodon* (Poaceae) are critical for elucidating some exine patterns, meiotic abnormalities, morphological apertures, and pollen viability from germplasm banks (Silva *et al*. 2018). Although the Erdtman acetolysis provides enough information on dispersal's ecological and evolutionary characteristics in many angiosperms, additional alternative techniques are recommended in fragile pollen grains (*e.g*., methods based on enzymatic treatments) to avoid changes in morphology (Silva *et al*. 2018). Furthermore, Padureanu & Patras (2018) performed a palynological characterization among hybrids in the genus *Vitis* (Vitaceae) to understand the relationships between morphology, germination potential, and pollen tube growth in the fertility of grapevines. In their study, they demonstrated that more homogeneous pollen size and tricolporate apertures positively affect the degree of fertility from pollen grains in different genotypes of vineyards. Recently, these investigations have been commonly applied in globalized agriculture systems to decrease external inputs (*e.g*., fertilizers or pesticides) and increase the adoption of integrated crop-livestock systems along with conservation agriculture towards sustainability (Therond *et al*. 2017).

Plant breeding programs may be necessary to complete climate change mitigation actions (Souza *et al*. 2017, Silva *et al*. 2018). De Haan *et al*. (2013) demonstrated the complementary nature of both "*in situ*" and "*ex situ*" conservation strategies from the Potato landrace cultivar collection in Peru. According to De Haan *et al*. (2013), the *ex situ* conservation will ensure the availability and use of unique genetic diversity, while *in situ* management will result in responsive evolution facilitating adaptation to changing environments. For these reasons, palynological applications of pollen grains take an essential role in germplasm banks, landrace, genotypes, and wild accessions for cryopreservation. Although both *in situ* and *ex situ* conservation are significant advances in ecology and evolution, Zimmerer *et al*. (2019) proposed more rigorous methodologies and innovative estimation techniques for monitoring agrobiodiversity, including stakeholder engagement. In practice, palaeoecological records provide information for such strategies by considering the ecological tolerance and ability to thrive in microrefugia for several plants (Vegas-Vilarrúbia *et al*. 2011).

Beyond the conservation of agrobiodiversity, alternative practices can be employed to restore natural habitats or abandoned agricultural lands using palynological tools. *Inter-situ* restoration, the establishment of species by their reintroduction to locations outside the current range but within the recent past range of the species, involves horticultural and agricultural techniques for the conservation of natural habitats (Burney & Piggot 2007). In fact, this type of restoration uses a list of fossil pollen that comes from adjacent sites to maintain the functions of the target ecosystem (Burney & Piggot 2007). For instance, Burney & Piggot (2007) documented the scope of *inter-situ* restoration of native palms because their seeds and pollen were abundant in pre-human sediments excavated from the Hawaiian Islands. Although the *ex situ* conservation of pollen diversity in botanical gardens (Sudarmono 2019), as well as the reintroduction of native species, may be important in the regeneration of natural habitats (Burney & Piggot 2007, Jackson & Hobbs 2009), certain aspects, such as the conservation of pollinators, can also be crucial. The research of Rodríguez-Riaño *et al*. (1999) demonstrated that germination of the pollen grains of some species from the Genisteae tribe occurs only after rupture of the stigmatic surface by tripping due to pollinator action during anthesis. Furthermore, this might be significant in the floral phenology of endemic plants because there is a more significant investment of resources in the perianth than in the reproductive structures, which is logical in flowers that must attract pollinators (Rodríguez-Riaño *et al*. 1999).

As plant-pollinator interaction will be relevant in conserving diverse landscapes, some palynological applications like pollen loads from mobile agents can play an essential role in fragmented ecosystems. For example, in Neotropical cloud forests, Borgella *et al*. (2001) showed that fragments as small as 10 to 20 ha represent valuable habitats for supporting hummingbird populations using pollen loads and species richness. In that study, specialized feeders were commonly found in larger fragments and native forests wherein the maintenance of plant species may be affected if such pollinators are no longer available (Borgella *et al*. 2001). For these reasons, similar studies are essential for the conservation of biological corridors and their contributions to other ecosystem services such as crops, pest control or habitat preservation (Ponnuchamy *et al*. 2014, Wood *et al*. 2014, Stewart & Dudash 2017).

Palynology: *an interdisciplinary perspective*. Recently, two novel approaches have linked palynology within interdisciplinarity: socioecology and historical ecology. The socio-ecological approaches can analyze ecological features of honey as a provisioning MABES through melissopalynology, i.e., the botanical origin and pollen content of honey (Matias *et al*. 2019). The method can be used for tracing floral phenology across years to understand the foraging preference of pollinators as spatio-temporal factors of interannual projects (Ponnuchamy *et al*. 2014). Honey production can also be involved in rural development projects based on an integrated landscape approach as part of circular economies in alternative food systems (Therond *et al*. 2017, Matias *et al*. 2019). For these reasons, in some developing countries, melissopalynology as an indicator of land-use intensification as well as the role of some institutions should be a priority for sustainability (Matias *et al*. 2019).

Historical ecology commonly applies palynological tools to understand agricultural legacies as part of environmental history based on paleoecological and archaeological approaches. Paleoecology primarily obtains pollen from sediments as indicators of management intensity, landscape configuration, vegetation cover changes, and plant functional groups (Johnson & Miyanishi 2008, Nogué *et al*. 2018). In contrast, archaeology explores palynomorphs to explain the relationships between climate change and cultural development using archival documents over the last 3,000 years (Szabó 2015, Mensing *et al*. 2018). Therefore, the following discussion provides the relevance of palynology by means of the socio-ecological and historical approaches.

Melissopalynology in agrobiodiversity conservation.- Ecological restoration is a type of subdiscipline that facilitates biodiversity conservation (Young 2000). Melissopalynology can be a powerful strategy in integrated conservation efforts in the interests of forest restoration while emphasizing the multiple ecosystem services (*e.g*., crop pollination, reproduction of wild plants) provided by honeybees (Kremen *et al*. 2007, Matias *et al*. 2019). In the Philippines, some indigenous communities have transformed the traditional non-timber forest product (NTFP) into community forestry enterprises for subsistence (Matias *et al*. 2019). For instance, Matias *et al*. (2019) demonstrated that including melissopalynology, household surveys, and key informant interviews sufficed to recognize the role of different national and international institutions for sustainability. Furthermore, they discussed the relevance of the landscape approach to accessing higher-value markets based on the organic characteristics of honey that may prompt the creation of management policies to maintain ecosystem services and functions (Matias *et al*. 2019). Research also examined the relationships between the foraging preferences of giant honeybees (*Apis dorsata*) and honey gathering as the social and ecological features of a system to detect fertilizers and chemical pesticides harmful to bees (Matias *et al*. 2019). Physicochemical and melissopalynological studies are complementary tests accepted by the Codex Alimentarius Commission and the International Honey Commission, among others, to assess the natural quality and honey botanical origin (Alfaro-Bates *et al*. 2010).

This approach is an example of alternative food system landscape management in a sustainable development framework as it increases the degree of ecosystem services and territorial embeddedness (Therond *et al*. 2017). In addition, the inclusion of some institutions, such as FAO and the World Health Organization (WHO), are usually indispensable to protect consumer health and promote fair practices in the food trade. In this context, biodiversity and ecosystem services can be adequately employed in terms of landscape management and restoration due to multilayered relationships (Mace *et al*. 2012). The apiculture, honey bees, and meliponiculture have ecological implications in some countries such as Argentina, Mexico, the United States, China, and Turkey. They are the biggest honey producers globally (Ramirez-Arriaga *et al*. 2016).

The legacy of agroforestry.- The palaeoecological approach encompasses two main factors in environmental history: land-use intensification and plant cover changes (Bürgi *et al*. 2017). Magnetic mineralogy of soils is a powerful tool to identify cultural practices such as “slash and burn”; commonly practiced in sites with high levels of deforestation (Evans & Heller 2003). In contrast, plant cover changes are usually studied by means of paleoenvironmental indicators such as pollen and other palynomorphs that are related to peopling and agriculture (Haas *et al*. 2013, Acosta *et al*. 2018, Nogué *et al*. 2018).

However, the research of Nogué *et al*. (2018) explored the relevancy of agroforestry as a practice that has contributed to the maintenance of tropical forests for the last 900 years (Figure 1). They used pollen as an indicator of past changes in vegetation and macroscopic charcoal as an indicator of biomass burning to identify the persistence of habitat-specialist trees over time. In that study, the results showed that sacred groves increased the forested habitat during the last 300 years, whereas agroforestry plantations displayed different trajectories between 800 and 50 cal. years B.P. Additionally, research suggests that some ecosystem services of provision and worship were sociocultural drivers in the persistence of native trees in Western Ghats, India (Nogué *et al*. 2018).

In some areas of North America, historical ecology has been applied as a tool for understanding long-term changes in agriculture, frequently in agroforestry systems well known as chinampas (González-Quintero & Sánchez-Sánchez 1991, Nichols 2015). In addition, palaeoecological studies in these wetlands are crucial to promoting conservation strategies because of their relevance to local and regional food systems in Mexico (Moreno-Calles *et al*. 2013).

Palynology in archaeology and cultural development.- The cultural development of agrarian societies is essential to the reconstruction of the environmental history of ecosystems in the archaeological context. Palynology is also crucial to studying cultural practices (extensive and intensive pastures, crops, and cultivated trees) which have had a decisive impact on current ecosystem services (Mazier *et al*. 2009, Boivin *et al*. 2016, Mensing *et al*. 2018). In fact, in some regions of southwestern Amazonia, archaeological research has shown the influence of anthropogenic activity on the creation of artificial forest islands in a seasonally flooded savanna: a human legacy of the Holocene (Lombardo *et al*. 2020).

Mensing *et al*. (2018) corroborated that by using essentially-palynological historical indicators at archaeological sites, it was possible to identify land-use changes due to sociopolitical and demographic transformations in Italy during the Roman Period. Although the research underlines the importance of some climatic indicators, such as the North Atlantic Oscillation and the Little Ice Age, Mensing *et al*. (2018) concluded that environmental change was more related to human activity than climate change. In the same research, Mensing *et al*. (2018) included documentation of non-pollen palynomorphs as indicators of sociopolitical decisions in landscape configuration during the last 2700 years, some of which were: 1) new priorities for wood and meat (*Glomus* and *Sporormiella*) as biological recorders of soil erosion and livestock during the medieval period; 2) the afforestation of oaks during the ascent of Charlemagne in the year 774 A.D.; 3) rural land management and agricultural intensification in the mid-9th century; 4) the medieval practice of coppicing and pollarding in trees between the year 1380 and 1400 A.D.; and 5) the creation of forest laws in the mid-18th century (Mensing *et al*. 2018).

Therefore, according to Mensing *et al*. (2018), restoration efforts must consider specific causes of environmental change to manage biodiversity in different localities. For instance, they found that humid conditions in mesic forests (e.g., *Alnus*, *Fagus*, *Carpinus*) were brought about by floodplain wetlands, and therefore restoration of forest ecosystems is not likely to be accomplished without the restoration of alluvial plains. These relationships could be explained by constructing a drainage system that eliminated all the floodplain forest circa 1750 AD and converted former wetlands into permanent agricultural fields with settlements in the Rieti Basin (Mensing *et al*. 2018). Additionally specific historical events were suggested as highly important to conservation, such as differences in coppicing rotation: medieval and mesolithic practices that facilitate the resprouting of many stems and more rapid forestation (Mensing *et al*. 2018). Furthermore, cultivated trees (e.g., chestnut, walnut, and olive) and wolf and bear populations' return were also identified as ecosystem services using palynological indicators and archival documents (Mensing *et al*. 2018).

At this time, coppicing in many woodlands can produce multiple ecosystem services like fuel and food, making it an essential tool for restoration and conservation management (Bunting *et al*. 2016). The role of these managed woodlands is then to develop synergies between food and energy production to enhance ecosystem services into integrated food-energy systems (Therond *et al*. 2017). Therefore, multi-service landscape management can provide opportunities to expand biodiversity-based farming systems in circular economies for sustainability (Therond *et al*. 2017).

Thus, historical ecology is included in the newly emerging discipline known as Agriculture Biogeography, which studies the origins and past geography of crops as well as considering long- and short-term aspects on large and small geographical scales (Katinas & Crisci 2018). Consequently, the palynological component in historical studies may be utilized as a methodological tool to create ecological spaces from the origin of agriculture to the present, thereby adding anthropogenic biomes into landscape approaches, according to Katinas & Crisci (2018).

Palaeoecology and archaeology play an essential role in some biogeographic patterns in temperate forests in Europe (Divisek *et al*. 2020). These predictive models underscore the importance of including fossil pollen as an indicator of past climate changes, human legacies, and biotic characteristics that affect temperate ecosystems' current richness and distribution. Divisek *et al*. (2020) showed that by combining environmental and historical data, it was possible to predict the species richness of habitat specialists by thematic maps throughout the Holocene. That study observed that historical factors always appeared among the best predictors of current species richness. They demonstrated that landscape history, anthropogenic disturbances, and temperature seasonality, among others, were important predictors for the current species richness of vascular plants in forests and grasslands of eastern Central Europe. Similar approaches have found modern pollen-vegetation relationships across a landscape mosaic in central Mexico (Castro-López *et al*. 2021). These pollen-vegetation ratio indices demonstrate local and human disturbances derived from the late Holocene and the last 500 years (Castro-López *et al*. 2021). In addition, indexes of diversity and dominance provide the representativeness of vegetation types in different landscapes (Chang-Martínez & Domínguez-Vázquez 2013, Castro-López *et al*. 2021).

Moreover, the relevance of palaeoecology was to recognize the interactions between different historical factors to understand the variation of biological and biogeographic richness over time. Some of these interactions could be explained by the formation of environmental gradients between forest-steppe and dry steppes in the Middle-Holocene, the expansion of agriculture in the Late Neolithic, and the suppression of organisms by climatic and ecological variations during the last 11,000 years (Divisek *et al*. 2020). Therefore, these studies have suggested the inclusion of historical factors in ecological modeling and the incorporation of more past climate changes, especially within the Holocene (Divisek *et al*. 2020).

Future directions for research. One of the significant challenges for palynologists is to create research and strategies for ecosystem management. Long-term approaches and interviews with key stakeholders can provide evidence to address uncertainties in restoration efforts (Davies 2011). Through paleoecology research, stakeholders can recognize the value of the past to balance the practical knowledge required for conservation and restoration goals; for example, whether some practices such as managed grazing or coppiced and pollard trees can enhance the regeneration of woodlands (Davies 2011). In the United Kingdom, these approaches have been implemented to increase the connectivity between woodlands fragments without neglecting natural and cultural factors. Davies (2011) showed periods of climatic and biotic adversity by using pollen assemblages to detect landowners' positive and negative management practices. Therefore, palaeoecological and palynological data can improve stakeholder expectations by recognizing historical legacies. This means that future directions for research must recognize different historical legacies of adaptive management (Davies 2011). Interdisciplinary approaches to paleoecology must incorporate quantitative contributions of microenvironmental variables, anthropogenic disturbances, and past climate changes as a strategy for adaptation to climate change.

Palynology and archaeobotany studies will have implications in developing countries, where social and ecological approaches play an essential role in conservation efforts. A clear example is a case of calling for the recognition of indigenous rights in Amazonia as a policy of ecosystem conservation (Franco-Moraes *et al*. 2019). These investigations have considered human management as an indicator of the maintenance of plant biomass and biodiversity composition that positively impact soil quality in ancestral forests (Franco-Moraes *et al*. 2019). Historical legacies of management practices are commonly studied by using oral histories, floristic inventories, ethnobotany, and edaphic variables, which can be implemented along with palynological experiments; however, pollen and other sources require special conditions for preservation (Franco-Moraes *et al*. 2019). Although it can be challenging to collect historical sources, the interdisciplinary perspective and landscape approach can make the goals of many projects feasible. For example, the forest with nutrient-poor soils (Franco-Moraes *et al*. 2019) as well as fertile soils, such as "*Terra preta del Indio"* (Bush & Silman 2007), can be a framework in neotropical regions with similar pluriethnic systems (Vegas-Vilarrúbia *et al*. 2011).

Finally, one challenge is generating predictive models, using paleoecology and biogeography to identify the percentages of current plant community distribution patterns, precisely because these measures contribute to the detection of synergistic effects between human impact and the environmental history of ecosystems. Therefore, modern pollen rain studies and paleoecology databases will be essential for applying diversity analysis and their implications for other experimental investigations into natural habitats (Jantz *et al*. 2014). On the other hand, palynological techniques to identify pollen grains from different floral resources will be crucial for cryopreservation, so alternative methods to decrease costs will be significant (Silva *et al*. 2018). Future lines of research have also considered topics such as mountain palaeoecology, archaeopalynology, agroforestry palynology for food security, and palaeoecology of historical legacies.

This review made it possible to recognize palynological perspectives: ecological evolution followed by interdisciplinary research. The genetic improvement of monocultures by means of palynological analyses is indispensable to understanding not only the trade-offs of ecosystem services but also the possibility of food system transitions for sustainability. Greater involvement of palynology can acquire fantastic value for the application of germplasm sources between *ex situ* and *in situ* conservation of agrobiodiversity and ecological restoration in natural and abandoned habitats.

Soil quality assessment using palynomorphs can support adaptive management of ecosystems by integrating aquatic and terrestrial systems. This interdisciplinary perspective also supports management strategies using the MABES framework because it includes multiple environmental services in a landscape approach. For these reasons, long- and short-term studies that include palynology have proven to help generate climate change adaptation and mitigation strategies. We conclude that the most critical aspect of palynology in food security and the conservation of biodiversity is the participatory inclusion of actors and stakeholders because they play a strategic role in the management and study of novel and natural ecosystems.

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