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Reassessing the Role of Anthropogenic Climate Change in the Extinction of Silphium

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The famed ancient herb, known to the Romans as silphium (Greek *silphion*), is widely regarded as the first recorded instance of human-induced species extinction. Modern scholars have largely credited direct exploitation (e.g., over-harvesting; over-grazing) as the primary cause of silphium's extinction, due to an overwhelming demand for the plant in ancient times. Recent research has revealed strict cold-stratification requirements for the germination of silphium's closest living relatives, revealing the likelihood that silphium shared these same germination requirements. Documented environmental changes in ancient Cyrenaica (e.g., widespread deforestation; cropland expansion) likely resulted in accelerated rates of desertification throughout the region as well as the direct disturbance of silphium's habitat, effectively eliminating the necessary conditions for silphium's successful germination and growth within its native range. Contrary to previous conclusions, this evidence suggests that anthropogenic environmental change was instead the dominant factor in silphium's extinction, marking silphium as the first recorded instance of human-induced climate-based extinction.

Keywords: silphium, silphion, climate, extinction, Cyrene, Cyrenaica, deforestation, desertification

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INTRODUCTION

In his renowned work, *Naturalis Historia* (77 CE), Pliny the Elder famously declared that the once-beloved North African herb, known to the Romans as silphium (Greek *silphion*), "no longer exists" (Bostock and Riley, 1855), making it the first species in written history to have been knowingly driven to extinction by humankind (Parejko, 2003). Given the overwhelming demand for silphium amongst the ancient Greeks and Romans, numerous scholars have concluded that its disappearance was due primarily to exploitative pressures such as over-harvesting and over-grazing coupled with the general difficulty in regards to its cultivation (Andrews, 1941; Amigues, 2004). While these factors inarguably played major roles in the extinction of silphium, the consequential impact of human-induced environmental changes in Cyrenaica (modern-day eastern Libya) has been largely overlooked in modern investigations of silphium's extinction. Both the strict native range of silphium and the widespread environmental changes throughout ancient Cyrenaica are well-recorded in the literature. However, a direct causational relationship of these factors has not previously been linked to silphium's extinction. In light of new evidence which reshapes our understanding of silphium's environmental germination requirements, we reexamine the role of localized climate change and direct habitat disturbance as the primary factors in the extinction of silphium.

GEOGRAPHY AND CLIMATE OF CYRENAICA

Applebaum categorized the geography of Cyrenaica into three regions: the northern coastal plateau, the gradually descending steppe, and the harsh desert in the far south (1979). From the Mediterranean coast, the elevation of northern Cyrenaica swiftly ascends southward through a combination of steep cliffs and flattened terraces. Moisture from the sea gives rise to substantially increased rates of seasonal rainfall while the cooler temperatures atop the high-elevation (800–900 m above sea-level) Jebel al-Ahdar plateau (also known as Jabal al-Akhdar) lead to an abundance of condensation in the form of dew (Applebaum, 1979; Saaed et al., 2019). As a result, the climate of the northern region is far more resilient to environmental changes than the vulnerable arid ecosystems to its south (Saaed et al., 2019).

The dense vegetation of northern Cyrenaica was historically the region's primary natural resource and its composition has been well-documented since ancient times. The ancient Egyptians, who traded with the indigenous Libyans, described the diversity of northern forests west of the Nile River (Saaed et al., 2019). In the 4th century BCE, Scylax listed numerous fruits that grew in Euesperides (modern Benghazi), including apples (*Malus* spp.), pomegranates (*Punica granatum*), pears (*Pyrus* spp.), almonds (*Prunus amygdalus*), olives (*Olea europaea*), and grapes (*Vitis vinifera*) (Saaed et al., 2019). Theophrastus later listed some of the trees present in Cyrenaica's forests including lotus (taxonomy disputed), cypress (*Cupressus* spp.), pine (*Pinus* spp.), acacia (possibly *Vachellia tortilis*), and thuon (*Tetraclinis articulata*) [also known as thyone (Saaed et al., 2019)] (Hort, 1916).

The highest rates of precipitation now occur where the city of ancient Cyrene once stood: about 500 mm per year in the modern period (Saaed et al., 2019), likely higher in ancient times (Applebaum, 1979). According to Herodotus, the indigenous Libyans directed the Greeks to settle there, for there was "a hole in the sky" above it, a reference to its plentiful rainfall (Godley, 1921), which supported the dense coastal forests and abundant wildlife that Cyrenaica was well-known for in the ancient world (Hort, 1916; Godley, 1921; Einarson, 1976; Saaed et al., 2019). Applebaum describes ancient Cyrene as a "desert oasis," similar in climate and landscape to mainland Greece (1979). The modern-day location of Cyrene averages about 18°C, sometimes reaching as low as 5°C in the depths of winter and up to 35°C in the height of summer (Saaed et al., 2019). Temperatures were likely lower in ancient times, evidenced primarily by the climatic changes described by Applebaum (1979) and supported by numerous paleoecological studies (Hunt et al., 2002, 2010; Simpson and Hunt, 2009), all of which will soon be discussed in greater detail.

The steppe begins just south of Cyrene. In contrast to the steep shift in elevation near the coast, the southern side of the plateau descends gradually. Every kilometer southward is marked by a progressively lowering annual rate of precipitation and rising average temperatures, ultimately giving way to the "stony wastes that fade into the Sahara desert" (Applebaum, 1979). The non-forested northern steppe was home to numerous shrubs, including thorny burnet (*Sarcopoterium spinosum*), giant fennel (*Ferula communis*), and wild thyme (*Thymus serpyllum*) (Applebaum, 1979). Most of Cyrenaica's agricultural production (primarily cereal grains such as wheat and barley) also took place in this region (Bostock and Riley, 1855; Applebaum, 1979). The successful cultivation of food crops relied heavily upon consistent rates of precipitation. The Jebel al-Ahdar plateau directly to the north (being comprised primarily of porous Miocene limestone) is extremely permeable, leaving very little runoff for use in crop irrigation. However, this same limestone also served as a parent material for the fertile red soils of both the northern steppe and coastal terraces, which were highly effective at retaining moisture. Precipitation in Cyrenaica is both regional and highly seasonal, with most occurring in the winter (October through May). This is reflected by the nomadic lifestyle that many of the indigenous Libyans practiced for millennia (Applebaum, 1979).

The restrictive native range of silphium rested in the drier southern steppe. Despite its lower elevation, diurnal temperature variation was more pronounced in this region than in the northern forests, likely due to differences in both humidity and abundance (or lack thereof) of insulating vegetation (Applebaum, 1979). According to Pliny's description, silphium did not tolerate moist fertile soils any more than it did hot desert sands. Within a narrow, semi-arid strip of land—about "thirty miles in breadth and 250 in length"—silphium grew as a "wild and stubborn" weed, seemingly boundless in its extent and unobstructed by the growth of any species but its own (Bostock and Riley, 1855).

TAXONOMIC CLASSIFICATION OF SILPHIUM

Silphium's taxonomic classification has been extensively studied through a multidisciplinary approach, paying special attention to ancient literature and artwork analyzed with a modern scientific perspective. Numerous scholars have conducted this style of research in hopes of identifying silphium or its closest living relative (Sprengel, 1807; Amigues, 2004; Miski, 2021). Silphium's classification as a large *Ferula*-like species within the Apiaceae family is undisputed amongst modern scholars (Amigues, 2004). While we remain skeptical that silphium's closest living relative can be determined with absolute confidence, we recognize that many of the plant's morphological features are broadly accepted in the modern literature, due in part to the combined presence of detailed ancient literary descriptions and artistic depictions of silphium's morphology (Bostock and Riley, 1855; Hort, 1916; Amigues, 2004; Miski, 2021). The following section, while not an exhaustive overview of current knowledge by any means, highlights the most notable and verifiable traits of the silphium plant and its living relatives.

Theophrastus and Pliny describe silphium's thick, perennial root—which grew to a cubit (about 0.5 m) in length—as having a fleshy interior and black-colored bark (Bostock and Riley, 1855; Hort, 1916). Incisions made into this root would release an exudate "like milk in appearance" from which a substance

FIGURE 1 | Young basal foliage and emerging stalk of *Ferula asafoetida* [photo by Patrick Verhaeghe (public domain)].

FIGURE 2 | Wild stand of mature *Ferula asafoetida* in the Kyzylkum desert [photo by Patrick Verhaeghe (public domain)].

known as *laser* (the primary product of the silphium plant) was produced (Bostock and Riley, 1855). Silphium's above-ground parts (i.e., foliage, stalk, and blossoms) regrew annually (Bostock and Riley, 1855; Hort, 1916). Large basal leaves were the first to emerge; Theophrastus described their appearance as celery-like while Pliny instead likened them to parsley (Bostock and Riley, 1855; Hort, 1916). These statements are not themselves satisfactory descriptions, as neither source specifies the exact features (e.g., size; leaflet arrangement; leaflet shape) upon which their comparison is based. Artistic depictions of silphium's foliage (both basal and cauline) on the ancient coinage of Cyrene are highlighted by Amigues, providing the necessary insight into their structure and shape (2004). These depictions reveal a compound leaf (like those of celery and parsley) divided into 5–7 round, oblong leaflets (whose shape are quite unlike those of celery or parsley) (Amigues, 2004). We see this arrangement mirrored in the basal (**Figure 1**) and cauline (**Figure 2**) foliage of *Ferula asafoetida*.

The English translation of Theophrastus' *Enquiry Into Plants*, provided to us by Sir Arthur Hort, states that silphium's stalk was "*Ferula* in size and nearly as thick" (1916), which itself would be greatly inexplicit given the morphological variability within the *Ferula* genus. However, a closer examination of the original Greek text reveals a more accurate translation, which instead reads "*narthex* in size..." (Hort, 1916). The name "narthex" refers specifically to a known species (*Ferula communis*), whose stalk reaches 2–3 m in height and 3–7 cm in diameter (Lamnauer, 2005). This interpretation is confirmed by Pliny's account (likely sourced directly from Theophrastus), stating that silphium's stalk was "like that of fennel-giant and of similar thickness" (Bostock and Riley, 1855). Giant fennel, like narthex, is a common name used only in reference to *Ferula communis*.

Depictions of silphium's stalk on ancient coinage also reveal a vertical striation (Amigues, 2004; Miski, 2021), an exceptionally notable feature that differentiates silphium from many modern *Ferula* species. Another distinctive feature of silphium was the opposite arrangement of its foliar branches which attached to the stalk with overlapping sheaths (Bostock and Riley, 1855; Hort, 1916; Amigues, 2004; Miski, 2021). This contrasts the alternate branching pattern of most large *Ferula* species (Miski, 2021). Further up the stalk, the sheathed branches gave rise to large flowering umbels, from which fruit developed. Silphium produced a double-seeded fruit that split into two separate carpels upon maturity (Amigues, 2004; Miski, 2021). These seeds were described as "leaf-like" by Theophrastus, who aptly named them "phyllon" (Hort, 1916). Cyrenaic coinage depicts silphium's fruit as distinctly heart-shaped, however, Miski recently proposed that these depictions instead represent two overlapping carpels—a stylistic choice meant to represent the number of seeds in each of the fruit rather than the true shape of the fruit itself (2021).

Among silphium's many proposed relatives, the stalks of *Ferula tingitana*, *Ferula drudeana,* and *Ferula asafoetida* all notably exhibit a fine vertical striation. Only two of these species (*F. tingitana* and *F. drudeana*) also display an opposite arrangement of their sheathed foliar branches (Sprengel, 1807; Amigues, 2004; George, 2006; Miski, 2021). The former species (*F. tingitana*) was among the first to be proposed as a close relative to silphium. This conclusion has since been widely refuted for reasons including its toxicity to both humans and animals, its extremely broad native range, and the poor resemblance of its fruit to those of silphium (Amigues, 2004). Even Sprengel, who originally proposed its relation, later retracted this conclusion and instead proposed *Laserpitium gummiferum*, which has since been reclassified as *Margotia gummifera* (Amigues, 2004).

Amigues supports the notion that *M. gummifera* is silphium's closest living relative in her detailed study of silphium's morphology (2004). Some characteristics of *M. gummifera* match what is known of silphium, such as its aromatic resin and vertically striated stalk. The fleshy roots, which reach up to a meter in length and have a reddish-brown bark, are similar to silphium's although not compellingly so. The compound basal leaves of *M. gummifera* exhibit a fern-like appearance, with leaflets that do moderately resemble parsley or celery in their shape. However, the stalk (measuring only 1 cm in diameter) drastically contrasts the notable thickness of silphium's stalk (Amigues, 2004). For these reasons, we reject Amigues' argument

FIGURE 3 | Stalk of *Ferula asafoetida*, featuring fine vertical striations [photo by Patrick Verhaeghe (public domain)].

regarding the relation of *M. gummifera* to silphium. We instead propose that *F. drudeana* and *F. asafoetida* are much more likely to be among silphium's closest living relatives.

In addition to the aforementioned similarities of its stalk and branch arrangement, the roots of *F. drudeana* resemble silphium's almost exactly, both in their size (up to 46 cm in length and 25 cm in diameter) and composition (fleshy interior, black-colored bark, and resinous exudate with a pleasant aroma). About 20 cm below the surface, these roots typically diverge into several thick branches (Miski, 2021), matching Pliny's description of silphium's roots as "numerous and thick" (Bostock and Riley, 1855). The double-seeded schizocarp of *F. drudeana* is also consistent with silphium's own fruit. However, its foliage fails to share a resemblance with silphium's in both shape and structure (Miski, 2021).

Likewise, nearly all of the morphological features of *F. asafoetida* closely resemble those of silphium, with the sole exception of its alternate branching pattern. Like silphium, *F. asafoetida* exhibits a fleshy perennial root (45 cm in length and 12–15 cm in diameter) with black bark and a milky exudate. This root occasionally retains a simple structure, like that of a carrot or parsnip, but often separates into numerous forks. The stalk (which regrows annually) ranges from 2.5 to 3.25 m in height at maturity. As previously noted, it also features a fine vertical striation (**Figure 3**) as well as sheathed foliar branches (George, 2006). We also find it worth noting that four of our ancient sources (Pliny, Arrian, Dioscorides, and Strabo) indicated an extremely close relation between *F. asafoetida* and silphium (Goodyer, 1655; Bostock and Riley, 1855; Chinnock, 1884; Hamilton, 1903). Both Pliny and Strabo refer to *F. asafoetida* as the "silphium" of Media (modern-day Iran), adding that its resinous exudate is inferior to that of Cyrenaic silphium (Bostock and Riley, 1855; Hamilton, 1903). Strabo even speculated that this distinction between *F. asafoetida* and Cyrenaic silphium "may be accounted for by the difference of places (in which they grow), or from the mode of extracting and preparing the juice (that each of the plants produce)," rather than the likelihood that they were separate, yet closely related species (Hamilton, 1903).

Lastly, the extensive list of silphium's medicinal and culinary applications, provided to us primarily by Pliny (Bostock and Riley, 1855), and reiterated by later authors (e.g., Goodyer, 1655), yield valuable insights into its potential phytochemical properties. Notably, the resinous exudate of both *F. drudeana* and *F. asafoetida* contain numerous compounds whose known medicinal effects closely mirror those of laser (Bostock and Riley, 1855; George, 2006; Mahendra and Bisht, 2012; Sood, 2020; Miski, 2021). The processed exudate of *F. asafoetida* [known simply as "asafoetida" or "hing" (George, 2006)] was frequently used in ancient times to either adulterate or substitute authentic laser due to its shared properties and uses (medicinal, culinary, or otherwise). However, the foul odor of asafoetida differed from the pleasant smell of silphium's resin and often revealed its unwanted presence in adulterated forms of laser (Bostock and Riley, 1855; Hamilton, 1903; Hort, 1916; George, 2006). This serves as a reminder that even the most similar modern species to the extinct silphium are imperfect in their likeness.

GERMINATION REQUIREMENTS

Species of the genus *Ferula* have gained notoriety for their common inability to reliably germinate under environmental conditions differing from those of their native habitats, due primarily to the abundant prevalence of morphophysiological seed dormancy and the resultant cold-stratification requirements within the genus (Fasih and Afshari, 2018). While there are exceptions to this (e.g., *Ferula tingitana*), evidence from our ancient sources strongly suggests that silphium was not among them. Theophrastus explicitly declared that silphium did "not admit to cultivation" (Hort, 1916). Pliny reiterated this, claiming that any attempt to cultivate silphium "will leave the spot where it has been sown quite desolate and barren" (Bostock and Riley, 1855).

The seed germination requirements of *F. drudeana* and *F. asafoetida* are well-recorded in the modern scientific literature; both require an extended period of cold stratification to break dormancy (Zarekarizi et al., 2011; Miski, 2021; Shanjani and Hoseini, 2021). The seeds of *Ferula gummosa* [the species from which galbanum, an ancient medical resin similar to laser, was derived (Goodyer, 1655)] and *Ferula ovina* also must endure prolonged exposure (4–8 weeks) to temperatures $\leq 5°C$ under moist conditions to reliably germinate (Fasih and Afshari, 2018; Shanjani and Hoseini, 2021).

The modern exploitation of *F. asafoetida*, which mirrors what we know of silphium's own decline, further supports its proposed relation. Commercial demand for the species' resin is high due to its numerous culinary and pharmacological uses (George, 2006; Zarekarizi et al., 2011). Successful cultivation of *F. asafoetida* has yet to prove commercially viable due to poor germination, leading to a strong dependence upon wild populations in order to meet the sustained demand for its resin and widespread concern for the species' continued survival (Zarekarizi et al., 2011; Shanjani and Hoseini, 2021).

Given that silphium's classification as a large *Ferula*-like species is well-established (Hort, 1916; Amigues, 2004), it is reasonable to speculate that silphium shared the germination requirements of its closest living relatives (e.g., *F. drudeana* and *F. asafoetida*) and other related species, as shown in the modern scientific literature. This conclusion is strongly supported by the written testimonies of Theophrastus and Pliny regarding silphium's own germination difficulties. If the previously stated argument is accurate, a lowered rate of seasonal precipitation or elevated winter temperatures would have effectively disrupted the capability of silphium's seeds to germinate in the wild. Numerous trends fueled by the expansion of ancient Cyrene likely caused both of these climatic changes to occur simultaneously in the form of desertification alongside direct habitat disturbance.

CAUSES AND IMPACTS OF ENVIRONMENTAL CHANGE IN ANCIENT CYRENAICA

Much of the available paleoclimatic data for North Africa is highly fragmentary in terms of both geography and chronology. Some more comprehensive investigations of the Mediterranean paleoclimate assess extended durations of time spanning many millennia, from the last glacial period to the present day (Cremaschi, 2003; Cheng et al., 2015). One such paleoclimate study measured speleothem oxygen-carbon isotopes from the Jeita Cave in the Levant region, which indicate a period of increased temperature and decreased precipitation during the time of silphium's decline (Cheng et al., 2015). In contrast, numerous geomorphological and paleoecological studies on the ancient climate of Tripolitania (northwest Libya) show that this region's macroclimate has remained relatively stable over the last three millennia (Barker, 2002; Cremaschi, 2003). While none of these studies directly address the local climate of Cyrenaica during Classical Antiquity, they do provide context regarding the broader climate conditions in North Africa (including that of Cyrenaica) over an extended period of time.

A much more detailed climate record is provided to us in the form of dendrochronological data from the valley of Wadi Tannezzuft in southwest Libya (Cremaschi et al., 2006). In this study, twenty samples of wood from the species *Cupressus dupreziana* were collected. The width of all visible rings (an indication of moisture availability at the time of growth) were measured for each sample. These rings were then subjected to radiocarbon dating so that all samples could be synchronized into one cohesive chronological model. The collective raw data were then detrended to produce a standardized model of ring width over time. The resulting model shows a period of wide rings (high moisture availability) between 500 BCE and 250 BCE following a large gap (∼3,000–1,500 BCE) in which no wood samples were available for study, which the authors suggest may be the result of poor wood preservation due to a period of excess moisture (Cremaschi et al., 2006). From this time, a steady trend of declining ring width was observed (aside from a smaller, yet significant gap in the data record from ∼100 BCE to the very beginning of the common era) which accelerated dramatically around the year 500 CE and extends into the modern period (Cremaschi, 2003; Cremaschi et al., 2006). These data support the notion that the climate of southwest Libya has consistently dried since the Hellenistic period (7th—1st centuries BCE) but does not demonstrate that this decline occurred rapidly until long after silphium's extinction was recorded.

However, there are some notable issues with the use of this dataset. Firstly, the plant family of Cupressaceae, to which the numerous species of cypress (including *Cupressus dupreziana*) belong, is generally regarded as unsuitable for dendrochronological research. While the species involved in this study does have an extensive lifespan, the width of its rings in relation to moisture availability at the time of growth has shown to be unreliable, as noted by the authors (Cremaschi et al., 2006). This concern is largely alleviated by the abundance of samples in the study, whose rings were radiocarbon dated and aligned accordingly, producing a much more representative model of ring width over time.

Secondly, there is little reason to believe that the climate of the Tannezzuft valley (which rests at the foothills of the Saharan Tassili n'Ajjer plateau) accurately reflects upon that of the Mediterranean coast of Cyrenaica (Cremaschi, 2003; Cremaschi et al., 2006). Furthermore, the decline of silphium [from its "golden age" in the 5th and 4th centuries BCE (Amigues, 2004) to its reported extinction in the 1st century CE (Bostock and Riley, 1855)], was both hyperlocal and comparatively rapid, and thus more detailed examinations of ancient microclimatic changes in silphium's narrow range would be necessary to provide any quantitative data of significant relevance.

One such source comes to us in the form of a palynological study that analyzed pollen and spore samples isolated from sediment deposits in the Jebel al-Ahdar region—the first investigation of its kind in Cyrenaica. Many of the taxa identified in these samples were typical of Libya's native steppe-land environments, such as trees (e.g., *Pinus*, *Quercus*, and *Juniperus*), shrubs (e.g., Rhamnaceae, Cistaceae, and Rosaceae), and wild grasses (i.e., Poaceae). However, others were more typical of cultivated lands such as cereal grains, olives, and arable weeds (e.g., Chenopodiaceae and Cruciferae), offering more direct evidence for extensive cultivation in this region. Furthermore, many samples showed clear signs of charring, which the authors speculate resulted from the intentional burning of vegetation. In all, this study suggests that significant land-use changes took place in northern Cyrenaica, characterized by the widespread clearing of vegetation, heavy grazing, an expansion of food crop cultivation, and significant soil erosion. Of particular note is the presence of olive tree pollen, a non-native species that was imported to North Africa for oil production by the Greeks. This effectively dates the adjacent pollen samples (and by extension the initial changes in land usage) to some time after Greek colonization in 631 BCE (Hunt et al., 2002).

A preliminary palynological study in the coastal-facing Haua Fteah cave (located ∼20 km north of Cyrene) found that 37% of the pollen samples were introduced via animals, primarily pigeon and sheep (Simpson and Hunt, 2009). This finding confirms what has been previously concluded regarding the use of Haua Fteah as a location for stalling livestock, a practice which began in the Hellenistic period and continues into the modern-day (Barker et al., 2008). Perhaps the most reliable research with paleoecological implications to have been conducted in Haua Fteah was the recent series of excavations led by the Cyrenaican Prehistory Project (CPP), which sought to reassess the initial findings of Charles McBurney from his excavations of Haua Fteah in the 1950s (Hunt et al., 2010). The findings of these excavations provide a detailed account of human occupation from the Late Pleistocene to the modern era. Of particular note is the presence of large inflows of eroded sediment layered between deposits of manure (from livestock stalling) and various anthropogenic artifacts. These deposits, which appear to have originated from the tilling of surrounding land for food crop cultivation, are primarily found above (but also directly beneath) a structure dated to the Graeco-Roman period, indicating that significant changes in land usage, resulting in periods of heavy erosion, began to take place just prior to its construction (Hunt et al., 2010; Douka et al., 2014).

These modern scientific studies confirm what has already been stated by our literary sources regarding the sudden changes in land usage and local climate conditions following the Greek colonization of Cyrenaica. As recorded by Theophrastus, the aforementioned thuon tree once grew there in great abundance but its rot-resistant wood became a popular material for the construction of furniture and home roofing, contributing to its rampant harvest (Einarson, 1976; Saaed et al., 2019). The timber of this region more broadly served as a lucrative export for Cyrene's growing economy in both the Hellenistic and Roman periods (Applebaum, 1979; Saaed et al., 2019). Alongside these economic drivers of deforestation, the growing population of Cyrene was also a major contributor, as densely forested areas were also the most suitable for the establishment of permanent settlements. We also find that this clearing of forested land was expressly permitted "by license of the temple authorities" in the 4th century BCE Cyrenaean Cathartic Law of Apollo (Applebaum, 1979).

Among the most recent regions within northern Cyrenaica to have been deforested was Teucheira (also known as Tocra), which remained forested up until the 14th century CE. Observations of this region provide us with perhaps the most analogous example of environmental impacts from deforestation in Cyrenaica. Applebaum records the presence of ancient farmsteads in Teucheira that "remain in places where the soil has been eroded to bedrock" as a result of deforestation (1979).

Another example of environmental impacts from deforestation can be found in *De Causis Plantarum*, in which Theophrastus recorded his observations of the climatic effects of deforestation in Philippi. He tells us that nearly all of the trees were cut to make way for the expansion of cultivated land, which allowed sunlight and wind to reach where they could not before. This made the air less humid and caused the groundwater to recede almost entirely. Freezing temperatures (once common) became a significantly less frequent occurrence (Einarson, 1976). We see this trend closely mirrored in the expansion of ancient Cyrene, whose deforestation is recorded to have resulted in less reliable rainfall, higher and less stable temperatures, lower levels of soil organic matter, and an increased prevalence of soil erosion (Applebaum, 1979; Saaed et al., 2019). The two latter impacts likely hindered the soil's ability to retain moisture, driving further desertification and reducing agricultural productivity (Mirzabaev et al., 2019).

The second primary driver of environmental change in ancient Cyrenaica was the lack of sustainable cropland management. Prior to Greek colonization, the various groups of indigenous Libyans generally lived symbiotically with one another from an ecological perspective. In the north, an agrarian lifestyle dominated, relying on fertile soils and consistent rainfall to nourish food crops. Others lived a nomadic lifestyle as shepherds, spending the rainy winter seasons in the southern steppe and migrating north in the summer when their livestock were lacking water and fresh pasture. The northern agrarians benefitted by leaving their land fallow in the summer and allowing the nomads to graze sheep upon it. In doing so, the soil was fertilized with rich manure and given the opportunity to rest between seasonal plantings (Applebaum, 1979).

Initially, the Greeks continued the agricultural practices of the indigenous Libyans but the growing pressures of a rapidly expanding population in Cyrene and demand for cereal grains in Europe ultimately led to the adoption of more intensive cultivation systems. Furthermore, most large landowners rented their estates to tenant farmers, who had a strong tax incentive to maximize production (Bostock and Riley, 1855; Applebaum, 1979). Consequently, more forested land was cut to make room for the expansion of food crop production (Applebaum, 1979).

As the forests endured continued destruction and new arable northern land became increasingly scarce, growers began sowing summer crops between their winter plantings of barley. The introduction of summer crops led to conflict with the nomads, whose sheep could no longer graze in the north to escape the seasonal droughts on the steppe (Applebaum, 1979). In retaliation, the nomadic "barbarians" (as Strabo described them), knowing how reliant Cyrene's economy was on the export of laser, "attempted to destroy all [of] the [silphium] roots" in the southern steppe (Hamilton, 1903). Strabo claims that silphium was "nearly lost" as a result (Hamilton, 1903), likely bolstering the predestined decline in silphium's population due to anthropogenic environmental changes.

By the 4th century BCE, Cyrene had a dense population, which Applebaum believes to have resulted in a serious cropland shortage based on the relation of numerous factors (e.g., population dynamics, cultivation techniques, types of crops cultivated, and expected yields) to the availability of arable land (1979). The factors considered in this estimation (despite having been approached conservatively) are numerous and some bear a significant degree of uncertainty due to the scarcity of available data, thus conclusions drawn from it should be considered accordingly. On this account, Applebaum explained his reasoning in further detail, stating that the newly acquired preference for wheat in Europe forced Cyrenaic farmers to shift away from their traditional cultivation of barley, which was viewed as the "food of slaves and animals" (1979). The Romans (another importer of grains from Cyrene) have long preferred wheat in their own culinary preparations (Applebaum, 1979; Parejko, 2003). During this period, the population of Cyrene (which accounted for roughly 80% of Libya's total population) is estimated to have been no less than 135,000 individuals, of which roughly 10,000 were slaves and 50,000 were indigenous Libyans, both of whom were likely to have consumed barley while the remaining 75,000+ likely consumed wheat (Applebaum, 1979). Barley was much better suited for Cyrenaica's short growing season and nearly twice as productive per unit of area (Parejko, 2003). The resulting decline in yield led to further southward expansion of cultivated land in order to sustain the previous level of production (Applebaum, 1979).

The resulting intrusion of cultivated land into silphium's habitat was likely detrimental, even to well-established plants. Theophrastus noted that "as the land is brought under cultivation and tamed, [silphium] retires, plainly showing that it needs no tendance but is a wild thing" (Hort, 1916). Such language not only confirms that silphium's habitat was brought under cultivation but also that silphium could not tolerate the resultant ecological disturbance of its environment. We also find that the timeline of silphium's infamous decline correlates closely with the aforementioned changes of land usage (Amigues, 2004). This would suggest that direct habitat disturbance may have also been a significant driver of silphium's extinction irrespective of the species' germination requirements, further supporting our central argument that environmental factors were of higher significance than direct exploitation.

Silphium's exorbitantly high value and luxury status (Bostock and Riley, 1855) bring into question why Cyrenaic farmers would knowingly disturb its habitat for the cultivation of relatively low-value food crops. This is perhaps explained by the fact that most growers were tenant farmers, who were highly incentivized to maximize crop yield due to tax pressures (Applebaum, 1979). A similar mentality is reflected in Pliny's testimony that these same sharecroppers found it "more profitable to departure flocks of sheep upon [silphium]" (which greatly improved the flavor of the meat and increased its value accordingly) than to harvest the plant itself (Bostock and Riley, 1855). In doing so, farmers may have been exploiting a legal loophole, as we know from Theophrastus that strict "regulations" were imposed by the Greeks "for *cutting* the [silphium] root... having regard to previous cuttings and the supply of the plant" (Hort, 1916).

On a related note, the clear lack of evidence for non-anthropogenic ecological drivers of extinction in the ancient literary record is elevated in its significance by our knowledge of silphium's immense value; that is to say such factors (predatory, pathogenic, or otherwise) would have been highly notable to our ancient sources and thus the absence of related evidence strongly suggests that none were of any major concern.

The Romans took control of Cyrenaica in the early 1st century BCE (Applebaum, 1979). By this time, silphium's continued survival was likely already destined for failure. A recent report by the Intergovernmental Panel on Climate Change cited deforestation, cropland expansion, and over-grazing as leading contributors to desertification: a process characterized by both an increase in temperature and a decrease in precipitation. Once set into motion, desertification can be extremely difficult to reverse (Mirzabaev et al., 2019). Even if the harvest of silphium had ceased entirely under Roman occupation [which most certainly did not occur (Bostock and Riley, 1855)], silphium's wild population could not have survived on its own due to the desertification of Cyrenaica initiated during the Hellenistic period.

These climatic changes, paired with the likely germination requirements of silphium (extended periods of cold-stratification under moist conditions), would have pushed the species' potential range northward, where those conditions could be met. Even in the event that the environmental changes of ancient Cyrenaica had taken place at a sufficiently gradual rate for silphium's realized range to migrate naturally, the expanding area of land under cultivation in the north would have prevented this from taking place. The most likely scenario is in fact quite the opposite: a progressive southward infringement of cultivated land into silphium's native range.

By nearly all accounts, the poor environmental and cropland management of the Greeks was further intensified under Roman occupation, making it unsurprising that silphium's extinction was ultimately recorded in the 1st century CE (Hunt et al., 2002, 2010). During this same period, we find strong evidence for increasing resource pressure in Cyrenaica. One notable study analyzed the shells of edible marine mollusks, which appear to have been a significant food source for the inhabitants of Cyrenaica since at least 12,760 BCE. Shell samples were collected from four locations in Cyrenaica (including a late-Roman farmstead) although most were excavated from the Haua Fteah cave. The disproportionate abundance of larger marine shell specimens indicates that the mollusks were intentionally collected as a food source. During the Roman period, the mean shell diameter decreased to levels not seen since the end of the last ice age. While this finding does not have any direct implications on the extinction of silphium, it does indicate an abnormally heavy reliance of the Romans on marine mollusks for nourishment due to increased dietary stress—a possible result of severe environmental changes on land (i.e., decreased precipitation, increased temperature, loss of soil organic matter, soil erosion, etc.) leading to poor crop yields. By contrast, the size distribution of modern shells is fairly even and the mean diameter is higher than any other period in recorded history, affirming that predation by humans was the primary factor impacting the size of excavated shell specimens rather than the aforementioned climatic changes, which still impact the region today (Hunt et al., 2011).

The climate of modern Libya (over 95% of which is classified as desert) does not consistently meet the necessary conditions for cold-stratification to occur in any of its regions (Saaed et al., 2019). Notably, neither *F. asafoetida* nor *F. drudeana* can be found in climates resembling that of North Africa in the modern day but rather in their colder native regions of Central Asia and Anatolia, respectively (George, 2006; Miski, 2021). The best available candidate (in terms of its proposed relation to silphium) that is still found in North Africa (*F. tingitana*), has shown to be a relatively poor match based on morphological and phytochemical features (Amigues, 2004).

Therefore, as a corollary to our main argument, we disagree with any suggestion that silphium or its closest living relatives could exist in North Africa today due to the present climate conditions. Such conditions (as previously stated) were likely initiated on a microclimatic scale (poor environmental and cropland management by the Greeks and Romans) and more recently exacerbated on a macroclimatic scale [atmospheric greenhouse effect and continued environmental degradation in the modern period (Mirzabaev et al., 2019)]. The facts that the closest likely relatives to silphium are present in colder climates outside of North Africa, and that the remaining species in North Africa are poor matches to silphium, further support the notion that silphium's successful germination was highly dependent upon environmental conditions conducive to cold-stratification. This conclusion upholds our central contention that a localized change in climate due to deforestation and cropland expansion was a major, if not the dominant, factor in silphium's extinction.

DISCUSSION

No single factor can be solely faulted for the extinction of silphium, but rather a deadly convergence of many. In addition to environmental changes, silphium's high value and luxury status are widely believed to have fueled rampant over-harvesting, heavy grazing, and even occasional vandalism (Hamilton, 1903; Andrews, 1941; Applebaum, 1979; Parejko, 2003). The latter set of factors bear less significance however, as even in their absence, the anthropogenic change of Cyrenaica's local climate would likely still have produced inadequate conditions for silphium's successful germination and growth. This argument also offers a compelling explanation for the failure of numerous attempts made to rescue the species, such as enclosing silphium stands with fencing to deter grazing livestock (Chinnock, 1884) and implementing strict regulations dictating the amount of silphium that could be harvested at any given time (Hort, 1916). In light of the presented evidence, it is now plausible to argue against the notion that these conservation strategies were not effectively implemented or enforced, but rather, they failed to address the primary driver of silphium's decline entirely.

Andrews noted that early investigations of silphium's extinction proposed the change of Cyrenaica's local climate as a contributing factor, but proceeded to entirely disregard this argument due to both the rapid pace of decline in silphium's wild population and the typically gradual progression of climatic changes (1941). He instead argued that over-harvesting and lack of adequate management under Roman rule were the primary causes (Andrews, 1941). This has remained the leading narrative ever since (e.g., Amigues, 2004) other than perhaps Parejko's brief reference to environmental degradation in ancient Cyrenaica (2003).

In contrast to Andrews and the wider narrative that direct exploitation was the primary driver of silphium's decline, we now know that climate-induced extinctions and other ecological effects can indeed occur quickly (Mirzabaev et al., 2019), helping to explain silphium's rapid disappearance. Furthermore, we must recognize that silphium, like other climate-sensitive species, cannot survive on averages. If the necessary environmental conditions for silphium's germination failed to occur for only a short duration of time, given its continued exploitation, such an occurrence would almost certainly have been sufficient to deplete its population beyond the point of recovery.

What we know of the famed silphium plant in the modern-day, from characteristics described by our ancient sources, reveal a plant that only germinated within a remarkably narrow band of geography in which a particular microclimate had been sustained. The human-induced change of this microclimate, therefore, had an outsized impact on the ability of silphium to germinate within its native range while cropland expansion to the north prevented the species from migrating to more suitable environments. For the previously stated reasons, we conclude that silphium not only represents the first recorded instance of species extinction at the hands of humankind (argued most recently by Parejko, 2003) but also the first instance of such extinction induced primarily by climate change of any cause or scale. This finding bears deep relevance in the modern world, which is plagued by environmental degradation, a rapidly changing global climate, and species extinction on a substantially wider scale than that experienced in ancient Cyrenaica.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

Initial research and drafting of the manuscript were primarily conducted by PP. The translation and analysis of non-English primary sources were conducted primarily by PR. Both PP and PR collaborated in the conception of the stated conclusions and the final editing of the manuscript. Both authors contributed to the article and approved the submitted version.

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