

A comment on the indicator capacity of *Artemisia* pollen in pre-Holocene paleoecology

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Abstract. In pre-Holocene paleoecology, *Artemisia* (Asteraceae) pollen is commonly considered an indicator of arid steppic environments in temperate regions. However, the >520 known species of this genus occur across a wide range of bioclimatic conditions. This paper comments on a recent comprehensive study that examined the identification of *Artemisia* pollen at the species level in relation to the bioclimatic conditions in which these species occur globally (Lu et al., 2022). Using SEM, three main pollen groups were identified, of which only one was indicative of arid temperate grasslands and deserts, while the other two corresponded to species from wetter biomes and generalist species, respectively. The authors concluded that there is no correlation between *Artemisia* pollen morphology and bioclimatic characteristics. Therefore, *Artemisia* pollen cannot be used as an indicator of any specific vegetation type or bioclimatic domain. The significant intrageneric pollen homogeneity within *Artemisia*, along with the need for SEM to distinguish the few defined pollen types, severely limits its indicator capacity in routine LM paleoecological studies. As a result, *Artemisia* pollen records still require additional paleoecological interpretation methods, such as assemblage analysis and modern-analog approaches, though none can replace paleoenvironmental reconstructions based on pollen-independent proxies.

Keywords. *Artemisia*, pollen morphology, bioclimatic features, paleoecology, pre-Holocene

1. Introduction

According to the World Flora Online (WFO) Plant List (<https://wfoplantlist.org/>; last accessed 27 Feb 2025), the highly diverse Asteraceae genus *Artemisia* comprises over 520 accepted species of herbs and shrubs—trees are absent. *Artemisia* is found on all continents except Antarctica and is particularly significant in the Northern Hemisphere, especially in temperate Eurasia and North America, while being much scarcer or entirely absent in the tropics and the Southern Hemisphere (Fig. 1). Its center of origin and primary diversification is Central Asia, with the Mediterranean and Northwestern America serving as secondary speciation areas (Wang, 2004; Sanz et al., 2008; Malik et al., 2010). Although *Artemisia* is generally regarded as a key component of arid and semi-arid vegetation, particularly steppes, its species span a broad bioclimatic range, occurring in diverse biomes from forests to deserts and across both wet and arid climates (Lu et al., 2022).

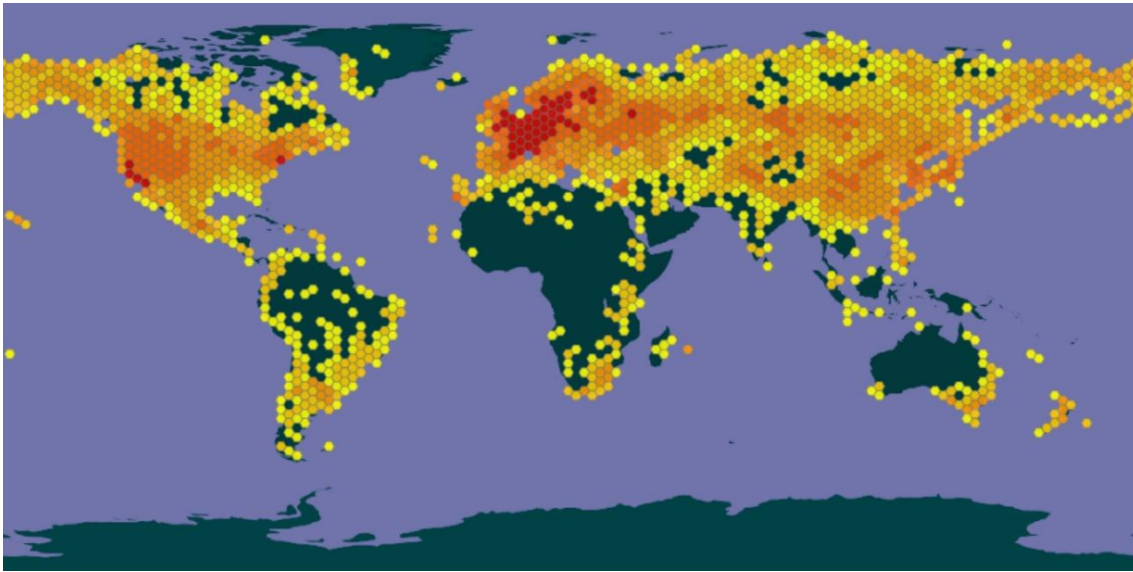


Figure 1. Worldwide distribution of the genus *Artemisia* (Asteraceae). Colors represent the documented occurrence frequency, from high (red) to low (yellow). Downloaded from the Global Biodiversity Information Facility (GBIF) (<https://www.gbif.org/>; last visited 27 Feb 2025).

The oldest fossil pollen records of *Artemisia* date back to the Eocene-Oligocene, followed by an intra-Asian Miocene expansion and subsequent dispersal to Europe and North America (Wang, 2004; Sanz et al., 2008). The pollen of *Artemisia* is highly distinctive and easily distinguishable from other Asteraceae genera, making it particularly useful in paleoecological studies worldwide. However, identifying this pollen at the species level is challenging due to its morphological homogeneity under a light microscope (LM). As a result, paleoecological literature typically refers to *Artemisia* pollen without further taxonomic resolution, significantly limiting its indicator capacity, especially given the vast number of species distributed across diverse biomes and environmental conditions.

The paleoecological interpretations of *Artemisia* pollen records vary according to the human influence. The Holocene has been characterized by the global human expansion and the Neolithic revolution, during which stable settlements and intensive agricultural activities replaced former hunter-gatherer practices. This shift in agricultural practices facilitated the expansion of *Artemisia*, which is considered a reliable indicator of intensive and extensive grazing practices associated with neolithization (Roberts, 2014).

This comment focuses on pre-Holocene times, when human impact was minimal (Pleistocene) or inexistent (Neogene), and vegetation change were driven by non-anthropogenic factors. The main aim is to discuss a recent paper by Lu et al. (2022), which examines the relationship between *Artemisia* pollen morphology at the species level and bioclimatic conditions. This is the first global and phylogenetically comprehensive study specifically on this subject and has potential to influence paleoecological interpretation of Pleistocene and Neogene records where *Artemisia* is a relevant component.

2. Antecedents

Some precursors to the work by Lu et al. (2022) exist in the European Pleistocene, particularly in the Mediterranean region. Glacial phases in this area were typically characterized by cold, steppe-like landscapes dominated by *Artemisia* pollen (along with *Ephedra* and other Asteraceae), whereas interglacials were marked by deciduous forest communities with thermophilous elements (e.g., Zagwin, 1960). However, in some localities, particularly in the eastern Mediterranean sector, this pattern was disrupted or even reversed. For example, in an early Pleistocene (1.95–1.77 Ma) record from Zakynthos Island in the Greek Ionian Sea,

Artemisia pollen exhibited opposite trends, reaching its highest values during interglacial climates. This was indicated by $\delta^{18}\text{O}$ minima in the foraminifer *Globigerinoides ruber* measured in the same core (Subally et al., 1999).

This encouraged the development of modern-analog studies on a set of representative Mediterranean *Artemisia* species, which exhibited a wide range of specific—or idiosyncratic—environmental requirements across temperature and precipitation gradients (Subally & Quézel, 2002). Steppic representatives were largely dominant; however, while some species were independent of elevational vegetation belts, others required specific hydrothermal ranges and were distributed according to geographical and elevational patterns (Fig. 2). Thus, the seemingly anomalous interglacial *Artemisia* peaks recorded on Zakynthos Island were explained by differences in species composition compared to those that peaked during glacial periods in other localities (Subally & Quézel, 2002). These authors concluded that *Artemisia* pollen cannot be reliably interpreted as an indicator of glacial climates unless other independent proxies (e.g., stable isotopes) support this interpretation and/or the *Artemisia* pollen can be identified at the species level.

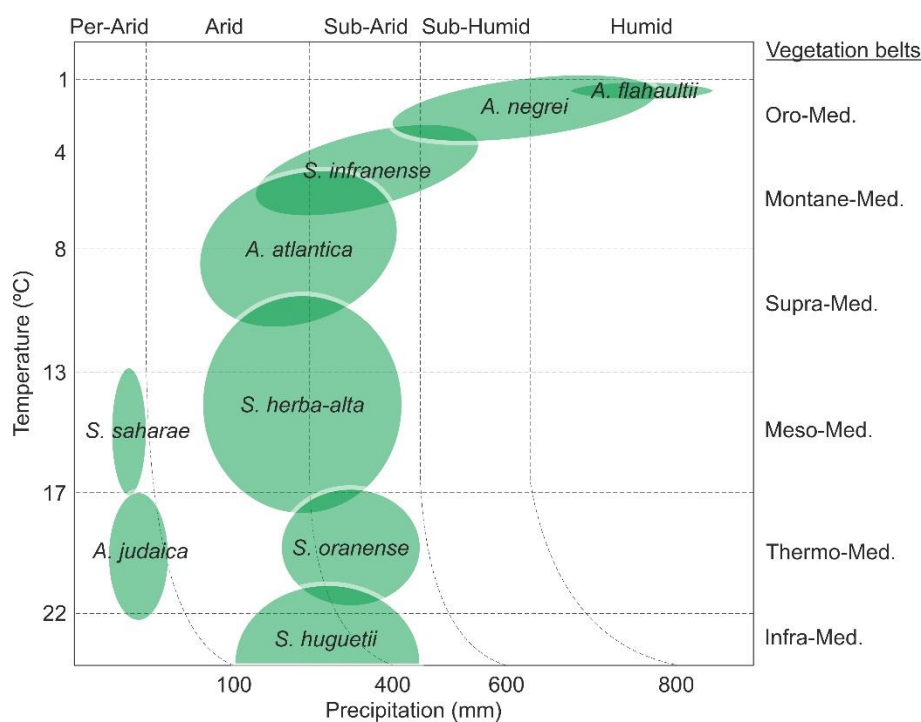


Figure 2. Distribution of Mediterranean *Artemisia* species (including *Seriphidium*) from north Africa sensitive to annual average temperature and annual total rainfall gradients. Modified from Subally & Quézel (2002). Abbreviations: A, *Artemisia*, Med., Mediterranean; S, *Seriphidium* (a subgenus from *Artemisia*),

3. First attempts

Between the works of Subally & Quézel (2002) and Lu et al. (2022), several pollen-morphological studies were conducted to distinguish *Artemisia* species or species groups using light microscopy (LM) and scanning electron microscopy (SEM) (e.g., Jiang et al., 2005; Ghahraman et al., 2007; Hayat et al., 2010; Hussain et al., 2019). However, most of these studies had a local or regional focus and primarily aimed to resolve taxonomic and/or phylogenetic issues rather than establish relationships between pollen morphology and the environmental requirements of the parent species. An exception was the work by Suc et al. (2004), who distinguished between cold and warm *Artemisia* steppes—the former typical of glacial phases and the latter occurring during interglacials—as previously observed by Subally & Quézel (2002).

These observations led Suc et al. (2004) to initiate an SEM study on pollen morphology in relation to environmental characteristics, primarily temperature (from megathermal to microthermal conditions) and edaphic factors (halophytic and psammophilous species) in the Mediterranean region. The pollen of megathermal species has moderately pointed but relatively broad spinules, giving it a somewhat verrucose appearance. In contrast, the pollen of mega-mesothermal, mesothermal, and meso-microthermal (temperate-cold) species tends to have less pointed spines, often interspersed with glomerules or micro-rugules. The pollen of microthermal (boreal) species features blunt spines resting on a nipple-like structure. Halophytic species exhibit a pattern in which the spines are more spaced out, with an apparent decreasing height gradient as temperature increases. A similar trend is observed in psammophilous species, though many of them are also halophytes. However, this classification was not further developed.

4. A global geographical-phylogenetic comprehensive study

The study by Lu et al. (2022) was motivated by the ongoing debate over the potential relationship between *Artemisia* pollen abundance and hydroclimatic conditions, particularly during the Neogene. While some researchers have regarded *Artemisia* pollen as a reliable indicator of aridity, others have argued that there is no correlation between *Artemisia* pollen and moisture availability.

To capture the full range of morphological variability in *Artemisia* pollen worldwide, Lu et al. (2022) selected 33 species representing the major *Artemisia* subgenera defined in phylogenetic studies (Sanz et al., 2008; Malik et al., 2017): *Dracunculus*, *Artemisia*, *Absinthium*, *Seriphidium*, *Pacifica*, and *Tridentatae*. Following an exhaustive LM and SEM analysis, Lu et al. (2022) quantitatively distinguished three main pollen types: SWS (short and wide spinules), LNS (long and narrow spinules), and SG (sparse granules). As in Suc et al. (2004), spinule shape and size were the primary distinguishing parameters. The SG type differs from the other two in granule density, with the Gs/Ss (granule spacing/spinule spacing) ratio always being ≥ 0.37 , whereas in the other types, it is ≤ 0.31 . The distinction between SWS and LNS is based on the D/H ratio (spinule base diameter/spinule height), which is ≥ 1.38 in SWS and < 1.38 in LNS. These diagnostic characteristics were measured using SEM. Using these parameters, along with other measured traits—polar length (P), equatorial width (E), exine thickness (T), pollen length (P), and perforation spacing (Ps)—Lu et al. (2022) constructed a dendrogram in which the established morphological groups were clearly distinguishable.

The next step was to compare this global-scale pollen-morphological classification with the worldwide distribution of the corresponding *Artemisia* species in relation to bioclimatic traits. This was done by mapping the occurrences of the studied *Artemisia* species (nearly 30,860 records) using GBIF and ArcGIS tools within the global terrestrial biome map of Olson et al. (2001). Climatic parameters at these coordinates were obtained from WorldClim (<https://worldclim.org>). The detailed results are available in the supplementary material of Lu et al. (2022) and are summarized in Fig. 3.

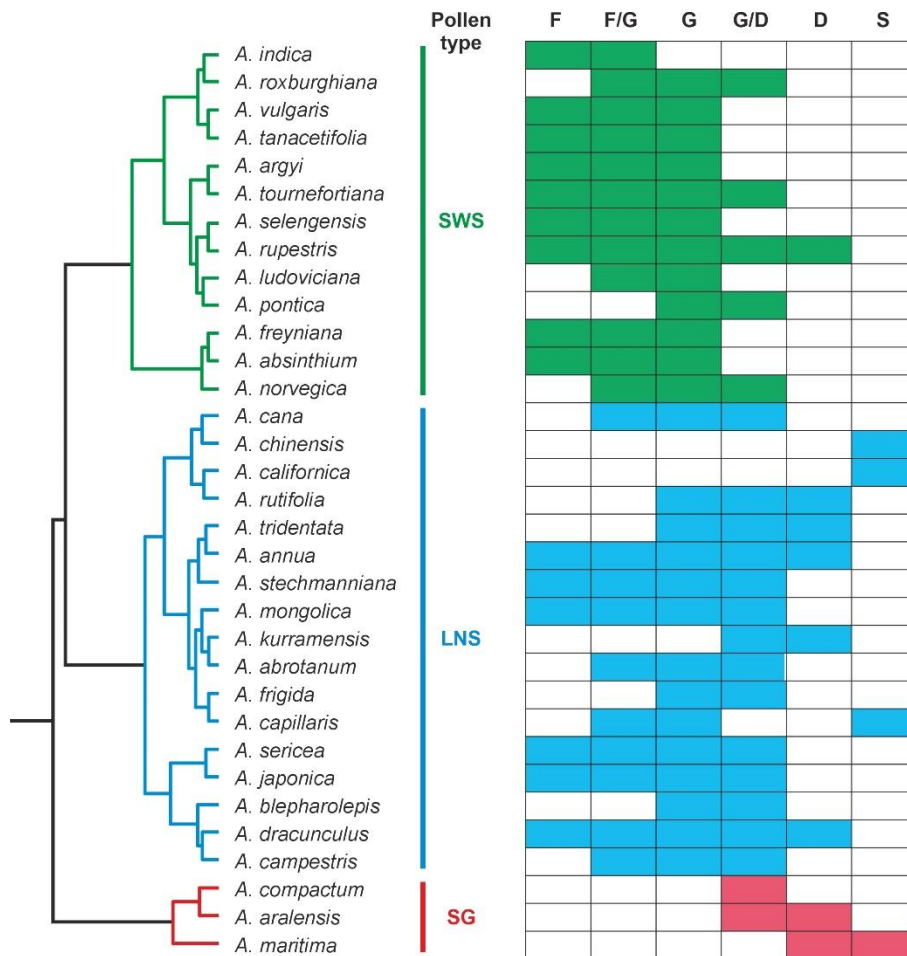


Figure 3. Cluster analysis using the quantitative characters mentioned in the text and habitat ranges of the *Artemisia* species analyzed. Modified from Lu et al. (2022). Pollen type abbreviations: SWS, small and wide spinules; LNS, long and narrow spinules; SG, sparse granules. Biome abbreviations: F, forest, G, grassland; D, desert; S, coastal saline.

Bioclimatically, the defined pollen types fall into four categories: 1) Species with SG pollen type correspond to *Seriphidium*, a low-elevation Eurasian subgenus found in dry grasslands, deserts, and saline/alkaline coastal environments; 2) Species with LNS pollen type are considered generalists, as they have a global distribution and occur in forests, grasslands, deserts, and coastal areas with the highest mean annual temperature (MAT); 3) Species with SWS pollen type also have a global distribution and occupy a wide range of habitats, but most are found in humid forests and grasslands with the highest mean annual precipitation (MAP); and 4) The coexistence of species with SG and SWS pollen types is indicative of dry grasslands and deserts. In summary, among the analyzed species, only those with SG pollen and some with LNS pollen can be used as indicators of arid biomes. The others show little correlation between pollen morphology and environmental characteristics.

5. Discussion

A remarkable strength of the study by Lu et al. (2022) is its global scope and its representation of the main *Artemisia* lineages defined in genus-wide phylogenetic studies. Thus, it can be considered the most comprehensive study to date on *Artemisia* pollen morphology from both geographical and taxonomic perspectives. The pollen-morphological groups defined (SWS, LNS, SG) appear to be globally consistent and likely represent the best classification possible with current technology. It seems that little remains to be done in this regard. The study by Lu et al.

(2022) represents a tremendous effort that will be valuable to many researchers, as all raw data are provided, facilitating further studies on this topic from different perspectives.

Lu et al. (2022) definitively demonstrated that *Artemisia* species occur across a wide range of bioclimatic conditions globally and that using *Artemisia* as a bulk category in paleoecological records as an aridity indicator may be misleading. The fact that only three morphological groups could be established confirms, at a global scale, the pollen-morphological homogeneity within the genus, as previously observed in more local or regional floras. These findings reinforce the difficulty of identifying *Artemisia* pollen at the species level, or even at the subgeneric level, which hinders more detailed environmental inferences based on species-specific traits, as proposed by Subally & Quézel (2002). Moreover, the diagnostic spinule characteristics used to define *Artemisia* pollen types must be measured with SEM, complicating their application in paleoecological studies, which are primarily conducted using LM. Therefore, the potential of *Artemisia* pollen as a standalone paleoenvironmental indicator remains difficult to determine.

6. Conclusions and recommendations

From the above observations, the following general conclusions can be drawn:

1. *Artemisia*, as a single pollen type, is not a reliable indicator of any particular vegetation type, a specific bioclimate or a small set of them.
2. The intrageneric morphological homogeneity of *Artemisia* pollen hinders identification at the species level, significantly limiting its indicator potential.
3. There is no clear correlation between the *Artemisia* pollen morphology-based groups and bioclimatic characteristics.
4. The few morphological groups distinguishable within *Artemisia* require SEM analysis, making routine paleoecological studies using LM impractical.

Therefore, the use of *Artemisia* pollen in pre-Holocene paleoecology requires support from additional methods, particularly assemblage analysis and modern-analog approaches based on the current niches of extant species and the communities they form. However, it is important to consider that the reliability of these approaches decreases over time, and it remains unclear how far back we can go while ensuring the persistence of individual niche characteristics and assemblage types (Rull et al., 2024).

The use of novel physico-chemical experimental techniques, such as Fourier transform infrared spectroscopy (FTIR) and FT-Raman spectroscopy (Kendel & Zimmermann, 2020), could aid in identifying *Artemisia* pollen at the species level. Regarding SEM, recent advancements in pollen counting using this method show promise for routine paleoecological analyses (Smyth et al., 2015). However, the use of independent physico-chemical and biological indicators within the same pollen records, as well as chronological correlations with nearby and/or standard paleoenvironmental records, remains the most reliable approach.

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