Challenges in using modern pollen analogs for Cenozoic paleoecology: examples from the European Neogene

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Abstract

The use of modern pollen analogs in paleoecology is well established in Quaternary studies; however, the reliability of this approach decreases with increasing geological age due to evolutionary changes. Establishing a definitive chronological boundary beyond which modern pollen analogs remain reliable is currently unfeasible. This limitation affects not only paleoenvironmental reconstructions based on the niche conservatism hypothesis for individual extant species, but also community- and biome-level reconstructions that assume compositional and environmental constancy over time. This paper discusses several case studies from the European Neogene—focusing on individual species, communities, and biomes—where the use of modern pollen analogs under the untested assumption of niche conservatism is common. These studies include: (1) quantitative paleoclimatic estimations using the climatic envelope of extant species, (2) comparisons between Middle Miocene European mangroves and present-day Middle-East mangrove communities, and (3) the use of *Artemisia* pollen as an indicator of dry steppe biomes and (4) the occurrence of taxodiaceous coastal marsh forests in Europe after the Miocene Climatic Optimum. The main conclusion is that assuming species' niche conservatism and extrapolating this assumption to communities and biomes is unwarranted and may lead to unsupported conclusions. Therefore, empirical testing of species' niche conservatism across the relevant time spans is essential. Alternative and complementary methods—such as the fossil community approach and the use of pollen-independent proxies (e.g., stable isotopes, biomarkers)—are strongly recommended.

Keywords

Modern analogs, niche conservatism, paleoclimatology, communities, biomes, Europe, Neogene

1. Introduction

The use of modern pollen analogs is common in Quaternary paleoecology and paleoclimatology, based on the assumption that the ecological and environmental requirements of extant species have remained constant over the last ~2.6 million years (e.g., Birks & Birks, 1980; Delcourt & Delcourt, 1991; Cronin, 2009; Bradley, 2015; Rull, 2020). This assumption has led to detailed quantitative estimates of climatic and other environmental parameters using transfer functions, which apply the environmental envelope of extant species to fossil pollen taxa (Birks et al., 2012). However, this assumed niche constancy—also known as niche conservatism (Wiens et al., 2010)—declines over time due to evolutionary processes, progressively reducing the likelihood of finding reliable modern analogs for fossil pollen taxa. Therefore, niche-conservatism uncertainty (NCU) increases with time, and establishing a chronological boundary for the reliability of modern analogs beyond the Quaternary is currently unfeasible (Fauquette, 2017; Matthaeus et al., 2023).

In spite of this, the use of modern analog approaches in Cenozoic paleoecology and paleoclimatology remains common. These methods range from detailed paleoclimatic estimates to reconstructions of past community and biome dynamics, based on the assumption that extant communities and biomes have also remained compositionally and environmentally stable over time. The concept of compositional stability also emerged from Quaternary studies (Prentice et al., 1996; Ni et al., 2010) and was later adopted for the Neogene (e.g., Mahler et al., 2022; Altoaguirre et al., 2023). Some macroecological surveys support this perspective. For example, phylogenetic niche conservatism—the tendency of lineages to retain niche-related traits through speciation events (Crisp & Cook, 2012), or more succinctly, the retention of ecological traits over time among related species (Wiens et al., 2010)—has been considered a major factor structuring vegetation types and biomes globally (Crisp et al., 2009). Similar results have been reported for the European Cenozoic (Lososová et al., 2020).

However, these studies rely on phylogenetic inference and modelling, rather than empirical paleontological evidence, and do not resolve the NCU conundrum, neither for species' niche traits nor for community or biome composition. Therefore, assuming niche conservatism across taxonomic, geographical, and temporal scales is unwarranted and may lead to questionable past ecological and biogeographical reconstructions. As a consequence, modern analog approaches that uncritically adopt niche conservatism as a premise should be approached with caution.

Among the many examples in the literature that rely on these assumptions, we have selected three from the European Mediterranean Neogene including inferences involving individual species, communities and biomes. The first case involves the assumption of climatic niche conservatism of extant species to quantitatively estimate Neogene climates, particularly paleotemperature and paleoprecipitation, which has been widely used in Europe (Utescher et al., 2014; Suc et al., 2018). The second example is the use of modern mangrove communities from the Middle East as modern analogs for those that existed along the northern Mediterranean coasts during the Middle Miocene Climatic Optimum (MMCO) (Plaziat et al., 2001; Popescu et al., 2021). This case was chosen in light of a recent study that provides a detailed description of Middle East mangroves and their environmental context (Waleed, 2024). The third example concerns the widespread use of *Artemisia* fossil pollen as a straightforward indicator of temperate, mostly cold and arid, steppe biomes (Zagwijn, 1960; Suc, 1984; Popescu et al., 2010). This case is revisited in response to a recent thorough study on *Artemisia* pollen morphology and the broad range of biomes inhabited by species of this genus (Lu et al., 2022). While these cases have been analyzed in detail in other publications, this paper provides a succinct summary.

The main aim of this discussion is to highlight the need to avoid using unsupported general modern-analog assumptions as premises for interpreting past ecosystems and their environmental features. The intention is not to dismiss the use of modern-analog approaches, but rather to improve their reliability by taking into account the specific characteristics of each taxon and community under study. A comprehensive review of the subject is beyond the scope of this paper, which focuses on specific case studies from the currently defined European continent.

2. Species level: paleoclimatic estimates

Pollen-based Cenozoic paleoclimatic estimates using modern analog approaches—such as the widely used Coexistence Approach (Mosbrugger & Utescher, 1997) or the Climate Amplitude Method (Fauquette et al., 1998), among others—assume climatic niche conservatism in individual species and community constancy over evolutionary timescales. In this framework, precise quantitative estimates of past climatic variables are obtained from fossil taxa that share pollen morphology with extant species—known as nearest living relatives (NLRs)—by transferring the climatic envelope of these NLRs to their assumed fossil representatives. These methods have been challenged from both theoretical and practical perspectives.

Theoretically, the assumptions of niche conservatism and community constancy have been considered unrealistic, as they remain empirically untested in most reconstructions. Testing climatic niche conservatism requires independent paleoclimatic and palynological evidence. Non-empirical methods—such as molecular phylogenetic inference and species distribution modeling—suggest that the presence or absence of niche conservatism in plants throughout the Cenozoic depends on both the geological timescale and the taxa under study, with no general rule being universally applicable (e.g., Svenning, 2003; Abbink et la., 2004; Byrstriakova et al., 2011; Loera et al., 2012; Martín-Hernanz et al., 2014; Weeks et al., 2014; Benítez-Benítez et al., 2017; Zhang et al., 2021; Vieira et al., 2023; Qian et al., 2024; Quirk et al., 2024; Fernández-Mazuecos & Glover, 2025; Liu et al., 2025). Therefore, niche conservatism in the target taxa over the time interval of interest cannot be assumed a priori.

Concerns have also been raised about the establishment of reliable botanical affinities, which largely depends on the taxonomic resolution achievable in the fossil pollen record—typically at the genus or family level—compared to NLRs. This is especially critical in genera and families with homogeneous pollen morphology. Another drawback is that modern-analog-based methods implicitly overlook the possibility that extinct species, as well as species originated after the time interval under study, with the same pollen morphology that extant taxa may be present in fossil assemblages. Additionally, the potential for modern-analog approaches to result in circular reasoning when studying vegetation responses to climate shifts has been highlighted. Reviews and discussions addressing these issues can be found in Grimm & Potts (2016), Lu et al. (2022); Matthaeus et al. (2023), Quirk et al. (2024) and Rull et al., 2024a).

Another untested assumption is that pollen morphology and ecophysiological traits linked to climatic requirements evolve in a similar manner. However, Krassilov (2000) showed that "sporophytic and pollen characters show only weak correlation over their evolutionary history." According to the author, in some cases, pollen morphology is a conservative trait compared to other plant characteristics, while in other cases, the opposite is true. There is no general rule that can be universally applied; each case requires specific analysis.

The chronological uncertainty associated to niche conservatism (NCU) would also apply to community composition. In this case, empirical palynological data show that the taxonomic composition of many communities has actually varied over time, even during the most recent Quaternary period, largely due to range shifts of extant species (Jackson & Williams, 2004; Williams & Jackson, 2007; Rull, 2020). These compositional changes have been even more pronounced throughout the Paleogene and the Neogene, due to evolutionary factors such as speciation and extinction, in addition to large-scale dispersal (e.g., Rull, 2024). Therefore, extant communities cannot be assumed a priori to be modern analogs for past Cenozoic communities.

From a practical standpoint, pollen-based paleoclimatic estimates derived from modern-analog methods have consistently shown significant discrepancies when compared with pollen-independent and modeling approaches (e.g., Kvaček, 2007; You et al., 2009; Herold et al., 2011; Goldner et al., 2014; Zhang et al., 2019; Salocchi et al., 2021; Botsyun et al., 2022; Gilson et al., 2022). According to Popescu et al., (2021), this could be due to the excessive weight that pollen-based methods assign to megathermal plants, particularly those from mangroves (see next section), in pollen-based paleoclimatic reconstructions.

In summary, given the current state of knowledge, pollen-based paleoclimatic reconstructions using modern-analog approaches should be interpreted with caution and await further developments that may improve their reliability, with emphasis on empirical paleoecological testing of previous assumptions. The use of pollen-independent methods of paleoclimatic estimation, especially those based on isotopic and biomarker proxies, is highly recommended (Subally et al., 2002; Rull et al., 2024a).

3. Communitiy level: Mediterranean mangroves

Mangroves are intertidal forest communities currently restricted to tropical and subtropical coasts between approximately 30°N and 30°S (Spalding et al., 2010). However, during the Miocene—particularly the Middle Miocene Climate Optimum (MMCO; 17–15 Ma), when global temperatures were 4–8 °C higher than today (Westerhold et al., 2020)—pollen records indicate that the northern limit of mangrove distribution extended to the northern Mediterranean coasts, reaching up to approximately 45°N (Plaziat et al., 2001; Popescu et al., 2021). These MMCO Mediterranean mangroves have been referred as *Avicennia*-only mangroves, as they were dominated by *Avicennia* (Acanthaceae) – one of the two globally distributed genera of mangrove-forming trees (Tomlinson, 2016; Duke, 2017) – whereas *Rhizophora* (Rhizophoraceae), the other conspicuous mangrove genus, along with other mangrove-forming tree genera, was absent (Popescu et al., 2021).

The MMCO *Avicennia*-only Mediterranean mangroves have been considered taxonomically and ecologically comparable to those currently found in the arid and semi-arid regions of the Middle East, particularly along the coasts surrounding the Arabian Peninsula (Jiménez-Moreno and Suc, 2007; Suc et al., 2018; Popescu et al., 2021). These regions represent the northernmost boundary of modern mangrove distribution, where *Avicennia* is the dominant mangrove-forming tree. If this comparison holds, modern Middle-East mangroves could serve as modern analogues for reconstructing the ecological characteristics of MMCO Mediterranean mangroves. However, this comparison has yet to be fully explored from biogeographical and paleoenvironmental perspectives (Rull et al., 2024b).

The Miocene *Avicennia*-only Mediterranean mangroves were considered impoverished mangroves located at the northernmost edge of mangrove distribution, likely reflecting a temperature-driven latitudinal pattern (Popescu et al., 2021). These authors estimated a mean annual temperature (MAT) of 18–20 °C and mean annual precipitation (MAP) exceeding 1000 mm/year, except in some localities of the Iberian Peninsula—particularly in the southwestern sector—where climates were drier (see also Postigo-Mijarra et al., 2009; Barrón et al., 2010). As mentioned above, these pollen-based estimates were higher than others based on pollen-independent proxies and paleoclimate modeling, which yielded MAT values of 11–17 °C and sea surface temperatures (SST) of around 20 °C (You et al., 2009; Goldner et al., 2011).

Regarding current Middle Eastern mangroves, a recent review covering most African and Asian coasts surrounding the Arabian Peninsula has revealed highly diverse environmental conditions (Waleed, 2025). MAT vary significantly across the region, ranging from 20 °C in the NE to 30 °C in the SE. SST can reach up to 28 °C in summer, while MAP is generally below 100 mm/year, with evaporation rates typically ten times higher. Additionally, the absence of large permanent freshwater sources limits sediment and nutrient supply essential for mangrove growth and results in hypersaline coastal conditions exceeding 40 ppt. These extremely hot, arid and hypersaline environments are generally unfavorable for mangrove development (Quisthoudt et al., 2012).

Only two mangrove-forming tree species—*Avicennia marina* and *Rhizophora mucronata*—are capable of surviving the harsh environmental conditions of the Middle East. *Avicennia marina* typically dominates the mangrove canopy, whereas *Rhizophora mucronata* is rare or entirely absent, found only in a few locations with some freshwater input (Waleed, 2025). Due to the intense environmental stress, both species exhibit stunted, dwarf growth forms when compared to populations thriving in more favorable climates. Overall, the sparse, low-stature, and species-poor *Avicennia*-dominated mangroves of the Middle East reflect a unique regional adaptation to aridity and related environmental pressures (Osland et al., 2017), rather than a pattern driven by latitude-dependent temperature gradients. In contrast, other Asian mangroves occurring at similar latitudes (approximately 10°–30° N), but under more favorable environmental regimes, rank among the most diverse and healthy mangrove ecosystems in the pantropical zone (Tomlinson, 2016; Duke, 2017).

These observations suggest that the present-day Middle East mangroves represent a latitudinal anomaly within the northern tropical/subtropical mangrove belt—one that is independent of the global temperature gradient and instead more closely linked to regional aridity and hypersalinity. Consequently, these extant mangroves are unlikely to serve as appropriate modern analogs for the Miocene Mediterranean mangroves, considered as a temperature-driven latitudinal feature. This view is further supported by the contrasting climatic conditions estimated for Miocene mangroves, particularly the absence of extreme heat and aridity. Additionally, some studies from the NE Iberian Peninsula do not support the presence of hypersaline conditions (Bitzer, 2004). Combined with the absence of a present-day northern latitudinal zone dominated solely by *Avicennia* mangroves, the above observations make it difficult to identify suitable modern analogs for the MCO Mediterranean mangroves. In the Southern Hemisphere, *Avicennia* mangroves occur in the Mediterranean antipodes (New Zealand and southeastern Australia), where minimum temperatures—a latitude-dependent factor—are the primary drivers of mangrove distribution and diversity (Osland et al., 2017). Further comparisons with these systems could offer valuable insights.

The available evidence suggests that potential modern analogs for MCO *Avicennia*-only mangroves would have thrived in mild, humid climates. Today, *Avicennia*-only mangroves occur sporadically, either as pioneering communities on recently formed mudflats or in hypersaline areas within broader mangrove ecosystems across tropical and subtropical regions (Thatoi et al., 2016). It is plausible that MMCO mangroves developed under similar conditions, though on a much broader regional scale. However, further research is needed to determine whether meaningful parallels exist between ancient and modern *Avicennia* stands. If no clear analogs can be identified, MMCO Mediterranean mangroves may represent an extinct mangrove type—a phenomenon not uncommon in mangrove history, particularly throughout the Cenozoic (Rull, 2024). In paleoecology, communities with no modern counterparts are relatively frequent, even during the Quaternary, when the species involved were already extant (Jackson and Williams, 2004; Williams and Jackson, 2007).

4. Biome level

4.1. Artemisia dry steppes

The presence of significant amounts of *Artemisia* (Asteraceae) pollen in fossil records has traditionally been considered an indicator of arid and semi-arid biomes, particularly steppes, in temperate regions (Wang, 2004). This interpretation applies to pre-Holocene records, as *Artemisia* species are common weeds and ruderal plants associated with human activities such as grazing and other intensive or extensive agricultural practices, which began to play a significant role during the Early Holocene Neolithization (Roberts, 2014). In the Neogene, steppes dominated by *Artemisia*, with *Ephedra* present, began to be important at the end of the Miocene (6.2-5.6 Ma) in the eastern Mediterranean area (Anatolian), coinciding with the Antarctic glaciation and the desiccation of the Mediterranean Sea. At the beginning of the Pliocene, these steppes expanded across the entire Mediterranean region, reaching the westernmost part during the Middle Pleistocene (Suc et al., 2018).

According to the most widely accepted view, the European Pleistocene was characterized by the alternation of cold steppes—dominated by *Artemisia*, *Ephedra*, and other Asteraceae—during glacial phases, and deciduous forests with thermophilous elements during interglacials (Zagwijn, 1960; Suc, 1984). However, Subally et al. (1999) noted that this pattern was disrupted, or even reversed, in some Mediterranean regions, with *Artemisia* reaching its highest values during interglacials, as indicated by independent isotopic proxies. The same authors analyzed the ecological niches of Mediterranean *Artemisia* species and found that, although steppe representatives were dominant, other species were distributed along environmental gradients of elevation—and thus temperature—and hydroclimatic conditions.

Subally & Quézel (2002) suggested that *Artemisia* peaks during glacial and interglacial periods may correspond to different species, and recommended identifying *Artemisia* pollen at the species level and incorporating independent paleoclimatic proxies.

The main limitation is that *Artemisia* pollen is highly homogeneous, making identification at the species level challenging—particularly under light microscopy (LM), which is the standard method used in pollen analysis. Some attempts have been made in this direction, but they primarily aimed to resolve phylogenetic questions rather than support environmental reconstruction (e.g., Jiang et al., 2005; Ghahraman et al., 2007; Hayat et al., 2010; Hussain et al., 2019). Suc et al. (2004) were the first to attempt linking *Artemisia* pollen morphology with environmental preferences. Using scanning electron microscopy (SEM), they found that the key distinguishing feature was the morphology and size of spinules, and they preliminarily associated these traits with various Mediterranean species differing in thermal and edaphic requirements. Unfortunately, this classification was not further developed and a single *Artemisia* pollen type continued to be used as an indicator of glacial steppes (e.g., Popescu et al., 2010).

Recently, Lu et al. (2022) conducted a comprehensive pollen-morphological study that included species from all known *Artemisia* lineages (Sanz et al., 2008; Malik et al., 2017), along with the biomes and vegetation types in which they occur globally, accompanied by corresponding environmental characterizations. The study confirmed the high level of intra-generic pollen homogeneity and reinforced the value of spinule morphological traits as key diagnostic features. Lu et al. (2022) were able to distinguish only three main pollen types within a genus comprising over 500 species (World Flora Online; https://wfoplantlist.org/). These pollen types were designated as SWS (short and wide spinules), LNS (long and narrow spinules), and SG (sparse granules).

Lu et al. (2022) highlighted the wide range of biomes and climatic conditions in which *Artemisia* species occur—from forests to deserts, including grasslands and coastal saline environments—across various climatic zones, with a particular emphasis on temperate regions. The three defined pollen-morphological types showed little correlation with bioclimatic zones. Species with the SWS pollen type have a global distribution and occupy a wide variety of habitats, with a slight preference for humid forests and grasslands. The LNS pollen type was characteristic of generalist species found in forests, grasslands, deserts, and coastal areas, typically in regions with higher temperatures. Species with the SG pollen type were associated with low-elevation open biomes, such as dry grasslands, deserts, and saline environments. In summary, only species with the SG pollen type—and some with LNS—can be considered indicators of arid biomes; the others lack clear indicator value.

It can be concluded that *Artemisia*, when treated as a bulk pollen category, is not a reliable indicator of any specific biome or vegetation type. The difficulty in identifying pollen at the species level, along with the lack of correlation between pollen morphology and environmental preferences, complicates bioclimatic interpretation. Moreover, the need for SEM to distinguish pollen types limits the applicability of the defined pollen-morphological groups in routine pollen analysis. As a result, the interpretation of *Artemisia* fossil pollen records still depends on supporting methods, such as the fossil assemblage approach or the use of independent paleoenvironmental proxies (Rull, 2025). It would be worthwhile to investigate whether recent advances—such as Fourier transform infrared spectroscopy (FTIR) (Kendel & Zimmermann, 2020) and automated pollen counting using SEM (Smyth et al., 2015)—could offer useful support.

4.2. Taxodiaceous tropical marshes

In the Mediterranean region, it is also common to interpret the dominance of pollen from the former Taxodiaceae family as an indicator of tropical coastal forested marshes, which likely replaced the European *Avicennia*-only mangroves after the MMCO during the southward migration of the main Mediterranean biomes (Suc et al., 2018). This interpretation is based on identifying this pollen as *Taxodium* type, encompassing *Taxodium* and *Glyptostrobus*, two genera of trees now restricted to tropical or subtropical latitudes outside Europe. This approach not only leads to questionable biome reconstructions, as explained in this section, but has also formed the basis for debatable quantitative paleoclimatic estimates, as discussed in Section 2. Once again, the problem lies in pollen identification at taxonomic resolutions not supported by morphological differences.

The now-abandoned family Taxodiaceae included nine genera—*Athrotaxis*, *Cryptomeria*, *Cunninghamia*, *Glyptostrobus*, *Metasequoia*, *Sequoia*, *Sequoiadendron*, *Taiwania*, and *Taxodium*—characterized by pollen with a protuberance (papilla) at the center of the aperture (leptoma). This papillate pollen is a common Cenozoic fossil in the Mediterranean region and has traditionally been identified as *Taxodium*-type or *Taxodium/Glyptostrobus*, with corresponding bioclimatic inferences mentioned above (e.g., Bessedik, 1985; Bessedik & Cabrera, 1985; Fauquette et al., 1998a, b; Jiménez-Moreno, 2005; Jiménez-Moreno & Suc, 2006). With the advent of molecular phylogenetics, Taxodiaceae was dissolved as a family and reclassified as a Cupressaceae subfamily (Taxodioideae) containing three genera—*Cryptomeria*, *Glyptostrobus*, and *Taxodium*—while the remaining six genera with papillate pollen were reassigned to four other subfamilies. This reclassification did not alter traditional fossil identification practices in the region (e.g., Jiménez-Moreno et al., 2010; Biltekin et al., 2015; Fauquette, 2017; Suc et al., 2018, 2020; Popescu et al., 2021).

However, a recent palynological study seriously questioned these interpretations. After a thorough and detailed morphological analysis of modern pollen, Bouchal and Denk (2020), concluded that distinguishing among the nine former Taxodiaceae genera based on pollen characteristics is "difficult if not impossible." They also highlighted that the extant species within these genera occupy a wide range of ecological niches, casting doubt on paleoenvironmental interpretations that rely solely on fossil pollen and their presumed modern counterparts. Consequently, the routine assignment of papillate Cupressaceae pollen to the *Glyptostrobus*–*Taxodium* group—while overlooking the ecological variability of the remaining seven papillate genera—rests on weak taxonomic grounds. As such, using papillate Cupressaceae pollen alone to indicate megathermal biomes and environments, such as tropical or subtropical coastal swamps, is not justified.

5. Discussion

The main drawbacks of using modern pollen analogs for the European Neogene stem from uncertainties surrounding niche conservatism (NCU) and its extrapolation to community- and biome-level taxonomic composition and environmental requirements. The most common approach is to assume niche conservatism and constancy in community or biome composition a priori, often without critical evaluation—an approach that can lead to unsupported conclusions. In the case of pollen, these assumptions are especially problematic due to additional factors, including limitations in pollen morphology and taxonomic resolution, difficulties in establishing accurate botanical affinities, and the possible presence of extinct species or taxa that evolved after the period under study. As such, finding empirical evidence for niche conservatism in the taxa examined over the relevant time span is essential. Identifying reliable modern analogs and clearly defining the spatiotemporal contexts in which they are applicable should therefore be a key objective.

Alternative and complementary approaches based on direct observation of the paleontological record—without reliance on potential modern analogs—are strongly recommended. One such method is the fossil community approach, which statistically defines fossil pollen assemblages based solely on paleontological evidence and incorporates pollen-independent paleoclimatic and paleoenvironmental proxies such as stable isotopes, biomarkers, and similar indicators (Rull et al., 2024a). This approach can be applied to individual species, communities, and biomes, and, combined with the use of pollen-independent paleoclimatic proxies, it may provide empirical evidence for testing niche conservatism. As a result, it can help reduce the NCU for the taxa and time interval under study. Paleoclimatic modeling can also contribute to testing niche conservatism, though the underlying assumptions and premises of the models must be carefully considered.

The challenges discussed here are not exclusive to the European Neogene and should be seriously considered in studies from other continents and Cenozoic time intervals. It should not be forgotten that empirical evidence constitutes the basis of scientific research, and that modelling and other theoretical approaches, while useful, cannot replace the direct observation of natural phenomena. In the words of Ricklefs (2012): "Whereas the origins of ecology were firmly grounded in direct observation of nature, the emergence of strong theory in ecology appears to have changed our perspective on natural history, to the point that observation is often used to serve theory rather than test predictions and find inspiration for new ideas." Special care should be taken with the untested and potentially unrealistic a priori assumptions underlying some modelling and theoretical ecological approaches.

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