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Plagues, famines, and fear: How insects influenced the course of human history

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Abstract

Throughout history, insects have been silent yet potent agents of change, shaping the destiny of human civilizations in profound ways. They have actively influenced the development of societies through their roles in ecological systems and their direct interactions with humans. As carriers of disease, destroyers of crops, and symbols of both fear and resilience, insects have repeatedly forced humanity to adapt and innovate. The transformative power of these small creatures lies not only in their biological characteristics but also in their ability to alter human demographic, economic, and cultural trajectories in unexpected ways. Epidemics such as the Black Death, carried by fleas, and the enduring scourge of malaria, spread by mosquitoes, illustrate how insects have influenced demographic patterns, disrupted economies, and altered the trajectory of empires (Cantor 2002). Meanwhile, infestations of locusts and other agricultural pests have driven famines that reshaped societies, spurring migration and social upheaval. Beyond these direct impacts, insects have left an indelible mark on human consciousness, inspiring fear, innovation, and even art, as they became symbols of both destruction and resilience. This article explores the multifaceted influence of insects on human history, examining their roles in catalyzing social, economic, and cultural transformations. By understanding these interactions, we not only uncover the profound interconnectedness of humans and nature but also gain insights into addressing modern challenges posed by insects in a rapidly changing world.

Key Words

Cultural Representations of Insects, Insect-borne Diseases and Warfare, Insects and Human History, Pollination and Agricultural Systems

Introduction

The entangled history of insects and humans is as ancient as civilization itself, or even older, with traces of their interaction embedded in archaeological evidence, classical literature, and cultural mythology. Far from being peripheral, insects have played foundational roles in shaping the ecological, economic, and even spiritual dimensions of human life. Long before the rise of cities or the mechanization of agriculture, they had already begun influencing the trajectory of human societies—at times as essential pollinators and decomposers, at others as devastating pests and vectors of disease.

In early mythological, religious and literary traditions, insects were often portrayed as omens or agents of transformation. In the "Book of Exodus", locusts serve as instruments of divine wrath; in classical works such as Aristotle's "Historia Animalium" (Thompson 1910) and Virgil's "Georgics", bees and beetles reflect the dual nature of insect agency—either as symbols of industrious harmony or as harbingers of agricultural collapse. Hesiod's "Works and Days" celebrates the bee as a paragon of order and collective labor, while locust swarms, sudden and uncontrollable, embody the unpredictability of nature and the fragility of human enterprise (Lombardo and Lamberton 1993).

The Neolithic revolution marked a turning point in human-insect relations. The rise of sedentary agriculture and food storage enabled the proliferation of pests such as the granary weevil [*Sitophilus granarius* (L.)], one of the earliest entomological threats to food security (Panagiotakopulu 2000). Simultaneously, irrigation and

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landscape domestication created ideal habitats for mosquitoes, notably *Anopheles* species, whose role in the spread of malaria significantly shaped ancient settlement patterns and demographic dynamics (Sallares 2002).

Beyond fear and management, insects were also studied with curiosity and intent. Classical thinkers like Aristotle laid the groundwork for observational entomology, while Pliny the Elder's "Naturalis Historia" compiled detailed accounts of both beneficial and destructive insect species, reflecting a nascent ecological awareness (Rackham 1938). These early interpretations foreshadowed many of today's entomological challenges—from pest control and disease surveillance to the vital role of pollinators in food production systems.

As human societies expanded, intensifying agriculture, trade, and urbanization, insects adapted in parallel, exploiting new microhabitats and interaction spaces created by anthropogenic change. Their resilience and biological versatility have embedded them not only in the material conditions of human development but also in its historical ruptures: wars disrupted by insect-borne illness, empires weakened by plagues, and economies transformed by silkworms, honeybees, and locusts.

This review proposes a re-examination of insects as historical agents whose activity has shaped key developments in military strategy, economic systems, public health, and cultural memory. To make sense of their complex entanglements with human systems, we propose a typology of entomological influence across four interlocking domains:

- Biopolitical Agents – Insects as vectors of disease and population-level disruption, reshaping demographics, health systems, and settlement patterns through pandemics and endemic illness
- Ecological-Economic Influencers – Insects as both destroyers and supporters of food systems, responsible for both famines and agricultural productivity through crop damage on the one hand and pollination, biological control and commodity production (e.g., silk, honey) on the other
- Military and Strategic Actors – Insects as factors in warfare, either as unintentional saboteurs through disease transmission or as intentionally deployed weapons within biological conflict.
- Symbolic and Cultural Figures – Insects as metaphors, omens, and mythic archetypes, shaping religious doctrine, literature, and moral cosmologies across civilizations.

This typology provides a structured lens for interpreting the diverse and overlapping ways in which insects have shaped human history—materially and metaphorically. While many of the examples discussed in this review draw from historical, entomological, and epidemiological sources, others engage symbolic texts and metaphysical framings. We distinguish clearly between these registers, treating cultural narratives not as empirical data but as reflections of how societies have projected meaning onto ecological phenomena. Rather than portraying insects as solitary historical drivers, we emphasize their interaction with broader structural dynamics: climate variability, governance regimes, labor systems, and symbolic worldviews. Insects, in this framework, are not deterministic agents, but catalytic forces whose biological capacities intersect with—and often expose—the vulnerabilities of human systems.

Materials and methods

This review adopts an interdisciplinary, historically grounded methodology, combining sources and frameworks from entomology, environmental history, epidemiology, economic anthropology, and cultural studies. The review draws on a wide array of sources. Primary materials encompass original documents such as historical chronicles, religious scriptures, and classical philosophical writings. Secondary materials include scholarly interpretations and analyses found in peer-reviewed scientific literature, literary criticism, and historical research articles. Primary and secondary materials were drawn from peer-reviewed scientific literature, historical chronicles, literary texts, religious scriptures, and classical philosophical writings. Key databases and academic repositories (e.g., JSTOR, PubMed, Scopus) were consulted between 2000–2024, with emphasis on works that address insect-human interactions across ecological, political, and symbolic dimensions.

Events were selected based on their relevance to entomological impact on human systems—including agriculture, warfare, trade, and collective memory. Comparative criteria included geographic diversity, temporal span (from antiquity to the present), and the documented role of insects as direct or indirect agents of disruption or transformation. Table 1 was constructed to synthesize major historical episodes of locust-related famines (selected as case study) and their socio-political consequences, based on documented cases from multiple historical periods and regions.

No new empirical data were collected; rather, the review was aimed to offer a synthetic reinterpretation of existing knowledge through a cross-disciplinary analytical lens, highlighting the central role of insects as structural actors in human history. In interpreting the historical influence of insects, this review avoided biological determinism by emphasizing their interaction with broader socio-political, environmental, and technological systems. While insects were treated as active agents of disruption or transformation, their impact was analyzed within the context of structural co-factors—including climate variability, trade networks, governance capacity, agronomic practices, and public health infrastructures (Waller and Gotway 2004). This approach acknowledges that entomological phenomena rarely act in isolation but instead intersect with pre-existing vulnerabilities and institutional dynamics to shape historical outcomes.

The centrality of insects in historical transformations: General issues

The dynamic relationship between insects and humans has deep ecological roots, grounded in the critical roles insects play as pollinators, decomposers, herbivores, and biocontrol agents. These functions are vital to ecosystem health and have historically underpinned the agricultural and economic systems upon which human societies depend. As pollinators, insects facilitated the rise and stability of sedentary farming communities. As herbivores and decomposers, they contributed both to soil fertility and to challenges in crop cultivation—stimulating cycles of adaptation, resistance, and innovation.

Among the most dramatic disruptions are those caused by agricultural pests such as locusts, whose capacity for rapid population growth and swarming behavior has led to recurrent episodes of food system collapse. These events often coincided with systemic vulnerabilities—such as climate anomalies or monoculture farming—that magnified their socio-economic impact.

Yet the historical influence of insects extends far beyond the agrarian sphere. Certain species have acted as vectors of disease, shaping the trajectory of human health and settlement patterns. Others, such as silkworms and honeybees, became linchpins of premodern economies and trade systems. Insects have also played strategic roles in warfare and appeared as potent symbols in religious, literary, and philosophical traditions, embodying both fear and fascination (Onaga 2012).

This section offers a conceptual framework for understanding how insects have functioned as both material forces and cultural figures. In the following paragraphs, we explore their impact across four interrelated domains: public health, agricultural economies, warfare, and symbolic imagination. Through this lens, we trace how insects have consistently shaped the contours of human history.

Insects and economy: Plague, pollination and silk

Insects have had a profound and paradoxical impact on economic systems throughout history — acting simultaneously as foundations of agricultural prosperity and agents of devastating loss. Their influence spans millennia, from ancient tax systems built around apiculture and sericulture, to catastrophic locust plagues that destabilized food security across continents.

Among the most destabilizing insect threats to agrarian economies throughout history are locusts, particularly the desert locust [*Schistocerca gregaria* (Forskål)]. Known since antiquity for their capacity to swarm in vast numbers, locusts have periodically inflicted catastrophic damage across Africa, the Middle East, and Asia. Ancient Egyptian, Mesopotamian, and biblical records often depict such invasions not only as agricultural crises but as events with religious or moral significance—such as in the Book of Exodus (Bucknell 2018; Beck 1939; Gurugram 2024), where a locust plague is portrayed as divine retribution.

Economically, the impact of locust outbreaks has been marked by their scale, unpredictability, and capacity to cross political boundaries. Historical accounts from the Ottoman Empire, Mughal India, and colonial North Africa show that these infestations did not merely destroy crops, but also precipitated famines, political unrest, and changes in land tenure and taxation systems (Lecoq and Cease 2022). Locust management has been ongoing for centuries, dating back to the early development of agriculture. For instance, historical records from China document over 3000 years of migratory locust outbreaks, with more than 800 recorded episodes.

These patterns underscore the locust's long-standing entanglement with human socio-economic systems. While the specific technologies and institutional responses have evolved, the underlying dynamics remain relevant today—particularly in the context of climate change and global food insecurity, as explored in greater detail in Section 4. Furthermore, historical evidence suggests that in addition to their destructive potential, locusts have also been utilized as an emergency food source in various societies. Their consumption—particularly in agrarian contexts marked by scarcity—complicates the binary framing of locusts as purely agents of devastation and underscores the ambivalent position they occupy in human–environment interactions.

If locusts embody destruction, the honeybee (*Apis mellifera* L.) represents an archetype of productivity and ecological harmony. Managed by humans since at least 2400 BCE in Egypt, bees have served not only as pollinators critical to crop yields but also as producers of highly valued commodities: honey and beeswax. In ancient Greece and Rome, apiculture was a regulated rural industry, with honey prized for its use in medicine, religious offerings, and food preservation, but also as the only available sweetener in a world without sugar. Beeswax was essential for candle-making, writing tablets, and artistic applications. The "Lex *Manciana*" and other Roman agricultural texts include detailed references to bee management and property rights over hives, reflecting the economic and legal significance of bees in Mediterranean rural economies (Crane 1999).

Pollination, though historically under-quantified, is now understood as a keystone ecosystem service with significant economic implications. The annual global value of insect pollination has been estimated at over $200 billion (Gallai et al. 2009), underscoring how ancient economic dependencies on bees have evolved into one of the most critical sustainability challenges of the 21st century. While *A. mellifera* remains the most economically prominent pollinator, recent research has emphasized the critical role of a broader diversity of insect pollinators, including bumblebees (*Bombus* spp.), solitary bees

(*Osmia* spp., *Megachile* spp.), butterflies, moths, hoverflies (Syrphidae), and beetles, particularly in the pollination of wild flora and also crops like tomatoes, berries, and almonds (Klein et al. 2007; Garibaldi et al. 2013). These non-managed pollinators contribute substantially to both crop yield stability and ecological resilience, yet many are disproportionately vulnerable to habitat loss, pesticide exposure, and climate change. Their has prompted conservation initiatives and landscape-level planning approaches aimed at supporting pollinator diversity beyond domesticated bee species. This broader entomological picture deepens our understanding of the economic and ecological interdependence between human societies and insect biodiversity — a relationship already visible in antiquity but now made urgent by contemporary environmental pressures.

Among domesticated insects, the silkworm (*Bombyx mori* Linnaeus, 1758) stands out for its role in shaping transcontinental trade and industrial development. Originating in China during the Neolithic period, sericulture spread via the Silk Road, transforming into a state-controlled sector in many empires — including Byzantium, Persia, and the Italian city-states.

By the 13th century, Italian silk production had become a major driver of urban economies in cities like Lucca and Bologna. Silkworm cultivation required an entire infrastructure of mulberry orchards, labor-intensive rearing techniques, and complex guild-based processing systems. This made sericulture both an economic opportunity and a source of vulnerability, as epizootics affecting silkworms could collapse entire regional economies (Federico 1997). Governments intervened with research institutes, disease monitoring, and sericultural schools — early examples of entomological investment at the state level.

The economic significance of insects also manifested in fiscal structures. In various historical contexts, honey and silk were taxable goods, subject to tariffs, levies, and royal monopolies. In medieval Europe (9th–14th centuries), beekeeping obligations were codified in manorial laws, particularly in Carolingian and later feudal systems. In the Abbasid Caliphate (8th–10th centuries), honey was collected as an in-kind tax within agrarian and market frameworks. Silk duties, introduced as early as the Tang Dynasty in China (7th–10th centuries) and later systematized under the Song and Ming Dynasties, were also pivotal to state revenue. In Europe, particularly in the urban republics and principalities of the 13th–16th centuries (e.g., Lucca, Venice, Florence), silk trade and taxation supported urban bureaucracies, contributing to both legal codification and economic centralization (Molà 2000).

The fiscal entanglement of entomological activity underscores how insects, far from being mere natural agents, were deeply implicated in political economies—serving as both productive resources and catalysts of agrarian vulnerability.

Insects have influenced the global economy both as biological assets and agricultural threats. Their capacity to destroy harvests or sustain entire industries underscores their dual role in economic history. Understanding the entomological foundations of trade, taxation, and rural production reveals the extent to which insects have not only adapted to human systems, but co-structured them — from imperial supply chains to peasant economies.

Epidemics and insects: Tiny carriers, massive collapse

One of the most devastating pandemics in human history—the Black Death (1347–1351) —originated and spread through the agency of a small arthropod: the oriental rat flea (*Xenopsylla cheopis* Rothschild), primary vector of *Yersinia pestis* (Lehmann-Neumann). Infesting black rats (*Rattus rattus* L.) that thrived in densely populated and poorly sanitized urban environments, these fleas proliferated along expanding trade routes such as the Silk Road, facilitating the rapid transmission of bubonic plague across Eurasia (Perry and Fetherston 1997). The demographic impact was catastrophic: an estimated 25 to 30 million people—roughly one-third of Europe's population—perished in the initial wave (Benedictow 2004 and 2021).

While fleas served as critical biological intermediaries, the scale and speed of the pandemic were the result of a broader socio-ecological matrix: climatic anomalies linked to the Little Ice Age, high urban density, weak public health infrastructure, and intensifying connectivity through commerce. Insects, in this context, were not isolated causal agents but accelerants within a system already strained by environmental and institutional fragility.

The plague's consequences were both immediate and transformative. Labor shortages destabilized feudal economies, empowered surviving workers, and accelerated the transition toward wage labor and urban growth (Herlihy and Cohn 1997). The shock to religious authority—unable to contain or explain the catastrophe—fueled growing skepticism and provoked spiritual introspection. Cultural responses such as the Danse Macabre and Boccaccio's Decameron (Holbein and Douce 1833; McWilliam 1995.) reflected widespread existential anxiety and a new awareness of human vulnerability. In this sense, *X. cheopis* functioned not merely as a disease vector, but as a catalyst of civilizational upheaval. If fleas reshaped medieval Europe, mosquitoes —particularly of the genus *Anopheles*—played an equally transformative role in the tropical and subtropical regions of the world, but also in temperate zones, where malaria profoundly shaped human settlement, land use, and public health strategies, as illustrated by historical cases such as the Pontine Marshes in Italy. As the primary vector for *Plasmodium* spp., the causative agents of malaria, *Anopheles* mosquitoes have significantly influenced human settlement patterns, land use, and imperial ambitions over millennia.

Archaeological and paleo-ecological data suggest that even early Mesopotamian communities were shaped by the need to avoid malarial wetlands, as chronic disease

burden in low-lying areas discouraged permanent habitation (Sallares 2002). With the expansion of agriculture and irrigation, particularly in colonial contexts, breeding grounds for mosquitoes multiplied. Malaria subsequently became entrenched in many parts of Africa, South Asia, and the Americas, profoundly affecting both indigenous populations and colonial settlers.

During European colonial expansion in the 18th and 19th centuries, malaria functioned both as an ecological barrier and a geopolitical determinant. Colonizers often struggled to maintain settlements in malarial zones, leading to the prioritization of highland or dry regions for administrative centers (Packard 2007). The disease was so pervasive that the differential immunity between Europeans and local populations occasionally altered military and economic outcomes. For instance, in sub-Saharan Africa, European powers often relied on locally recruited labor and intermediaries to mitigate the fatal toll malaria exacted on their own personnel (Padian 2008).

The colonial encounter also intensified environmental changes that exacerbated malaria transmission—deforestation, plantation agriculture, and water infrastructure created ideal larval habitats. Even into the 20th century, global eradication efforts—such as those employing DDT—were undermined by *Anopheles*' extraordinary adaptive plasticity and evolving insecticide resistance (Hemingway and Ranson 2000). Thus, the mosquito stands not only as a transmitter of pathogens, but also as a decisive agent in the epidemiological and political history of empires and states.

In the 21st century, globalization and rapid urbanization have facilitated the emergence and spread of insect-borne viral diseases with pandemic potential. *Aedes aegypti* L., a mosquito species originally native to Africa, has become a vector for several arboviruses—including dengue, Zika, chikungunya, and yellow fever—in various parts of the world. Its urban ecology, characterized by breeding in stagnant water accumulated in human-made containers -even very modest ones such as small vases for cut flowers, buckets, tires, and cisterns-, and a preference for biting during daylight hours, has enabled it to thrive in densely populated tropical and subtropical cities. The resurgence and expansion of dengue fever, now endemic in over 100 countries, exemplifies the entomological dimensions of modern global health threats. The 2015–2016 Zika virus outbreak in the Americas underscored *A. aegypti*'s ability to rapidly disseminate novel pathogens, with severe consequences for maternal health and public health infrastructure. Factors such as climate change, international air travel, and inadequate urban planning have converged to expand the mosquito's range and intensify its impact (Kraemer et al. 2015). *Aedes aegypti* has only been intercepted and has not established in Italy, contrary to *Aedes albopictus* (Skuse), of Asian origin, which is well spread in Italy, is strictly close in morphology, biology and behavior to *A. aegypti* and has also been reported as a vector of several arboviruses (Puggioli et al. 2017; Fortuna et al. 2024). Unlike *Anopheles*, which thrives in rural or peri-urban wetlands, both *A. aegypti* and *A. albopictus* are closely aligned with human behavior and built environments. The modern metropolis thus becomes not a refuge from nature, but a new habitat and amplifying environment for entomological threats. Controlling these mosquitoes requires not only technological innovation—such as sterile insect techniques (SIT) —but also systemic improvements in housing, water management, and community engagement (Bhatt et al. 2013; Malfacini et al. 2022).

In summary, the evolution of insect-borne pandemics reveals a persistent entanglement between insect biology, biology of microorganisms, environmental transformation, and socio-political systems. From *X. cheopis* to *A. aegypti*, insects have repeatedly operated as agents of epidemiological upheaval, reminding us that global health remains inextricably linked to ecological dynamics.

Insect-driven famines: Locusts, crops, and collapse

Locust plagues have haunted the historical and literary imagination of multiple civilizations, symbolizing the terrifying convergence of natural disaster and divine retribution. In the Book of Exodus 10:14–15 (Bucknell 2018), the eighth plague—swarms of locusts—was unleashed as a punishment against Pharaoh, described as so dense that "they covered the face of the whole land so that the land was darkened" (Grenzer 2024). This passage not only conveys ecological devastation but also represents a moral indictment, in which environmental catastrophe serves as divine justice.

In the Greco-Roman world, locusts also held symbolic and material significance. Pliny the Elder, in "Naturalis Historia" (Book XI, 35) (Gibson 2011), catalogued their biology and impact, noting how swarms would devastate crops and forests alike. His description is striking for its detail, acknowledging both the empirical destructiveness and the cosmic resonance of these insects. Similarly, Virgil's "Georgics" paint a vivid image of famine-inducing insects, warning of their overwhelming capacity to annihilate harvests and destabilize rural economies (Georgics I.177–186) (Miles 2021). These classical depictions emphasize how locusts were understood not merely as biological threats but as portents of disorder in both nature and society.

Such narratives reinforced a cultural association between insects and divine displeasure. Famine, induced by these voracious swarms, was not just a material condition but a sign of a broken harmony between humans and the natural (or divine) order. In many ancient traditions, the insect swarm became a moral metaphor—an embodiment of imbalance and hubris—that still echoes in contemporary discourses on ecological collapse.

Locust swarms such as those of *Schistocerca gregaria* undoubtedly caused (and cause) severe agricultural damage, but their impact on food security and social order must be situated within larger contexts. Climatic irregularities (such as unseasonal rains), monocultural farming practices, colonial land tenure systems, and weak

institutional responses all may compound the devastation. The entomological event can be catalytic, but not singularly determinative. Famine, in these cases, emerge from a complex interplay of ecological, economic, and political vulnerabilities — with locusts acting as accelerants within already precarious systems.

While ancient accounts emphasized the symbolic and theological meanings of locust plagues, contemporary entomology and climatology have revealed the complex ecological mechanisms underlying these phenomena. The desert locust (*S. gregaria*) is one of the most studied of these agents of famine, renowned [as other species, i.e., *Dociostaurus maroccanus* (Thunberg) and *Locusta migratoria* (Linnaeus)] for its capacity to shift from a solitary to a gregarious phase when environmental conditions—particularly vegetation density and humidity—cross specific thresholds. This phase polyphenism, driven by neurohormonal changes, enables the formation of vast, mobile swarms capable of covering hundreds of kilometers in a single day (Pener and Simpson 2009; Cullen et al. 2017; Zhang et al. 2019a, 2019b).

The ecological adaptability of *S. gregaria* has led to periodic agricultural disasters in regions spanning East Africa, the Arabian Peninsula, Iran, and the Indian subcontinent. Notably, the 2020–2021 outbreak in East Africa—exacerbated by unseasonal cyclones linked to climate change—devastated crops across Kenya, Ethiopia, and Somalia, affecting over 40 million people (FAO 2020). These swarms destroyed not only staple crops like maize and sorghum but also livestock fodder, threatening pastoral systems and amplifying existing food insecurity.

What makes modern locust plagues particularly alarming is their interaction with fragile agricultural infrastructures and monocultural cropping systems. In many affected areas, smallholder farmers rely heavily on a single harvest per season; thus, the loss of a single crop can trigger cascading effects—debt accumulation, displacement, and in extreme cases, famine. The vulnerability of these agro-ecosystems highlights the structural fragility induced by globalized food economies and the ecological risks of intensive land use.

In response, international organizations have attempted to institutionalize surveillance and control mechanisms. The Food and Agriculture Organization (FAO) has spearheaded early warning systems based on satellite imagery, meteorological modeling, and field reports. Despite these innovations, many national response systems remain underfunded or politically constrained, making coordinated action difficult during large-scale outbreaks (Brader et al. 2006). The persistence of these crises, despite technological advances, underscores the need for integrating ecological science with policy, infrastructure, and community-based resilience strategies (Therville et al. 2021).

Historically, locust-induced famines have functioned not only as crises but also as catalysts for transformation—forcing innovation, migration, and political unrest. In the pre-modern world, repeated agricultural failures often prompted the development of new agronomic techniques, diversification of food systems, and the restructuring of land tenure systems. For example, in colonial India, successive locust invasions in the late 19th century were compounded by drought and administrative inertia, contributing to deadly famines that led to rural uprisings and eventually spurred limited agrarian reforms (Zewde 2001). These entomologically driven crises and their socio-political consequences are synthesized in Table 1, which offers a comparative overview of key historical episodes in which locust plagues catalyzed agrarian change, migration, and political unrest.

In many contexts, mass migrations have followed in the wake of locust-induced famine, as rural populations sought refuge in urban centers or across borders. These displacements not only altered demographic patterns but often created new pressures on urban infrastructures, reshaping labor markets and socio-political dynamics.

Moreover, the fear of locusts has repeatedly mobilized collective action. In regions of the Sahel and Horn of Africa, local communities have developed traditional ecological knowledge (TEK), which includes systematic monitoring of environmental indicators to predict locust outbreaks, manual removal of egg masses, and the use of physical barriers or controlled burning to prevent the spread of swarms,—measures rooted in practices dating back to antiquity. However, these traditional empirical methods are now generally considered to have had little significant impact on large-scale locust invasions due to the desert locust's ability to disperse by flight and the speed of its movements (Dobson 2001; Mwikali et al. 2024). Such measures are essentially symbolic, or used as a last resort in the absence of modern surveillance and control tools.

In modern times, state actors and NGOs have increasingly sought to incorporate this knowledge into adaptive governance frameworks, although not always successfully (Folke et al. 2005).

Perhaps most striking is the enduring role of famine as a trigger for political upheaval. Food shortages caused or worsened by insect plagues have frequently undermined regimes and delegitimized state authority. The inability to ensure food security in the face of ecological threats often exposes systemic inequalities, galvanizing protest and, in some cases, revolutionary change (Carson 2002).

Thus, while locusts remain biological phenomena, their historical impact transcends entomology. They are socio-political actors whose presence has repeatedly provoked rethinking of how societies govern food, manage risk, and adapt to ecological stress. As Lecoq (2005) aptly observes, "the focus of locust control studies, if a sustainable solution is to be found, should not simply be the locust, but also humanity, its real motives, competing interests and organization strategies".

Recognizing this broader entanglement between insects, agriculture, and politics is essential to developing robust and equitable responses in an era of climate volatility and ecological interdependence. The historical locust swarms and their socio-economic impacts are summarized in Table 1.

Table 1. Sample of Notable Historical Locust Outbreaks and Their Socio-Economic Impacts.

Period / Event	Insect Species	Region Affected	Historical Impact	Societal / Institutional Response	References
Biblical Era (c. 13th century BCE, Exodus narrative)	*Schistocerca gregaria*	Ancient Egypt and Levant	Crop devastation described as divine punishment; symbolic of ecological catastrophe	Ritualized interpretations; absence of coordinated institutional response	Grenzer (2024); Lecoq and Cease (2022)
Classical Antiquity (Pliny the Elder, 1st c. CE)	Likely *S. gregaria* (southern Mediterranean) and *L. migratoria* (Europe)	Mediterranean Basin and parts of Europe	Pliny documents recurring agricultural collapses due to swarms	Imperial chronicling but no known large-scale state mitigation systems	Pliny the Elder, "Naturalis Historia"; Gibson (2011); Eco (2012)
1860s–1900s	*S. gregaria*	British India	Major famines compounded by drought and colonial neglect; thousands of deaths	Limited colonial intervention; later reforms in famine response policies	Nevo (1996); FAO (2020)
1915–1917	*S. gregaria*	Ottoman Levant (Palestine, Syria)	Locusts destroyed food supplies during World War I; famine and economic disruption	Regional administrative failures; societal breakdown and mass suffering	Lecoq and Cease (2022); Grenzer (2024)
1930–1950	*S. gregaria*	Africa, Middle East	Scientific foundations of preventative control defined by Uvarov; improved understanding of phase polyphenism	Early international cooperation; post-WWII FAO initiatives (DLCC)	Uvarov (1938); FAO (1968, 1972); Jago (1998)
1918–1985	*S. gregaria*	Africa, Middle East, South Asia	Three major invasion periods with widespread crop loss and famine	Gradual implementation of early control measures, aerial spraying, monitoring	Showler et al. (2021); Lecoq and Cease (2022)
1986–1989	*S. gregaria*	Sahel, West Africa	Significant modern outbreak, but controlled within two years due to proactive intervention	FAO-led regional coordination; improved international response	FAO (2020); Brader et al. (2006); Showler et al. (2021)
2020–2021	*S. gregaria*	East Africa, Middle East, Pakistan	Triggered by cyclonic rains; major food insecurity affecting over 40 million people	FAO-led response with drone surveillance, satellite forecasting, and biopesticides	FAO (2020)
2020–2022	*Dociostaurus maroccanus*	Sardinia (Italy)	Recent outbreaks damaging cereal crops and pastures; part of a long history of recurrent plagues in Mediterranean basin	Regional monitoring programs; emergency mechanical and chemical control; agroecological approaches	Lecoq and Cease (2022); Khairov et al. (2024)

Note: Historical records indicate that past invasions in Egypt and the southern Mediterranean were primarily caused by *Schistocerca gregaria*, while those affecting Europe (up to France and Germany) were due to *Locusta migratoria* originating from the Danube delta (Eco 2012). This table provides a sample of notable locust outbreaks across different historical periods and regions and does not aim to be exhaustive.

A closer reading of Table 1 reveals a clear typology of institutional responses to locust-induced crises, ranging from symbolic interpretation to coordinated international intervention. This typology can be grouped into three broad phases:

1. Ritual and fatalism (pre-modern era): in ancient and classical societies (e.g., Biblical Egypt, Pliny's Rome), locust plagues were framed through religious or metaphysical lenses, often interpreted as divine punishment. Institutional responses were minimal or nonexistent, relying instead on ritual practices or fatalistic acceptance.
2. Ad hoc administration and reactive governance (colonial and early modern periods): In British India and Ottoman Palestine, limited bureaucratic responses occurred. However, these were often reactive, under-resourced, and constrained by political priorities or colonial indifference. Locust swarms exposed administrative fragilities, often compounding the severity of famine and triggering unrest.
3. Surveillance and transnational coordination (late 20th – 21st Century):

The scientific foundations of a preventative control strategy for locusts — particularly for the desert locust (*Schistocerca gregaria*) — were defined by Boris Uvarov in the 1930s (Uvarov 1921, 1928, 1937). At the 1937 International Conference on Natural Disasters, Uvarov (1938) emphasized that invasions could be prevented by targeting hopper bands and swarms in localized outbreak areas, provided there was a solid understanding of the species' ecology and effective international cooperation.

These principles were quickly recognized at the global level, especially with the establishment of the Food and Agriculture Organization (FAO) in 1945, which laid the groundwork for coordinated action. In the 1950s, the FAO helped create the Desert Locust Control Committee (DLCC), which remains central to promoting joint surveillance and control measures. Since 1955, FAO member states have mandated the organization to coordinate desert locust monitoring and control activities, primarily through its Desert Locust Information Service (DLIS) — initially managed by the Anti-Locust Research Centre (ALRC) in London (1943–1978), and later by FAO in

Rome. The period between 1930 and 1950 is often seen as a turning point, when modern preventive control approaches emerged (Jago 1998). Since the 1960s, locust invasions have become less frequent, more limited in scope, and typically contained within one or two years. This is largely due to advances in monitoring (e.g., satellite imaging, GIS tools, drones) and the institutional strengthening of FAO, regional commissions, and early warning systems (FAO 1968, 1972; Hafraoui and McCulloch 1993; Magor et al. 2005; van Huis et al. 2007). However, challenges persist due to uneven funding, logistical constraints, and political instability — as illustrated during the delayed interventions of the COVID-19 pandemic (2020–2021).

Insects and warfare: Biological disruption and strategic vulnerability

Throughout history, insects have influenced the outcomes of military conflicts not merely as background elements of the battlefield environment, but as active disruptors of military capacity. Their role in warfare can be categorized into two primary modalities: (1) deliberate use as biological weapons and (2) unintended yet decisive factors in the spread of vector-borne diseases that altered the course of campaigns and wars (Harris 2002).

The use of insects as weapons predates modern biological warfare doctrines. In antiquity and the medieval world, insects were harnessed for their capacity to sow chaos, inflict pain, and spread disease. Beehives and wasp nests were catapulted or dropped onto enemy fortifications, particularly during sieges, exploiting the natural aggression of hymenopterans to disrupt enemy troops and create panic within defensive positions (Lockwood 1987).

Historical accounts from Roman, Chinese, and later European sources recount how defending armies would intentionally weaponize bees or hornets to deter invaders, often using local knowledge of swarming behaviors to optimize impact. In 198 CE, during the siege of Hatra in Mesopotamia, defenders allegedly used clay pots filled with venomous insects against Roman attackers, combining psychological terror with physical threat (Lockwood 2008). These tactics underscore the extent to which insects were perceived not only as natural nuisances but as biological allies capable of tactical intervention.

Far more consequential than direct weaponization was the role of insects in the epidemiological and ecological destabilization of armies and empires. From antiquity to the modern era, insect-borne diseases and pest-induced famines have not only impaired military effectiveness but also catalyzed political collapse and societal transformation. One of the earliest examples is the Plague of Athens (430 BCE), vividly described by Thucydides, which likely involved typhus, or another epidemic disease transmitted by fleas (*X. cheopis*) or lice (Nelson et al. 2007). The epidemic killed an estimated one-third of the city's population, including its leader Pericles, undermining the Athenian war effort, eroding morale, and contributing to Athens' eventual defeat in the Peloponnesian War. In the 5th century CE, the invasions of Attila the Hun coincided with a period of widespread ecological crisis, including locust infestations that devastated crops across the Eastern and Western Roman Empires (Eco 2012). Historical evidence suggests that past invasions affecting Egypt and the southern Mediterranean were caused by the desert locust (*Schistocerca gregaria*), whereas those that extended into central and northern Europe — including regions that are now France and Germany — were due to the migratory locust (*Locusta migratoria* Linnaeus, 1758), originating from the marshlands of the Danube delta. These migratory locust invasions in Europe ceased a few centuries ago, largely due to anthropogenic changes in their breeding areas (Lecoq 2022).

Chroniclers such as Priscus and Procopius recount how these environmental shocks, including famine and disease, weakened the empire's resilience and contributed to its political fragmentation (Blockley 1983; Dewing 1941). Locusts (*S. gregaria*), already symbolically associated with divine punishment in Roman and Christian traditions, played a tangible role in precipitating food insecurity and social unrest. These compounded pressures helped dismantle centralized Roman governance and accelerate the transition toward localized, feudal economies. Shortly thereafter, the Justinianic Plague (541–542 CE), caused by *Y. pestis* and transmitted by fleas, devastated the Byzantine Empire, killing between 25 and 50 million people (Eisenberg and Mordechai 2020). The resulting labor shortages and fiscal collapse significantly undermined Emperor Justinian's ambitions to reunify the Roman territories, altering the trajectory of European history and reinforcing the geopolitical shift toward the early medieval period. This entomological vulnerability persisted across centuries. During the Roman Empire, endemic malaria in the Pontine Marshes and Tiber Valley shaped military logistics and settlement patterns, limiting the empire's capacity to project power into affected regions (Sherman 2017). In the 19th century, the role of *Anopheles* mosquitoes became dramatically evident during the French campaign in Haiti (1801–1803), where more than 30,000 soldiers of Napoleonic troops died of malaria and yellow fever. This epidemiological catastrophe played a decisive role in the success of the Haitian Revolution, marking a turning point in colonial resistance and European military decline in the Caribbean. Lice-borne typhus also proved lethal during the Napoleonic Wars, particularly in the failed Russian campaign of 1812, where epidemic typhus (*Rickettsia prowazekii* da Rocha-Lima, 1916, transmitted by body lice and not to be confused with typhoid fever caused by *Salmonella enterica* subsp. *enterica* serovar Typhi (Schroeder and Edwards 1962) killed more soldiers than combat (Booss and Bia 2025). The pattern repeated during World War I, especially on the Eastern Front, where typhus spread rapidly in trench conditions, prompting early innovations in

public health such as delousing stations and chemical insecticides. In each of these episodes, insects did not merely accompany the march of history—they shaped it from within, acting as ecological catalysts and biological saboteurs that exposed the vulnerabilities of imperial systems. Their role in undermining military strength, triggering famine, and facilitating population collapse makes them indispensable subjects (though often overlooked) in any analysis of warfare, power, and resistance across time.

The entomological dimension of warfare also catalyzed innovations in military medicine and vector control, laying the groundwork for modern entomology and epidemiology. The identification of mosquitoes as the vector of malaria (Ross 1897) and of yellow fever (Reed et al. 1900) prompted large-scale interventions in military planning and colonial infrastructure, from draining swamps to distributing quinine rations. During the construction of the Panama Canal, U.S. Army doctors implemented entomological surveillance and larvicidal measures to control *A. aegypti* populations, transforming entomology into a tool of imperial expansion and labor discipline (Mitchell et al. 2002). Thus, insects did not merely challenge armies; they shaped military-scientific responses, contributing to the professionalization of disease ecology and the militarization of public health. Insects have exerted a profound influence on the conduct and outcome of wars. Whether deployed as weapons or acting as invisible saboteurs through disease, they have demonstrated a capacity to shape geopolitical outcomes and military strategies (Felton 2012). Understanding the historical entanglement between insects and warfare reveals the necessity of integrating entomological and microbiological insight into military history, while also foregrounding the roots of contemporary approaches to vector control and disease mitigation in conflict zones.

Cultural memory and symbolism

Before proceeding, it is important to clarify the interpretive approach taken in this section. While earlier parts of this review emphasize empirical evidence of insect-driven disruption—such as disease transmission or agricultural collapse—this section examines the symbolic life of insects in myth, religion, and literature. These cultural texts are not treated as direct historical records, but as reflective surfaces through which societies encoded fear, awe, and moral interpretation of ecological events. In this sense, insects operate here not as causal agents, but as discursive figures, whose meanings are shaped by cultural context and serve as indices of broader socio-environmental anxieties.

Throughout human history, insects have occupied a profound and often ambivalent position in cultural memory, religion, and symbolic systems. Their representation in myths, sacred texts, and literary traditions reflects not only biological familiarity but also deep-rooted psychological and societal projections. Insects embody both the awe of order and the terror of chaos, functioning as potent metaphors for human anxieties and aspirations.

Insect imagery is prominent in diverse religious and mythological frameworks. The honeybee (*A. mellifera*), for instance, has long been associated with sacredness, diligence, and social harmony. In ancient Egypt, bees symbolized the soul and were tied to the Pharaoh's divine authority (Ransome 2004). Greek and Roman sources viewed bees as messengers between worlds, often linked to the Muses and prophetic insight (Carlson 2015).

In stark contrast, the locust appears as a destructive force in multiple religious texts, not only in the Book of Exodus (Exodus 10:1–20), but also in the Book of Revelation (9:3–11); in this Book, apocalyptic locusts are unleashed as instruments of torment, described with scorpion tails and human faces — an unsettling hybridity reflecting eschatological fear (Horn et al. 2009).

Similarly, the "Lord of the Flies" (Beelzebub) — a name derived from the Philistine deity associated with flies — evolved in Judeo-Christian tradition into a demon embodying decay and corruption (Wedeck and Baskin 2019). Flies in literature and theology often symbolize death, pestilence, and moral decline, a connotation echoed in works such as William Golding's "Lord of the Flies", where they represent societal breakdown and latent savagery.

The cultural imagination attributes a dual symbolic function to insects. Bees, as agents of pollination and producers of honey, embody communal industriousness, ecological balance, and even immortality through their representation in funerary iconography (Carlson 2015). Conversely, locusts and flies reflect collective trauma: they are associated with agricultural devastation, disease, and divine wrath, as seen in both historical records and prophetic literature (Nevo 1996).

An anthropological perspective reveals that locusts are not solely symbols of catastrophe, but also integral to cultural traditions and subsistence strategies in some indigenous societies. In the cerrado regions of Mato Grosso, Brazil, locusts have long been a key component of the local ecosystem and diet, particularly among the Nambiquara, Baikiri, and Parecis tribes. As early as the 1930s, Claude Lévi-Strauss noted that locusts were consumed by the Nambiquara (Lévi-Strauss 1948, 1979). Subsequent studies (Setz 1983, 1991; Lecoq and Pierozzi Jr 1995) document traditional harvesting techniques of *Rhammatocerus schistocercoides* (Rehn), which is captured, toasted, and incorporated into daily meals. Beyond their dietary role, Parecis mythology attributes to locusts foundational significance: one myth describes a locust arising from the leg of a heroic figure, Miore, and inadvertently giving fire to humanity (Pereira 1986). These narratives highlight a deep and long-standing relationship between humans, locust populations, and fire management practices that favor grass regrowth and sustain ecological balance.

This dichotomy highlights a broader anthropocentric projection: insects as reflections of the human condition — industrious when society thrives, catastrophic when moral or ecological order collapses.

Insects often serve as mnemonic agents of catastrophe and resilience. Their cyclical appearances — like locust swarms or seasonal bee movements associated with transhumant beekeeping — embed them in agricultural calendars and oral histories, reinforcing their symbolic resonance. Cultural responses to insect phenomena can be viewed as mechanisms of resilience, preserving ecological awareness and spiritual narratives through ritual, myth, and art (Merritt 2013).

Modern literature continues this tradition: Kafka's "The Metamorphosis" (1915), where the protagonist transforms into an insect, explores alienation and the loss of humanity, while insect imagery in post-apocalyptic fiction underscores environmental collapse and existential dread (Peroikou 2019).

The symbolic life of insects reveals their integral role in shaping and preserving cultural memory. From the divine industriousness of bees to the apocalyptic terror of locusts, these creatures serve as mirrors of human civilization's values, fears, and ecological consciousness. Their ambivalent symbolism — oscillating between chaos and order — underscores their enduring place in the collective imagination, making them critical subjects for entomological humanities research.

Conclusion: From vectors to forces of history

Insects have long occupied a paradoxical yet profoundly transformative position in human history — not merely as vectors of disease or agents of agricultural ruin, but as organisms deeply entangled in the shaping of civilizations. Their presence, while often invisible or overlooked, has continuously challenged the illusion of human sovereignty over nature, revealing instead a world in which our systems — economic, political, symbolic — are deeply intertwined with those of the smallest creatures. Far from being passive background figures, insects emerge as biological agents with political, economic, and cultural significance, whose influence has permeated both the visible and invisible structures of history.

Historically, insects have operated at critical fault lines, i.e., where empires rise and fall, where agricultural regimes collapse, where trade routes flourish or break down, and where belief systems evolve in response to fear, scarcity, and awe. The philosopher Michel Serres, in "The Parasite" (1980), saw the parasite not merely as a biological phenomenon, but as a structuring force within systems of exchange and power — disrupting, destabilizing, and generating new orders. In this sense, insects have not only damaged the old but have often provoked reorganization, spurring innovation, resistance, and adaptation.

The locust, for instance, embodies both ecological devastation and symbolic rupture. In "The Book of Joel" (Bucknell 2018), locusts are described in cascading succession — "What the cutting locust left, the swarming locust has eaten..." — evoking not just famine, but the total collapse of ecological and spiritual order. And yet, such catastrophes have historically led to institutional innovation, from agronomic reforms and grain storage systems to the development of early meteorological observations. Conversely, the honeybee has long served as a metaphor for social harmony and collective labor. In Virgil's "Georgics" (Miles 2021), the hive mirrors the structure of Rome itself — hierarchical, disciplined, and unified. This symbolism reemerges in early modern political philosophy: for Hobbes, the beehive represents the centralized power of the state; for Mandeville, in "The Fable of the Bees" (1714), it becomes a metaphor for the moral contradictions of capitalist society, where private vices paradoxically generate public good (Semler 2018).

These literary, religious, and philosophical examples show that insects do not appear in history merely as biological realities, but as discursive figures — creatures through which humans have explored fundamental tensions between order and chaos, morality and survival, control and collapse. In Kafka's "Metamorphosis" (1915), the insect is no longer a symbol of nature but of existential alienation. The unnamed creature into which Gregor Samsa transforms externalizes the deep anxieties of modern life: invisibility, dehumanization, and the erosion of relational bonds in an industrialized society.

Beyond metaphor, insects have acted as disruptive material forces: destabilizing military campaigns through disease, triggering famines that undermined imperial rule, and shaping economic systems through their labor (as in apiculture and sericulture). From the Roman malaria zones to the typhus-infested trenches of World War I, and from silk diplomacy to locust-driven migration, insect life has been inseparable from human geopolitical outcomes.

Even in the present, their agency persists — not only biologically, but symbolically and systemically. The resurgence of *A. aegypti* and *A. albopictus* in global cities, the dramatic decline of pollinators, and the locust plagues exacerbated by climate changes signal more than ecological alarm bells; they mark the insect as a sentinel of systemic fragility. Insects have become both indicators and agents of planetary health — mirrors through which we confront our vulnerabilities in the Anthropocene (Potts et al. 2010).

Ultimately, insects have rarely acted in isolation. Their historical significance lies not in unilateral causation, but in how their biological capacities intersect with—and expose—the structural dynamics of human societies: governance systems, environmental management, economic dependencies, and cultural imaginaries.

Understanding insects, then, is not a niche concern of biology or entomology, but a gateway to rethinking human history, governance, and future-making. It requires an integrated approach — one that brings together environmental history, epidemiology, political ecology, and cultural theory — to make sense of how these small, ancient organisms have played oversized roles in shaping our collective fate. To study insects is, in part, to study

ourselves: our fears, our dependencies, our myths, and the systems we build in response to the nonhuman world. In this light, insects emerge not only as subjects of science or symbols in story, but as forces of history — capable of tracing, interrupting, and remaking the human condition.

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