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Review Article

Plants in the shadows: Bridging the gap in paleoecology and paleoart

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ABSTRACT

Paleoart, long considered peripheral to paleoscience, has become a powerful medium for visualizing extinct life and landscapes. Yet its historical trajectory has been dominated by zoocentric traditions, where plants are relegated to vague backdrops despite their central role in Earth system dynamics. This review examines the epistemological and cultural consequences of such plant blindness, situating paleoart at the intersection of paleontology, paleoecology, and landscape studies. We provide a critical historical synthesis, tracing the representation of vegetation from nineteenth-century phytocentric pioneers to the consolidation of animal-centered canons and the persistence of clichés that obscure paleobotanical data. Drawing on case studies across the Paleozoic, Mesozoic, and Cenozoic, we show how integrating fossil pollen and spores, macrofossils, taphonomic and multiproxy records—transforms paleoart into a form of visual scientific modeling that reveals ecological interactions, climatic drivers, and biogeographic patterns invisible in faunal reconstructions alone. Beyond historiography, we evaluate methodological frameworks for translating fragmentary data into coherent visual ecosystems, emphasizing the role of taphonomy, landscape reconstruction, and explicit protocols of inference. Particular attention is given to recent botanical paleoart that has redefined the visual vocabulary of deep time, replacing repetitive templates ("monkey puzzles and parking lots") with floristically accurate reconstructions anchored in paleobotanical evidence. Finally, we highlight the Quaternary record, where paleoart remains less developed despite the abundance of high-resolution palynological, anthracological, and macrofossil archives. Here we present original reconstructions from the Iberian Peninsula that illustrate how glacial refugia, ecological mosaics, and vegetation dynamics can be made visible through art. These examples demonstrate that paleoart, when botanically informed, is not ancillary illustration but a methodological extension of paleoecology.

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1. Introduction

How many scientific careers have been sparked by a sudden fascination—an accidental glimpse of a painting in a museum, an exhibition display, or even those mid-twentieth-century commercial products that, in their kitsch way, portrayed dinosaurs and other "prehistoric beasts"? The answer is likely more than we imagine. For many students of evolution, such moments of visual impact can be compared metaphorically to the contingent events of Earth's geobiological history: small, chance encounters with images that set in motion long intellectual trajectories. This is the enduring power of paleoart. Once considered a decorative or nostalgic curiosity, paleoart today stands as a genuine scientific–cultural practice. It generates aesthetic experiences while simultaneously offering images of life in the deep past, functioning not only as illustration but as a vehicle of knowledge and imagination.

We are, after all, visual creatures. "Seeing comes before words," as Berger (1959) once observed. Even the word *theory* derives from the Greek *theorein*, meaning "to see" or "to contemplate." Every discovery begins from this act of *theorein*—a perception shaped by accumulated experience and open to the possibility of surprise. In contrast, the transition during the Romantic period from "natural philosophy" to "science" marked a conceptual rupture. Etymologically, *philo-sophia* meant the "love of wisdom about natural things," whereas *scio* in Latin simply meant "to know." The shift was not merely terminological: it ushered in reductionist tendencies that became institutionalized in academic systems and curricula.

The consequences remain with us. Many teachers lament how brilliant students turn away from scientific careers because they see little space for creativity. Generations have been lost to a narrow conception of science as the rote memorization and regurgitation of facts. We have failed to convey that science depends deeply on human imagination. We have allowed bureaucratic frameworks to shape curricula that strip away the thrill of discovery and the intellectual adventures of exploring intricate natural structures. As a result, students are rarely invited to experience those fleeting but transformative *Eureka* moments, or to approach nature with the fresh, imaginative lens that fosters genuine insight. Paleoart is intimately connected to this state of intellectual excitement. By making visible what is otherwise absent, it encourages curiosity, nurtures creativity, and reminds us that to understand the past—and science itself—we must not only analyze but also *see*.

Our review advocates for the role of plants in paleoart, with particular attention to their taxonomic, geobotanical, and landscape components in the visual reconstruction of past terrestrial ecosystems, from the Paleozoic to the Holocene. Our objectives are to define and professionally contextualize paleoart, to examine historical examples of artworks that have treated fossil flora and vegetation with scientific accuracy, to highlight persistent errors and misconceptions concerning fossil plants, and finally to present original cases of paleovegetation reconstructions.

2. Paleoart: Scope and practice

Paleoart is best understood as an interdisciplinary practice at the intersection of art and paleontology (Lescaze et al., 2017). Its commonly recognized purpose is to reconstruct and represent extinct organisms and their ecosystems on the basis of available scientific evidence, producing visualizations that are both scientifically grounded and aesthetically compelling (Hallett, 1986). It should be clearly distinguished from prehistoric or cave art created by early humans, which belongs to a completely different cultural and historical domain.

The practice of paleoart typically begins with extensive research,

including the examination of fossil material, collaboration with paleontologists, and comparison with modern analogues. In the case of vertebrates, reconstructions often proceed "from the inside out," starting with the skeleton, followed by musculature, integumentary structures such as feathers, scales, or fur, and finally their ecological setting (Terakado, 2017). For other groups, including plants, invertebrates, or microbial life, the methodology may differ and relies on preserved structures, comparative morphology, taphonomic evidence, and ecological analogues as well as paleoecological proxy data—including pollen and spores, plant macrofossils, charcoal, and other sedimentary indicators—that provide the empirical basis for reconstructing past vegetational environments (Amorós, 2023; Amorós, 2024). Paleoart can take two- or three-dimensional forms, ranging from illustrations and animations to sculptures and digital models. It also extends to the reconstruction of entire environments, not just organisms, and requires attention to palaeoecology and palaeogeography. Its realization depends on a sustained dialogue between scientists and artists, but also engages the audience, whose perception of prehistoric life is profoundly shaped by these visual reconstructions (Amorós, 2024). At the same time, artists retain a degree of interpretive freedom, which must nevertheless remain within the bounds of scientific plausibility to avoid drifting into pure fantasy.

Beyond its technical and aesthetic aspects, paleoart often functions as an experimental space where scientific knowledge is translated into artistic form, sometimes fostering new questions and insights that were not anticipated in the early stages of research (Amorós, 2023). In this sense, paleoart exemplifies the shared cognitive creativity of science and art. Despite long-standing perceptions of separation between "the two cultures" of science and the humanities (Snow, 1961), it illustrates how collaboration across these domains can generate integrative knowledge and contribute to a "third culture" (Brockman, 1995). At the same time, paleoart raises conceptual and definitional challenges central to understanding its scientific, artistic, and cultural role, which will be addressed in the following section.

Over its two-century trajectory, paleoart has employed a wide range of artistic media, each shaping both the aesthetics and epistemic possibilities of reconstruction. Early works were typically executed as pen-and-ink plates or lithographs, prioritizing clarity of line for scientific illustration. The nineteenth century saw the flourishing of watercolor and oil painting, techniques embraced by Unger and Kuwasseg, Knight, Burian, and others, whose atmospheric renderings depended heavily on brushwork and colour layering. The mid-twentieth century introduced acrylics, enabling rapid drying and vivid chromatic effects that supported increasingly dynamic scenes. Since the 1990s, digital tools—3D modeling, photogrammetry, retrodeformation, biomechanical simulation, and tablet-based painting—have expanded the technical repertoire of paleoartists, while contemporary explorations include computer-assisted rendering and, more recently, the cautious use of AI-based generative systems. These media do not merely represent stylistic choices but reflect evolving relationships between artistic practice, scientific evidence, and the communicative aims of paleoart.

3. Defining paleoart: between scientific illustration and inclusivity

3.1. Between scientific illustration and paleoart

Scientific illustration focuses primarily on clarity and accuracy in the depiction of observable structures, with the main objective of supporting research or education. Paleoart, by contrast, is a form of visual reconstruction that necessarily goes beyond the strictly documentable (Amorós and Carrión, 2025; Carrión et al., 2024a; Carrión et al., 2024b). It seeks to restore extinct organisms and ecosystems by filling the gaps left by the fossil record through scientifically informed extrapolation, and by presenting them within a broader ecological and often narrative context.

This distinction historically begins with naturalists who made their own illustrations and continues with a synergistic evolution between scientists and artists, culminating in the current expansion of geo-paleontological literature and the professional development of paleoart (Manucci and Romano, 2022). Paleoart undoubtedly derives from, and incorporates, a substantial component of scientific illustration, which in the case of paleobotany has a long tradition and has produced artworks of outstanding anatomical and morphological resolution (e.g. de Saporta, 1879; Seward, 1898, 1900, 1908, 1919; Kidston and Lang, 1917, Kidston and Lang, 1920a, Kidston and Lang, 1920b, Kidston and Lang, 1921; Eames, 1936; Harris, 1961; Boureau, 1967; Gensel and Andrews, 1984; Anderson and Anderson, 1985; Meyen, 1987; Vakhrameev, 1991; Stewart and Rothwell, 1993; Cleal and Thomas, 1994, 1999, 2009; Niklas, 1997, 2016; Kenrick and Crane, 1997; Bateman et al., 1998a, 1998b; White, 1998; Gensel and Edwards, 2001; McLoughlin and McNamara, 2001; Carrión, 2003; Wagner, 2006; Wagner et al., 2003; Kenrick and Davis, 2004; Crepet et al., 2004; Carrión et al., 2006; Traverse, 2007; Davidson, 2008; Nichols and Johnson, 2008; Taylor et al., 2009, 2015; Tidwell, 2010; Friis et al., 2011; Willis and McElwain, 2014; Devesa and Carrión, 2017; Edwards et al., 2019; Krings et al., 2022).

3.2. Definitional debates and the problem of zoocentrism

When Mark Hallett coined the term paleoart in the late 1980s, he described this discipline as the art of "bringing the prehistoric past to life". His approach emphasized preparatory research and consultation with paleontologists, followed by the creation of reconstructions that gave movement, behavior, and vitality to extinct animals. This framing was highly influential, particularly in the popularization of dinosaurs and other vertebrates, and remains central to how paleoart is perceived today (Antón and Sánchez, 2004; Gurney, 2009; Witton et al., 2014; McDermott, 2020).

Yet this definition is implicitly zoocentric. Hallett's idea of restoring life mainly, though not exclusively, relies on bodily gestures, facial expressions, and overt behavioral cues that are readily associated with animals. Plants, by contrast, present a greater challenge: many of the most significant aspects of their biology—growth, phenology, seed dispersal, pollen transport, ecological interactions, or root systems hidden underground—may be slow, microscopic, or invisible to the human eye, and therefore resist straightforward visual translation (Sanisidro and Barrón, 2016; Amorós et al., 2021; Burjachs et al., 2016; Waterhouse Hawkins, 1875–1894; Carrión et al., 2024a), a difficulty compounded by the importance of substrate, soil properties, and geological context in shaping plant form and ecological function. Plant life is harder to capture artistically than animal behavior. This difficulty underscores an anthropocentric bias: animals resonate because they mirror us, while plants demand a more abstract and conceptual effort to visualize convincingly. This challenge is further amplified by the spatial framework of plant life, which unfolds simultaneously across microscopic, organismal, and landscape scales, making visual synthesis inherently complex.

At the same time, it is important to acknowledge that the dominance of animal-centred imagery in paleoart has historically fulfilled legitimate communicative, cultural, and aesthetic functions. Early paleoart cannot be judged by contemporary multiproxy standards, as its primary aims were often narrative, emotional, and pedagogical rather than strictly documentary. The widespread use of dramatic faunal protagonists—giant herbivores, fierce predators, and iconic "deep-time" creatures—responded to the expectations and imaginaries of their audiences and became firmly anchored in the collective conception of prehistoric life. Over the last two decades, however, a multidisciplinary and increasingly ecological approach has expanded the representational scope of paleoart, shifting attention from individual animals to whole environments and their interactions. Our critique of "plant blindness" is therefore not intended to diminish the artistic, communicative, or

historical value of these animal-centred traditions, but rather to highlight the long-standing structural imbalance that has limited botanical representation and, consequently, the full ecological potential of paleoart.

Several recent contributions have recognized this imbalance. Witton (2020) noted that "paleoartistry may be better described as the process of illustrating credible contemporary interpretations of prehistoric animals, where testable aspects accord with fossil data, and non-testable aspects are based on well-researched inference." Although this statement reflects the general zoocentric tendency, Witton himself also acknowledged the importance of botanical illustration in paleoart, and has published reconstructions of plants with impeccable botanical accuracy from the Crato Formation, and the Carboniferous of Scotland. In the same vein, science writer Riley Black (2025) has argued that "alone, a dinosaur is meaningless" and that "plants are often the missing part of our paleontological daydreams… Plants are the aliens that live in the yard." Her point is that the very ubiquity of plants—their essential role in our lives—has made us stop being impressed by their complexity and by the ways our existence intersects with theirs. If paleoart is to encompass the full spectrum of past life, it cannot remain tied to the zoocentric paradigm of "bringing to life." A more inclusive approach requires redefining paleoart as the sustained and synergistic collaboration between scientists and artists, oriented primarily toward research and evidence.

3.3. Toward an inclusive definition

Ansón et al. (2015) surveyed one hundred paleontologists from eleven countries to assess how the term paleoart is understood and valued. Their results showed broad agreement that paleoart is essential for both outreach and intra-scientific communication, and that scientific accuracy is a prerequisite for any work to be considered paleoart. At the same time, they revealed the absence of a universally accepted definition, as the term is often conflated with broader categories of "paleoimagery" and remains vulnerable to conceptual ambiguity. The authors also pointed to persistent problems such as plagiarism, outdated iconographies, and scientifically unsupported images—phenomena they described as "paleoartism."

A definition should not become a corset that constrains too tightly, especially in botany, where classifications and concepts have undergone numerous transformations with the advent of new fossil, embryological, and molecular data (Niklas, 1997; Rothwell et al., 2014; Devesa and Carrión, 2017). A botanical example illustrates this well: the concept of the flower. In a widely influential textbook, Strasburger et al. (1980) defined the flower as a structure "originating from short shoots of limited growth provided with microsporophylls and megasporophylls." Yet such structures also occur in non-angiosperm seed plants (Taylor et al., 2009). By this morphologizing definition, all seed plants would bear flowers. This raises the paradox of whether the sporangiophores of sphenophytes or even the reproductive structures of some red algae (Carrión, 2003) should also be regarded as flowers. A more practical approach is to define the flower—tautologically but usefully—as the reproductive organ of angiosperms, thus avoiding confusion with the myriad anthophytic organs known from the fossil record (Stewart and Rothwell, 1993; Taylor et al., 2009, 2015). In a similar vein, any attempt to define who qualifies as a "professional paleoartist" encounters a comparable conceptual difficulty. A strict definition risks becoming as problematic—and ultimately as tautological—as the morphological definitions of the flower discussed above. In practice, one could say that a paleoartist is simply someone who produces paleoart, regardless of whether their background is primarily artistic, scientific, or a hybrid of both. This inclusive understanding reflects the current landscape of paleoart, which is shaped by practitioners with diverse training and roles. Although perhaps not of critical importance, clarifying the fluid and heterogeneous nature of this term provides conceptual transparency in the introductory section of a review paper.

4. Paleokitsch and paleoimagery

Amorós and Carrión (2025) have recently examined the aesthetic phenomenon of kitsch in paleoart, coining the term paleokitsch to describe cases where reconstructions lose their scientific function and become ornamental, playful, or fetishized. Drawing on classical aesthetic theory (Benjamin, 2021; Dorfles, 1973; Eco, 2007; Amorós, 2025), they argue that while paleoart aspires to convey knowledge about the deep past, it has often been absorbed into consumer culture and popular entertainment in ways that trivialize its meaning. From the Victorian era onwards, dramatic scenes of monstrous creatures—such as those painted by John Martin or Archibald Willard—blurred the line between reconstruction and sensationalism, reinforcing cultural anxieties rather than paleontological accuracy. In this sense, paleokitsch does not denote a style but a value regime, in which prehistoric figures are rendered as hybrid icons—part biblical, part mythological—responding more to expectations of spectacle than to fossil evidence.

The discussion also highlights the impact of reproducibility (Benjamin, 2021; Lipps et al., 2022). Paleoartworks originally created for museums or scientific dissemination lose their "aura" when reproduced as posters, toys, or advertising logos—iconically, the Sinclair Oil dinosaur. Recontextualized in children's rooms or candy wrappers, such images undergo a semantic shift that distances them from their scientific origin and incorporates them into popular culture as decorative commodities (Clements et al., 2022). Finally, Amorós and Carrión (2025) stress the relevance of "paleoimagery" (Buscalioni, 2015), referring to speculative visualizations that proliferate online, often with little relation to scientific consensus. While these productions sustain fascination with prehistory, they dilute the epistemic credibility of paleoart by privileging spectacle over accuracy. In sum, paleokitsch underscores the vulnerability of paleoart to commodification, reproduction, and cultural appropriation. Unlike "paleoartism" (scientific inaccuracy), paleokitsch signals a shift in value systems, where images are detached from their evidential grounding. Both categories raise ethical questions for paleoartists working at the interface of science, art, and popular culture—and both contribute, in different ways, to reinforcing the zoocentric and plant-blind tendencies we address in the following sections.

5. Plant blindness in paleoart

If paleokitsch illustrates how spectacle can trivialize prehistoric life, plant blindness reveals a subtler but equally pervasive distortion: the systematic neglect of vegetation in reconstructions of deep time (Balding and Williams, 2016). In most paleoart, animals dominate while plants appear as indistinct scenery, despite being the organisms that regulate climate, hydrology, and atmosphere, and that often provide the very proxies on which reconstructions depend (Buscalioni, 2016; Vujaković, 2019; Beerling, 2007). This imbalance is not simply aesthetic but epistemological. To omit plants from paleoart is to obscure key drivers of evolutionary and Earth system change. Stephen Jay Gould's influential critiques of linear and progressive iconographies (Gould, 1989, 1993) remain paradigmatic: while he denounced animal-centered teleologies, his own visual tableaux all but erased vegetation, which never appeared as a protagonist. His justification—that zoocentrism is "understandable because we are animals" (Gould, 1993, p.16)—captures precisely the anthropocentrism that sustains plant blindness. While the communicative effectiveness of animal-centred scenes is undeniable—particularly in paleoart created for broad public audiences—this does not eliminate the representational bias that arises when animals systematically occupy the visual and narrative centre. In paleoart with scientific aims, such emphasis can obscure ecological relationships and underrepresent key botanical or environmental elements.

Multiple mechanisms explain the persistence of this bias. Perceptual research shows that humans detect animals more rapidly than plants, reinforcing the sense that vegetation is narratively inert (Balas and

Fig. 1. Engraving from *Physica Sacra* by Johann Jakob Scheuchzer (1672–1733), corresponding to the third day of Creation. The scene shows the Earth "covered with trees, grasses, and innumerable plants, a logical consequence of its fertility, further emphasized by fruits, ears of wheat, roots, and seeds" (Amorós, 2023). Notably, angiosperms, the most recently evolved reproductive plant group, prevail in the composition. Public domain/CC0.

Momsen, 2014). Haines (1999) notes how cinematic conventions and CGI further reinforced animals as the "active heroes" of deep-time reconstructions, marginalizing plants as static scenery. Educational surveys confirm the imbalance: less than 15 % of curricular content typically addresses plants, with measurable consequences for recognition skills and interest among students (Brownlee et al., 2021; Prokop and Fančovičová, 2023).

Parsley (2020) has framed this as plant awareness disparity (PAD), while Stroud et al. (2022) speak of a "botanical education extinction," where diminished teaching reduces public awareness, professional expertise, and funding, creating a self-reinforcing cycle. Jose et al. (2019) emphasize that this asymmetry extends into research agendas and institutional priorities, structurally marginalizing botany even within biology itself. As Sanisidro and Barrón (2016) and Spagnuolo et al. (2024a, 2024b) warned, reconstructions the neglect of flora not only weaken scientific rigor but also undermine public understanding of paleoenvironments. Overcoming plant blindness therefore requires both epistemological and cultural reform.

6. The Imprint of Landscape in Paleoart

If plant blindness reduces vegetation to scenery, the concept of landscape reminds us that environment itself is constitutive of paleoart. Landscape here is not a neutral backdrop but the expression of primordial nature, the very medium through which prehistoric organisms existed. This places paleoart within a long cultural history of landscape painting, where humans projected their relationship to nature through artistic representation. Yet, as John Berger (1959) and Kenneth Clark (1971) observed, landscape as an autonomous genre has declined in modern art, overshadowed by abstraction and conceptualism. Paleoart, however, remains fundamentally indebted to landscape, even if its zoocentric tradition long neglected paleobotanical reconstruction. Seen in this light, paleoart can be interpreted as an act of resistance (Deleuze, 1985, in Agamben, 2017): not against the union of art and science, but against the dissociation of landscape from the organisms that inhabited it. To depict an animal without its environment risks reducing paleoart to mere illustration, whereas its true essence lies in restoring deep time in its complexity of interactions.

Fig. 2. *Duria Antiquior* (c. 1830) by Henry Thomas de la Beche, watercolor on paper. Displayed at the National Museum of Cardiff, Wales. In this small watercolor, more than thirty living beings are depicted, over half of them engaged in acts of predation. This work became, in its time, a revolutionary milestone in shaping perceptions of prehistoric life. Public domain/CC0.

The paleoartist's task differs from that of a conventional landscape painter. Whereas the latter transfers visual information directly from observation, the paleoartist must construct an inner landscape from fossil data, ecological analogies, and scientific inference. The prehistoric scene exists only as an intellectual and imaginative construct, demanding meticulous preparatory work to preserve the unity of the landscape. The result is not a transcription of reality but a hybrid vision—scientific and artistic, evidential and interpretive. In this sense, paleoart affirms the ontological primacy of landscape. Deep-time worlds—whether populated by hominins, reptiles, or plants—can only be understood through their environments: wild, unforgiving, and inseparable from the beings that inhabited them. To ignore this is to impoverish the biodiversity of the past; to embrace it is to celebrate, through art, the indivisible bond between life and environment.

7. Historical Survey

Although the term "paleoart" is relatively recent, the impulse to give visual form to beings of the past long predates the birth of paleontology as a scientific discipline. As early as Antiquity, scholars have speculated about the influence of fossils on certain aspects of classical mythology (Mayor, 2011; Romano and Avanzini, 2019). As Mayor Iborra and Tapia Gutiérrez (2020) emphasize, those monstrous images should not be read simply as fantasies, but rather as cultural mediations that translated the unknown into the available visual languages, in an attempt to make sense of incomprehensible remains. In Renaissance and Baroque Europe, more tangible examples emerged, such as the *Lindwurm statue of*

Fig. 3. Works from the collaboration between Unger and Kuwasseg. **(a, b)** A selection of two of the 14 sequential lithographs produced by Rottmann (1851) after the works of Kuwasseg, depicting the "development of the Earth" through different geological stages. Source: Historical Archive of the University of Padua: https://phaidra.cab.unipd.it/. Public domain. **(c)** *The Coal Period*. From *The Primitive World in its Different Periods of Formation* 1851 by Joseph Kuwasseg. A swampy forest of lycophytes (*Lepidodendron*) with tree ferns and a bryophytic ground layer defines the botanical scene. Colección Neue Galerie, Landesmuseum Joanneum. Public Domain/CC0.

Klagenfurt (1590), inspired by a woolly rhinoceros skull, or Athanasius Kircher's illustrations in *Mundus Subterraneus* (1678), where dragons and giants probably echoed fossil findings from caves and quarries (Rudwick, 2008; Witton, 2020; Romano, 2024).

In this line, Amorós (2024) highlights the importance of Johann Jakob Scheuchzer's monumental *Physica Sacra* (1731–1735), known as the "Copper Bible" for its 748 copperplate engravings. A Swiss physician and naturalist, Scheuchzer integrated his fossil collections and his vision

Fig. 4. Some 19th-century paleoartists who paid attention to the paleobotanical component of the landscape. **(a)** *View of a forest and swamp during the Coal Period* by Riou (Figuier and Riou, 1863). **(b)** *Life Forms in the Carboniferous*. From *Die Geschichte der Erde* by Rossmässler (1863). A swamp forest dominated by *Calamites, Sigillaria*, lepidodendralean trunks, and giant ferns, is depicted. Images digitally restored by W. Griem at www.geovirtual.cl. Public Domain/CC0. **(c)** *Keuper in the Germanic Basin* by Ludwig (1861). **(d)** *Triassic landscape* by Neumayr (1897). Note the similarity with Ludwig's work. **(e)** Jurassic according to Siegmund (1877). **(f)** *Pliocene landscape* by Siegmund (1877).

of natural history into a narrative that followed biblical chronology step by step, from Genesis to the Apocalypse. What made the *Physica Sacra* distinctive was that its illustrations went beyond devotional scenes, incorporating landscapes and organisms rendered with unusual naturalistic detail: barren mountains on the Third Day of Creation, followed by a world suddenly covered in plants and fruits; fishes, mollusks, and quadrupeds depicted in lush settings, some of them explicitly alluding to known fossils; and, finally, the creation of man within a Central European landscape, complete with carefully described trees and botanical features (Fig. 1). The elaborate Baroque frames that surrounded the vignettes, inherited from the emblematic tradition, added a didactic and moralizing tone, yet the core of the imagery conveyed a genuine scientific interest in nature. In this emphasis on landscape and the coexistence of plants and animals, one can recognize a singular precedent of the paleoartistic sensibility—oscillating between the sacred and the biological—and anticipating the central role that landscape would later play in the discipline.

At the dawn of the nineteenth century, Jean Hermann in Strasbourg produced the first anatomical sketches based on a pterosaur fossil (Taquet and Padian, 2004), and shortly thereafter Roman Boltunov attempted to reconstruct the appearance of a mammoth from a Siberian find (Witton, 2020). In the 1820s, Georges Cuvier and other naturalists began to explore how musculature could be restored onto fossil skeletons, while William Conybeare caricatured William Buckland surrounded by extinct hyenas in their cave habitat—perhaps the first scene that sought to recreate a vanished ecosystem (Rudwick, 1992). A true foundational milestone arrived in 1830 with *Duria Antiquior*, the celebrated watercolor by Henry De la Beche inspired by Mary Anning's discoveries on the Dorset coast (Rudwick, 1992; Davidson, 2008) (Fig. 2). For the first time, marine reptiles were depicted interacting within a geologically realistic framework, inaugurating a narrative mode of paleoart (Sharpe and Clary, 2022; Amorós, 2023). The importance of *Duria Antiquior* lies not only in being one of the "first" paleoartworks, but in breaking with the conventions of purely pragmatic

illustration: until then, fossil organisms had been represented in isolated plates, devoid of landscape, in the manner of scientific illustration (McDermott, 2020; Amorós, 2024). By contrast, De la Beche's small watercolor condensed more than thirty creatures interacting tumultuously in a single space—many of them devouring one another—and projected onto the scene an unprecedented narrative and emotional forcé.

From there, reconstructions proliferated, ranging from Goldfuss's illustrations in 1831 to the life-sized dinosaurs of London's Crystal Palace in 1854 by sculptor Benjamin Waterhouse Hawkins, which brought these images into the public sphere and popular culture (Rudwick, 1992; Jäger et al., 2018). As Witton et al. (2014) have pointed out, these sculptures also marked the beginning of "commercialized paleoart," with replicas and printed guides aimed at general audiences, anticipating the central role dinosaur iconography would hold in modern visual culture.

The second half of the nineteenth century and the early decades of the twentieth consolidated what is now regarded as the "classical" stage of paleoart, shaped by the emergence of artists whose works defined the prehistoric imaginary for generations. In the United States, Charles R. Knight combined deep anatomical knowledge with a vibrant pictorial style that gave his creatures striking life and movement. His murals at the American Museum of Natural History in New York and the Field Museum in Chicago set the popular iconography of dinosaurs and established the aesthetic direction of the field (Paul, 2000; Milner, 2012). In Europe, Zdeněk Burian (1905–1981) became an international reference through illustrations of extraordinary atmospheric and landscape realism (White, 2012). Rudolph Zallinger (1919–1995), in turn, left a monumental legacy at Yale's Peabody Museum of Natural History. Together, Knight, Burian, and Zallinger, as we shall see later, defined the aesthetics of classical paleoart and established the visual frameworks through which twentieth-century society imagined Earth's deep past.

This paradigm began to falter with the so-called "Dinosaur Renaissance" between the 1970s and 1990s (Lucas, 1901; Milner, 2012; Kosemen, 2013). Dinosaurs came to be seen as active, warm-blooded animals, closely related to birds (Bakker, 1975). The paleoart of this period, led by artists such as Douglas Henderson, Mark Hallett, Michael Skrepnick, and Luis Rey, among others, was characterized by greater dynamism and a pursuit of anatomical accuracy, in line with scientific advances (Paul, 1997; Witton, 2020; Amorós, 2023). In the late twentieth and early twenty-first centuries, paleoart consolidated as a professional practice closely associated with paleontological research. Authors such as Mauricio Antón, with his extensive work on fossil mammals, Davide Bonadonna, Mark Witton, Óscar Sanisidro, Robert Nichols, Brennan Stokkermans, Gabriel Ugueto, Jay Matternes, Danielle Dufault, among many others (see White and Naish, 2022), exemplify the full integration of paleoart into contemporary scientific production (Supplementary Table 1).

In the last decades, digital technologies and online diffusion have transformed paleoart into a global, diverse, and increasingly participatory community (Antón, 2007; Ansón et al., 2015; Terakado, 2017). Yet, as Witton et al. (2014) have noted, this expansion has not been free of challenges: plagiarism and the reiteration of visual clichés have at times constrained creativity. The *All Yesterdays* movement (Conway et al., 2012) arose as a reaction to such inertia, not only breaking away from inherited tropes but also questioning the very role of speculation in paleoart. Speculation has always been part of the discipline—Gregory Paul, for example, anticipated feathered dinosaurs before fossil evidence was available—but the 2010s debate helped establish a more explicit ethics of "reasoned speculation," encouraging diversity of plausible depictions while avoiding ungrounded excesses (Romano and Manucci, 2022). At the same time, digital platforms, blogs, and social networks created a global arena for exchange, while accessible software enabled even non-professionals to produce reconstructions in two and three dimensions. Recent surveys have identified more than six hundred active paleoartists worldwide, highlighting both the vitality and the precariousness of the profession (Romano and Manucci, 2022). Meanwhile, digital tools such as 3D scanning, retrodeformation, and biomechanical modeling have brought paleoart closer to analytical research, not by turning it into a purely scientific procedure, but by enriching the evidentiary basis on which visual reconstructions are built, without displacing traditional painting and sculpture.

From the earliest speculative sketches to today's digital reconstructions, the history of paleoart reveals not only the shifting aesthetics of prehistoric life but also the enduring negotiation between evidence and imagination. Its trajectory shows that paleoart is neither a passive derivative of science nor a purely artistic endeavor, but a space of critical interplay where knowledge and creativity converge (Turner, 2019). The future of the discipline, we contend, lies precisely in cultivating this dialogue—rigorous yet imaginative, scientific yet cultural—that has defined paleoart since its inception. Yet one component has remained persistently underrepresented: the botanical component. It is to this neglected perspective that we now turn.

8. Botanical paleoart: antecedents

Botanical paleoart refers to reconstructions where flora and vegetation landscape are treated as central subjects, grounded in paleobotanical data rather than as decorative backdrops. Although most historical practice was overwhelmingly zoocentric, notable exceptions show how a plant-centered approach can both expand the epistemic reach and enrich the aesthetic range of paleoart (Bressan, 2012). In what follows we highlight a series of cases—beginning with the nineteenth-century collaboration between Franz Unger and Joseph Kuwasseg—that exemplify this alternative lineage and anticipate recent plant-literate developments.

8.1. Franz Unger and Joseph Kuwasseg: a phytocentric collaboration in paleoart

The collaboration between the Austrian botanist Franz Unger (1800–1870) and the landscape painter Joseph Kuwasseg (1802–1877) stands as a landmark in the history of paleoart and, more specifically, of paleobotanical visualization. Unger, a physician, botanist, paleontologist, and pioneer of plant physiology, sought to reconstruct past landscapes by integrating fossil evidence into systematic accounts of vegetation. His *Die Urwelt in ihren verschiedenen Bildungsperioden* (1851), followed by later works (Unger, 1864), combined scientific text with a suite of fourteen lithographs derived from Kuwasseg's watercolors, executed with extraordinary naturalistic precisión (Fig. 3a-c).

Kuwasseg's painterly sensibility was decisive: trained as an architectural and landscape watercolorist, he emphasized atmosphere, topography, and botanical diversity. Many of the plates minimize or even omit fauna, compelling attention to floristic structure. In this sense, the series constitutes one of the earliest systematic attempts at a "paleoart of plants". Gould, however, dismissed the plates as "empty" scenes populated only by plants with few animals in the distance (cited in Vujaković, 2019), overlooking the scientific and artistic innovation of presenting ecosystems through their dominant organisms—plants.

As Amorós (2024) underscores, the Unger–Kuwasseg project marked a turning point: the images do not follow the spectacular, action-centred conventions typical of many early nineteenth-century animal scenes, but instead present carefully constructed landscapes in which paleobotanical evidence drives the narrative. This naturalistic approach reflected Unger's broader intellectual project, including his *Versuch einer Geschichte der Pflanzenwelt* (1852), where he advanced pre-Darwinian ideas of common ancestry for all plant lineages. The plates, published in large format by Leopold Rottmann, circulated in exhibitions and lectures and can still be seen today at the Universalmuseum Joanneum in Graz (Fig. 3). Collins (2018) emphasizes their attention to floristic diversity, particularly in the seventh plate depicting the expansion of land plants during the Keuper Sandstone. This phytocentric emphasis

Fig. 5. **(a)** *Triassic Life of Great Britain* (1887) and **(b)** *Carboniferous Coal Swamp* (1875) by Benjamin Waterhouse Hawkins. Art Museum, University of Princeton, New Jersey. **(c)** *Early Land Plants* by Charles Knight (1932): one of the few explicitly plant-centered reconstructions by the Knight (Amorós, 2024), depicting a typical scene of the earliest forest ecosystems with arborescent lycophytes resembling *Lepidodendron*, tree ferns, *Asteroxylon*, small horsetails, and understory vegetation akin to *Psilophyton* and *Sadownia*. Public Domain/CC0.

not only anticipated later efforts to integrate paleobotany into holistic reconstructions of Earth history but also contributed to early evolutionary interpretations of plant diversity. Taken together, the Unger–Kuwasseg collaboration must be recognized as a foundational episode in the history of paleoart.

8.2. Rudolph Ludwig: the geological framing of prehistoric landscapes

The German scholar Rudolph August Bernhold Sebastian Ludwig (1807–1865) offered another significant, though often overlooked, contribution to the nineteenth-century visualization of deep time. Trained as a botanist, paleobotanist, and geologist, he produced *Das Buch der Geologie* (Ludwig, 1861), a richly illustrated synthesis intended to popularize Earth history for a wide readership. The work is distinctive for its systematic use of landscape compositions to convey the succession of Paleozoic, Mesozoic, and Cenozoic intervals (Amorós, 2024). Ludwig emphasized geological processes—stratification, facies, depositional environments—while at the same time offering detailed reconstructions of paleovegetation. His Carboniferous scenes depict dense swamp forests of *Calamites, Stigmaria, Sigillaria,* and tree ferns (Fig. 4c). Triassic reconstructions highlight arid facies and a scarcity of fossils, which Ludwig interpreted as evidence of desert climates and eolian deposition. Other images show storm-felled bennettitalean trunks, Muschelkalk coastal settings, or Keuper facies rich in equisetalean shoots and lepidodendralean trees.

8.3. Louis Figuier and Édouard Riou: La Terre avant le déluge (1863–1872)

Louis Figuier (1819–1894) was among the most prolific popularizers of science in nineteenth-century France. His *La Terre avant le déluge* (1863, 1867, 1872) offered a sweeping narrative of Earth history that combined fossil evidence with a didactic framework still partly anchored in the biblical flood tradition. While indebted to earlier works such as Unger's *Die Urwelt* (Unger, 1851), Figuier's book stood out for the breadth of its imagery and its explicit aim to make paleontological knowledge accessible to a broad audience (Vujaković, 2019). To visualize deep time, Figuier collaborated with Édouard Riou (1833–1900), who produced a series of nineteen "ideal landscapes," each corresponding to a geological period (Fig. 4a). Riou had been a disciple of Gustave Doré and the creator of the illustrations that accompanied Jules Verne's books. Although several were modeled on Kuwasseg's earlier illustrations for Unger, Riou introduced dramatic atmospheric effects and narrative detail that enhanced their appeal to lay readers (Rudwick, 1992). Among the most striking is the *View of a forest and swamp during the Coal Period*, which foregrounds dense arboreal vegetation and abundant smaller plants, closely aligned with the floristic composition of Carboniferous paralic basins in Central Europe and North America (Figuier, 1872).

8.4. Ferdinand Siegmund: Untergegangene Welten (1877)

Ferdinand Siegmund (mid-nineteenth century) was a Bohemian-born journalist and editor—originally trained in medicine in Prague and Vienna—who developed a prolific career as a scientific popularizer. His volume *Untergegangene Welten – Eine populäre Darstellung der Geschichte der Schöpfung und der Wunder der Vorwelt* (Lost Worlds: A Popular Presentation of the History of Creation and the Wonders of the Prehistoric World), published in Leipzig in 1877, sought to synthesize paleontology and evolutionary debate for a broad readership (Amorós, 2024). Siegmund foregrounded the prehistoric environment with a strong botanical emphasis. His illustrations span a wide range of geological periods—Pliocene, Devonian, Triassic, Jurassic, Permian, Cretaceous, and Carboniferous—and are meticulously composed to highlight lush vegetation and fossilized remains in the foreground, lending both visual richness and scientific credibility to the scenes (Fig. 4e). For Siegmund—as for predecessors such as Unger, Ludwig, and Figuier—-plants were not mere scenery but central actors in the narrative of Earth history. The later marginalization of this approach in twentieth-century paleoart reflects broader cultural and methodological shifts, including the rise of cinematic aesthetics that privileged dynamic animal protagonists (Vujaković, 2019).

8.5. Edna P. Plumstead: Gondwanan Coal Forests and early Botanical Paleoart

Edna P. Plumstead (1903–1989), a leading authority on *Glossopteris* floras and one of the most influential paleobotanists working in the southern hemisphere, also produced a body of visual work that deserves recognition within the history of botanical paleoart. Her volume *Three Thousand Million Years of Plant Life in Africa* (Plumstead, 1969), published as part of the Alex L. du Toit Memorial Lectures, contains some of the earliest scientifically grounded reconstructions of Gondwanan coal forests. These images, accompanied by extensive explanatory notes, depict ecosystems dominated by *Glossopteris, Gangamopteris, Cordaites, Sphenophyllum*, and other characteristic elements of Permian floras from the Transvaal and adjoining regions. Plumstead approached paleoart from a rigorously paleobotanical standpoint. Her illustrations integrate morphological, stratigraphic, and taphonomic observations, synthesizing decades of research on the anatomy, affinities, and ecological roles of Gondwanan seed ferns. Particularly notable is the annotated fold-out plate depicting a southern hemisphere coal forest, in which each taxon is identified by lettered codes and described in detail—an uncommon level of botanical precision for her time. The reconstruction emphasizes physiognomic diversity, growth habits, and ecological gradients, thus offering not merely a scenic landscape but a coherent visualization of a complex paleoecosystem grounded in fossil evidence. Although less widely disseminated in the northern hemisphere than European works of the nineteenth century, Plumstead's reconstructions constitute a crucial milestone in the development of plant-centred paleoart.

8.6. Emil Adolf Rossmässler: Die Geschichte der Erde (1863)

Emil Adolf Rossmässler (1806–1867; often written Roßmäßler in the original German) was one of the most versatile German naturalists of the nineteenth century: a botanist, zoologist, malacologist, educator, and political democrat. Strongly influenced by the Humboldtian tradition, he conceived of science as a cultural force and dedicated his career to disseminating natural history among the wider public (Prüfer Leske, 2019). His commitment to popular science was inseparable from his political and pedagogical convictions, particularly the idea that knowledge of nature was essential for social reform and democratic education (Prüfer Leske, 2019).

In his widely read *Die Geschichte der Erde* (Rossmässler, 1863), he offered an accessible synthesis of Earth history for educated readers, illustrated with nearly one hundred figures (Fig. 4b). In works such as *Der Wald* (1862) and *Das Wasser* (1858), Rossmässler argued that forests and hydrological systems should be understood as central actors in Earth's history, to be protected through knowledge and education (Rossmässler, 1858, 1862). In this sense, his Carboniferous landscape can be seen not only as paleoart but also as an early ecological manifesto. Although today Rossmässler is better remembered for his *Iconographie der Land- und Süsswasser-Mollusken Europas* (1835–1858) and for his political activity during the Revolution of 1848, his contribution to the visual culture of deep time deserves recognition (Prüfer Leske, 2019).

8.7. Melchior Neumayr: Gradualism and paleoartistic landscapes

Neumayr (1886-1887) was one of the leading figures of late nineteenth-century paleontology. Appointed to one of the first chairs of paleontology at the University of Vienna, he made substantial

Fig. 6. An emerging figure in the field of botanical paleoart, Zeinner de Paula. **(a)** The extraordinary plant biodiversity of a Gondwanan refugium during the Permian at the Cerro Chato outcrop. The vegetation is dominated by lycophytes (trunk of *Lycopodiopsis derbyi* on the left), ferns and sphenophytes (mainly undergrowth), pteridosperms, and gymnosperms (Ferraz et al., 2025). **(b)** The Missão Velha Formation (Upper Jurassic–Lower Cretaceous, Araripe Basin, NE Brazil). The landscape depicts a braided fluvial system with alluvial plains under marked seasonality. In the foreground, tall trees of Araucariaceae and Podocarpaceae/Cupressaceae dominate, corresponding to the fossil woods *Agathoxylon* and *Metapodocarpoxylon*. To the left, cycads and pteridosperms are shown, while moist areas near watercourses support ferns. In more open and probably drier zones in the background, shrubby gnetaleans and conifers of Cheirolepidiaceae appear, adapted to xeric conditions. Altogether, the reconstruction illustrates the coexistence of xeric and mesic communities under a semi-arid climate with wet seasons, as inferred from fossil woods and palynological assemblages (Conceição et al., 2025). Images courtesy of Zeinner de Paula.

Fig. 7. Reconstruction of Turonian–Santonian West Antarctica (Klages et al., 2020; artwork by James McKay), depicting a polar rainforest with podocarp and araucarian conifers, tree ferns, and diverse angiosperms, reflecting the southernmost known Cretaceous terrestrial flora. Courtesy of Johann Klages.

contributions to the study of ammonites and freshwater mollusks, while also shaping the methodological identity of German paleontology. In *Die Stämme des Thierreiches* (1889), he defined the task of the discipline as demonstrating that "all animals and plants evolved from one or a few basic forms by gradual transformation" (Neumayr, 1889, cited in Tamborini, 2015). He thus defended Darwinian gradualism, arguing that the fossil record revealed slow and cumulative change rather than abrupt discontinuities. At the same time, Neumayr opposed the introduction of statistical methods into paleontology, which he believed would undermine Darwinian theory and reduce paleontology to an auxiliary of geology. Instead, he championed *Formenreihen*—morphological series reconstructed through comparative anatomy—as the only reliable evidence for evolutionary transformation (Neumayr, 1878, 1889; Tamborini, 2015). Although primarily remembered as a methodologist, Neumayr also engaged in the visual representation of deep time. His two-volume *Erdgeschichte* (1886–1887) included a series of "ideal landscapes" for different geological periods (Fig. 4d).

8.8. Benjamin Waterhouse Hawkins: The ideal paleo-landscape

Benjamin Waterhouse Hawkins (1807–1894), best known for his Crystal Palace dinosaur sculptures, also produced a remarkable pictorial cycle that enriches the visual culture of paleoart. Commissioned by Arnold Henry Guyot for the Princeton University Museum of Geology in the 1870s–1880s, his seventeen paintings (fifteen preserved today in the Princeton University Art Museum) span environments from the Paleozoic to the Cenozoic, revealing Hawkins as a landscape painter as much as a sculptor. Unlike the dramatic zoological scenes that dominated nineteenth-century paleoart, Hawkins often gave primacy to environment (Fig. 5a-b). In *Triassic Life of Germany*, reptiles appear only as marginal silhouettes, while nocturnal atmosphere and framing vegetation dominate the scene. In *Carboniferous Coal Swamp*, animals recede almost entirely, foregrounding lepidodendralean trees and diffuse light. This consistent treatment of light and horizontality aligns Hawkins more with Romantic landscape traditions than with the spectacle-driven imagery of many contemporaries (Clark, 1971). Paintings such as *Tertiary Mammals of Europe* (1894) convey biblical calm and a sense of lost paradise, integrating plants and animals within a unified atmosphere. Through this series, Hawkins articulated an "ideal paleo-landscape": not a literal transcription of prehistoric nature, but a reimagined harmony of light, vegetation, and fauna. As Witton (2020) argues, he deserves recognition as the first "grand master" of paleoart, not only for his Crystal Palace sculptures but also for this unprecedented attempt to visualize entire prehistoric ecosystems. Hawkins was an innovator who transformed paleontology into a public spectacle and laid foundations for its institutionalization.

8.9. A rare botanical turn in the vertebrate-centred oeuvre of Charles R. Knight

Charles R. Knight (1874–1953) stands as a pivotal figure in the history of paleoart. His work fused anatomical mastery, painterly sensibility, and visionary foresight, shaping the prehistoric imagination of museums and popular culture alike. Manucci and Romano (2022) describe Knight as "an authentic time-traveler in spirit," noting that his partial childhood blindness sharpened rather than hindered his perceptual acuity. Rejecting photography, he reconstructed a "living" prehistoric world through fossils and anatomy, relying on dissections and taxidermy at the American Museum of Natural History. Under the mentorship of Edward D. Cope and Henry Fairfield Osborn, he developed a studio method that combined sculptural maquettes with close scientific consultation, producing some of the most iconic early dinosaur images and consolidating paleoart as a vehicle of science communication.

Amorós (2024) interprets Knight's approach to landscapes as an unprecedented turn toward the pictorial. His vibrant palette—cadmium yellows, radiant greens, turquoises, purples, and oranges—melded fauna and environment into unified chromatic fields; each brushstroke functioned, in Ortega y Gasset's terms, as an "algorithm of the whole canvas." The parallels with Monet are striking: the light–shadow interplay in *Laelaps* (1897) recalls *Grainstacks*, capturing motion and atmosphere, while *Brontosaurus* (1898) echoes the shimmering reflections of *The Japanese Bridge* in a Mesozoic domain.

Yet Knight was not especially attentive to botanical taxonomy. His

Fig. 8. *Alexander Island* by Robert Nichols (Witton, 2020). An illustrative reconstruction of the Cretaceous, ~120 million years ago, depicting the Antarctic Peninsula with *Ginkgo*, cycads, *Taeniopteris*, *Phyllopteroides*, *Aculea*, tree ferns, and spermatophytes in the background. A dinosaur is partially visible, camouflaged behind the trunk of the *Ginkgo*. Based on the PhD work of Jodie Howe, University of Leeds. This image is associated with the 2005–2010 BAS science programme GEACEP (*Greenhouse to Ice-House Evolution of the Antarctic Cryosphere and Palaeoenvironment*). Courtesy of the artist, Robert Nichols.

vegetation often dissolved into impressionistic masses, subordinated to atmosphere. A notable exception is the *Devonian Forest* mural at the Field Museum, depicting the Gilboa forests of New York (Fig. 5c). For this work, Knight consulted paleobotanist Winifred Goldring to maximize fidelity, but even here the plants are rendered in loose strokes, privileging atmospheric impression over strict taxonomic detail (Spagnuolo et al., 2024a, 2024b). Knight's oeuvre thus illustrates both the power and the limits of an artistically dominated vision of prehistoric landscapes. His rare botanical turn enriched the visual culture of paleoart, yet it remained an exception within a corpus overwhelmingly focused on vertebrates.

8.10. Zdeněk Burian: Botanical ambience without plant-blindness

Zdeněk Burian (1905–1981) is often regarded as the most naturalistic of the classic paleoartists, yet his landscapes carry a distinctly impressionist charge tempered by academic discipline. His scenes feel "painted from life": animals move with unforced fluency; muscles surface only when light or action demands it; and eyes, defined with a few strokes, convey alertness or torpor without theatrics (Amorós, 2024). This apparent ease masked a rigorous control of proportion and form, rooted in speed of eye and hand. Historically, Burian ranged across almost every interval of deep time, working closely with scientists—first with Josef Augusta, later with Zdeněk Špinar and Vratislav Mazák—and helped to define the mid-century "dreamlike aura" of paleoart without sacrificing credibility (Manucci and Romano, 2022).

For our purposes, his treatment of vegetation is central. Burian often concentrated masses of foliage in motion, softening contours into cottony clumps while overlaying sharper trunks and branches—an effect reminiscent of Camille Corot (Amorós, 2023). He tended to push microdetail to the ground plane—grasses, soil, stones rendered with virtuoso shorthand—while backgrounds dissolved into tonal fields near a high horizon. The result is an ecosystem that "breathes": wind-laden grasses, humid air, glints on water—botanical ambience rather than strict botanical taxonomy (Amorós, 2024).

Crucially, Burian was not plant-blind. His *Geological Series* of the 1950s–1960s included terrestrial panels in which flora received genuine paleobotanical weight, often produced with specialist input, notably from František Němejc (Lavas, 2016). The Middle Devonian panel, for instance, features identifiable plant architectures such as *Hyenia* and *Calamophyton* together with the lycophyte *Protolepidodendron*. The Carboniferous swamp canopy is anchored by *Lepidodendron* and *Sigillaria*, balanced with *Cordaites* and the tree fern *Psaronius*, producing a coherent coal-swamp physiognomy rather than generic greenery (Lavas, 2016). A Triassic reconstruction published in Augusta and Burian (1956) is especially detailed, with a cryptogamic understory of ferns and equisetaleans, overlaid by *Ulmannia*, *Baiera*, *Voltzia*, *Ginkgoales*, *Taxodiaceae*, pine- and cypress-like forms, and giant sequoias. Equally striking are the forest architectures of the Jurassic—prominently *Bennettitales*, ginkgos, and conifers—and the Miocene (conifers) (Špinar and Burian, 1972, 1995; Lavas, 2016). Burian's paleoart thus demonstrates how atmospheric impression and paleobotanical knowledge can be combined without contradiction.

Fig. 9. Paleoecological reconstruction of the middle Eocene Jianglang flora (Tibet), depicting a subtropical valley ecosystem along the Bangong–Nujiang Suture Zone (Zhou et al., 2023). The scene integrates a diverse assemblage of angiosperms (*Ailanthus*, *Lagokarpos*, *Cedrelospermum*, *Koelreuteria*), together with gymnosperms and ferns, capturing the composition and structure of this "Shangri-La" ecosystem. Artwork courtesy of Alex Boersma.

8.11. Zallinger: A Renaissance fresco of deep time

Rudolph Zallinger (1919–1995; Pulitzer Prize for Painting in 1949) belongs to the cohort of mid-century masters who carried paleoart decisively into the public sphere. His landscapes are unique in reviving pre-Renaissance and Renaissance strategies—especially the construction of space through graduated size and placement of volumes rather than atmospheric recession. In *The Age of Reptiles* (Yale Peabody Museum, 1943–1947), this method produces a panoramic fresco where clarity extends across every plane: leaves, stones, and horizons are rendered with equal precision, while chromatic fields progress in measured bands reminiscent of Joachim Patinir (Amorós, 2024). The mural functions almost like a didactic cycle, its unified light and colour linking all epochs of deep time.

Amorós (2024) interprets the painting as a vast "garden program": each interval is densely planted with carefully distinguished forms, so that the mural reads as a floristic encyclopedia embedded within a continuous landscape. Surfaces are immaculate and vegetation carries a decorative charge comparable to Roman garden frescoes, yet remains taxonomically informative. This duality—immersive unity versus the figure–ground logic of animals set within vegetal matrices—constitutes the "Zallinger paradox," resolved by consistency of light, colour, and botanical structure across the 33-m sweep. The botanical content is extensive: Devonian *Eospermatopteris* and early sphenopsids along waterways; Carboniferous *Lepidodendron*, *Sigillaria*, calamites and tree ferns such as *Psaronius* in swamp physiognomies; Permian cordaitalean

Fig. 10. Paleoecological reconstruction of the Miocene Konservat-Lagerstätte of McGraths Flat (Australia), illustrating a diverse rainforest flora and an exceptional faunal assemblage (McCurry et al., 2022). The scene highlights ecological interactions such as pollination, herbivory, and predation, capturing the complexity of Miocene rainforest ecosystems. Artwork courtesy of Alex Boersma.

conifers (*Cordaites*) and drought-tolerant elements; Triassic conifers such as *Araucarioxylon* and seed plants like *Bjuvia*, *Wielandiella* and *Macrotaeniopteris*; Jurassic bennettitaleans (*Williamsonia*, *Cycadeoidea*), araucarians, and wetland ferns and horsetails (*Neocalamites*, *Schizoneura*); and Cretaceous gymnosperms, ginkgos, palms (*Sabalites*), pandanaleans (*Pandanus*), and early magnoliid-grade angiosperms (Volpe, 2010). His later *The Age of Mammals* (1961–1967) also foregrounded vegetation, explicitly tracking shifts in climate and landscape in western North America, with plants serving as chronological and ecological markers rather than background décor (Gauthier and Hickey, Yale Peabody Museum, n.d.).

9. Recent developments in botanical paleoart

9.1. From "monkey puzzles and parking lots" to plant-literate paleoart

Throughout much of the 20th century, vegetation in paleoart was reduced to a narrow repertoire of motifs—typically araucarians, cycads, *Williamsonia*, palms, and tree ferns—applied indiscriminately across sites, ages, and climates. This impoverished visual vocabulary neglected most known Mesozoic seed-plant diversity and fostered repetitive imagery in which dinosaurs appear on barren ground punctuated by a few distant araucarias. Kirk Johnson described this convention as "monkey puzzles and parking lots" (Johnson and Troll, 2007; Spagnuolo et al., 2024a, 2024b). The problem was not confined to dinosaurs:

Fig. 11. Paleoartistic reconstructions of the Barremian Las Hoyas ecosystem (Spain) by Óscar Sanisidro. (**a):** aerial perspective of the wetland mosaic with ponds dominated by charophytes and microbial mats; this illustration was featured on the cover of the book *Las Hoyas: A Cretaceous Wetland* (Poyato-Ariza and Buscalioni, 2016). (**b):** ground-level view showing *Weichselia*, *Frenelopsis*, early angiosperms, and associated vegetation framing a subtropical wetland landscape. Artwork courtesy of Óscar Sanisidro.

reconstructions of mammalian ecosystems often relied on equally formulaic vegetation backdrops, showing little ecological or temporal differentiation. Angiosperms—though dominant in most post-Cretaceous floras—were frequently reduced to indistinct green masses, their diagnostic traits too rarely translated into recognizable silhouettes. Such conventions reinforced a tendency to treat plants as mere scenery rather than evidence-bearing components of paleoecosystems.

In recent decades, however, landmark museum projects have emphasized flora as data rather than décor (Supplementary Table 1). The Ancient Colorado Mural Series at the Denver Museum of Nature & Science, directed by Kirk Johnson and executed by Jan Vriesen, Donna Braginetz, and Gary Staab, reconstructed the botanical landscapes for

Fig. 12. Reconstruction of the early Vallesian (~10.3 Ma) ecosystem of Höwenegg (Germany) (Uhl et al., 2024), showing a lake-margin mosaic with grasses, herbs, and shrubs, and a mixed mesophytic forest dominated by *Populus*, *Quercus*, *Ulmus*, and other broadleaved trees. Courtesy of Óscar Sanisidro (paleoartist) and the Hessisches Landesmuseum Darmstadt.

stratigraphically constrained localities of the Denver Basin (Johnson and Raynolds, 2006; Johnson and Stucky, 2006) (https://denverpublicart.org/activity/ancient-colorado/). Jay Matternes's Cenozoic murals for the Smithsonian narrated North American ecosystem change, especially the rise of grasslands, with plants as ecological drivers (Carrano and Johnson, 2019) (https://www.si.edu/exhibitions). Mary Parrish produced plant-centered reconstructions of the Carboniferous rainforest collapse and of latest Cretaceous floras (Montañez, 2016; Sutton, 2019) (https://naturalhistory.si.edu/education/teaching-resources/paleontology).

9.2. Botanical paleoart in scientific publications and collaborations

A parallel development took place in scientific publications, where paleobotanical data became central to visual reconstructions. Barreda et al. (2012) illustrated the Cretaceous/Paleogene floral turnover of

Fig. 13. Paleoartistic reconstruction of a Carnian (Late Triassic) ecosystem during the Carnian Pluvial Episode (CPE), illustrating the profound ecological turnover discussed in Dal Corso et al. (2020). Plants: araucariaceous and cheirolepidiaceous conifers, bennettitaleans (e.g., *Pterophyllum*), cycads (*Nilssonia*), marattialean ferns (*Asterotheca*), and sphenophytes (*Neocalamites*). Animals (left to right): dicynodonts, a primitive mammal, a prosauropod, a crocodylomorph archosaur, and a theropod dinosaur. The scene emphasizes the emergence and radiation of floristic and faunal groups that became emblematic of Mesozoic ecosystems under the humid pulses of the CPE. Artwork by Davide Bonadonna, kindly provided by the artist and the MUSE (Museo delle Scienze, Trento).

Patagonia with scenes by F. Guillén depicting ferns, palms, conifers, Cheirolepidiaceae, and podocarps. DiMichele et al. (2023) commissioned Mary Parrish to reconstruct both an Early Devonian patchwork of *Pertica* (*Trimerophyton*), *Sciadophyton*, *Rebuchia*, *Sawdonia* and *Drepanophycus* with *Prototaxites*, and a late Paleozoic scene of insect oviposition and herbivory with *Edaphosaurus* feeding on *Supaia*. Wang et al. (2012) presented Ren Yugao's reconstructions of an early Permian peat forest preserved in volcanic ash, populated by marattialean tree ferns, noeggerathialeans (*Paratingia*, *Tingia*), emergent *Sigillaria* and *Cordaites*, taeniopterid and pterophyll foliage, climbing *Sphenopteris*, and a herb layer of *Sphenophyllum* and *Nemejcopteris feminaeformis*—an explicit ash-fall T0 snapshot.

Peng et al. (2025) integrated a series of reconstructions by D.H. Yang to visualize vegetational succession across the end-Permian crisis in the South Taodonggou Section (Xinjiang, China). The sequence of images conveys not only the dramatic ecological upheaval but also the remarkable survival and rapid reassembly of plant communities. *Pleuromeia*-like lycopsids dominate some scenes, evoking their role as opportunistic colonizers, while larger arborescent forms—possibly conifers—anchor the forested refugia. Through the progression of panels, the viewer perceives how seed ferns, horsetails, and gymnosperms reestablished structure, providing habitats that sustained *Lystrosaurus* and other tetrapods. Slater et al. (2015), with artwork by Pollyanna von Knorring, presented a paleoartistic reconstruction of a Middle Permian glossopterid-dominated mire in the Lambert Graben, depicting open woodlands of *Glossopteris* with subordinate cordaitaleans, an understorey of herbaceous lycophytes and ferns, and sphenophytes along lake margins.

Recent South American studies provide further examples of the integration of paleoart into paleobotanical research. In the case of the Late Jurassic–Early Cretaceous conifer assemblages from northeastern Brazil, Conceição et al. (2025) incorporated reconstructions by Zeinner de Paula to visualize the physiognomy and ecological settings of a unique floristic association, translating fossil data into coherent environmental imagery (Fig. 6b). Similarly, Ferraz et al. (2025) employed Zeinner de Paula's artwork to depict the Guadalupian paleoflora of the Cerro Chato outcrop (southern Paraná Basin), emphasizing lycopsid dominance together with glossopterids, pecopterids, and sphenopsids, all framed within humid lacustrine habitats that acted as biodiversity refugia during episodes of aridification (Fig. 6a).

Other striking contributions include Klages et al. (2020), who presented a reconstruction by James McKay of Turonian–Santonian West Antarctica, generously shared for this study. The scene illustrates podocarp and araucarian conifers (*Podocarpidites, Trichotomosulcites*), tree ferns (*Cyathidites*), bryophytes (*Stereisporites*), and proteaceous and magnoliid angiosperms (*Peninsulapollis, Beaupreaidites, Tricolpites*) (Fig. 7). Additional palynological evidence points to a remarkably diverse flora including *Osmundacidites* (osmundaceous ferns), *Rufforddiaspora* (gleicheniaceous ferns), and further Proteaceae (*Proteacidites*), revealing a complex rainforest mosaic. This site represents the southernmost Cretaceous terrestrial record known, documenting a polar rainforest flourishing at ~82° S under greenhouse conditions. The artwork captures ecological structure with a dense fern ground layer giving way to conifer and angiosperm canopies, while volcanic relief and snow-capped peaks suggest strong climatic and topographic gradients. Beyond its aesthetic impact, the scene conveys a powerful palaeobiogeographic lesson: Antarctica, now a frozen desert, once sustained highly productive and taxonomically diverse forests, underscoring the long-term sensitivity of high-latitude ecosystems to global climate forcing.

Similarly, McElwain et al. (2021) in *Tropical Arctic* combined decades of fieldwork and fossil plant research with highly detailed illustration to reconstruct Greenland's vegetation across the Triassic–Jurassic boundary, a period of climatic upheaval and faunal turnover. Marlene Hill Donnelly's reconstructions are grounded in abundant fossil material from East Greenland—leaves, seeds, and palynological data—depicting lush forested landscapes of ferns, cycads, ginkgophytes, and extinct groups such as *Czekanowskia*, alongside tree forms with distinctive venation and even signs of environmental stress such as leaf chlorosis. The visual sequence moves from pre-extinction richness through collapse and gradual recovery, highlighting the persistence of resilient plant lineages in the Arctic under greenhouse

Fig. 14. Artistic reconstructions made by Davide Bonadonna informed by one of us (Evelyn Kustatscher). **(a)** Kungurian (early Permian) moment in which the reptile *Tridentinosaurus* observes the volcanic eruption that will doom it. The vegetation includes conifers *Walchia* and *Feysia* (in the background, partly obscured by ignimbrite), and in the foreground small lycophytes reminiscent of *Selaginellites*. for the special exhibition "At the Shade of the Supervolcano of Bolzano" (South Tyrol Museum of Natural Sciences, Bolzano). **(b)** The Middle Triassic *Megachirella* (Simões et al., 2018), resting on a conifer trunk within a low-latitude terrestrial ecosystem of the Dolomites (Italian Alps). The vegetation includes, from left to right, *Taeniopteris* (cycad), *Schytophyllum* (seed fern, in the background), a fern (foreground), *Bjuvia* (cycad), *Lycopia* (lycophyte), and *Neuropteridium*. **(c)** Bletterbach ecosystem (Wuchiapingian, Late Permian), illustrating a deltaic setting associated with the transgressive event immediately below the Cephalopod Bank within the Gröden/Val Gardena Sandstone. The scene depicts a rich late Permian low-latitude ecosystem, with vegetation represented by *Baiera*, *Pecopteris*, horsetails, *Taeniopteris* (cycad-like plants), *Ortiseia* (shrubby conifer), and *Quadrocladus* (araucarioid conifer). Faunal elements include, from right to left, a captorhinid, gorgonopsids feeding on pareiasaurs, archosauriforms, and a neodiapsid. The paleoecological framework for this reconstruction follows Bernardi et al. (2017). Artwork created for the Bletterbach Geoparc.

conditions. This collaboration between experienced paleobotanists such as Jennifer McElwain and Ian Glasspool and a versatile artist like Marlene Hill Donnelly stands as a fine example of how botanical paleoart can render the deep past accessible while remaining faithful to fossil evidence.

In this terrain of professional collaborations, several well-known natural history artists have contributed decisively. Robert Nicholls, with a career spanning more than three decades and collaborations with museums, universities, and publishers worldwide, has produced murals, models, and illustrations for institutions such as the Natural History Museum (London), *National Geographic*, and the BBC. His reconstructions combine anatomical precision with ecological and botanical context, presenting vegetation as an integral and dynamic component of prehistoric worlds. Nicholls's versatility across media—from detailed paintings to large-scale dioramas—demonstrates a rare capacity to merge scientific accuracy with artistic imagination, creating scenes that are at once informative, atmospheric, and memorable. Robert Nicholls's reconstructions of West Antarctica inverted animal-first conventions, foregrounding taxa such as *Cyathea*, Podocarpaceae, and Araucariaceae (Fig. 8).

The work of Alex Boersma (https://www.alexboersma.com/), situated at the intersection of scientific illustration, paleoart, and transitional art, likewise stands out for the refinement with which it captures the morphological details of fossil plants and their ecological interactions. Boersma achieves immediate taxonomic definition in her depictions of vegetation. Her professional trajectory underscores this precision: she has collaborated with institutions such as the American Museum of Natural History, Harvard University, NOAA, and the

Fig. 15. Reconstrucciones de paleopaisajes vegetales por W.B. Myers. **(a)** *Aglaophyton beach*, **(b)** *Carboniferous riverbank,* **(c)** *Cordaites and Araucaria sunset,* **(d)** *Cordaites and Araucaria rainstorm.* Images Courtesy of Walter B. Myers (https://www.arcadiastreet.com/).

Australian Museum, and her artwork has graced the covers of leading journals including *Nature, PNAS*, and *National Geographic*. Her technique, blending delicate watercolor with digital enhancement, conveys clarity and atmosphere in equal measure, rendering vegetation with a sense of presence and vitality that shapes the entire scene. Recently, Zhou et al. (2023) featured Boersma's reconstruction of the middle Eocene Jianglang flora in Tibet, synthesizing diverse angiosperms (*Ailanthus, Lagokarpos, Cedrelospermum, Koelreuteria*), gymnosperms, and ferns in a subtropical valley (Fig. 9). In another significant contribution, Boersma produced a reconstruction of the Miocene Lagerstätte of McGraths Flat, Australia (McCurry et al., 2022) (Fig. 10). This exceptional Konservat-Lagerstätte preserves not only an outstanding diversity of plants—including mesophyllous rainforest taxa such as *Nothofagus, Cryptocarya, Myrtaceae, Lauraceae, Proteaceae (Banksia), Casuarinaceae (Gymnostoma)*, and Araucariaceae (*Agathis*), together with lianas like *Lygodium* and a wide array of ferns and bryophytes—but also an extraordinary assemblage of animals, from insects and spiders to fish and feathers. The site captures ecological networks with remarkable fidelity, documenting interactions such as pollination, herbivory, and predation. Boersma's reconstruction translates this paleoecological complexity into an image where biodiversity and ecological interplay are foregrounded, underscoring the importance of McGraths Flat as one of the key Miocene windows into rainforest ecosystems worldwide.

Although primarily focused on vertebrate paleontology, Óscar Sanisidro has also produced significant works in the realm of pictorial paleoecology (Delgado Buscalioni and de la Cita García, 2019; Sanisidro, 2024). Two of these are highlighted in this paper. The Barremian *Konservat-Lagerstätte* of Las Hoyas (Spain) offers one of the most detailed windows into Early Cretaceous wetlands, where both aquatic and terrestrial vegetation are preserved alongside an exceptionally diverse fauna (Fig. 11a). This mosaic landscape is characterized by shallow ponds carpeted with charophytes and microbial mats, bordered by pioneering angiosperms such as *Montsechia vidalii* and *Ranunculus ferreri*, and flanked by thickets of the cheirolepidiaceous conifer *Frenelopsis* and the tree fern *Weichselia reticulata* among other ferns. Additional conifers (*Brachyphyllum*, *Pagiophyllum*, *Sphenolepis*, *Cupressinocladus*) and cycads or bennettitaleans form more open stands, while traces of seasonal fire suggest recurrent disturbance in this subtropical setting. The Upper Miocene (early Vallesian, ~10.3 Ma) reconstruction of Höwenegg, exhibited at the Hessisches Landesmuseum Darmstadt, portrays a mosaic of lakes and wetland margins surrounded by a mixed mesophytic forest (Fig. 12). The scene by Oscar Sanisidro emphasizes grasses and herbs—Poaceae, Cyperaceae, Amaranthaceae, Asteraceae, *Plantago*, *Rumex*, and marginal *Characeae*—alongside shrubs such as *Buxus*, *Vitis*, and *Podogonium*. The arboreal layer is dominated by *Populus* (the most common leaf type recovered), with *Ulmus*, *Betula*, *Quercus*, *Gleditsia*, *Platanus*, *Salix*, *Cinnamomum*, *Laurophyllum*, *Ficus*, *Sapindus*, *Fagus*, and *Celtis lacunosa* also represented. Sanisidro's artwork conveys not only the faunal richness of Höwenegg, but also the structural and taxonomic diversity of its plant communities, integral to understanding the paleoecological dynamics of the outstanding paleoneological site (Uhl et al., 2024).

Davide Bonadonna (http://www.davidebonadonna.it/) is another artist who successfully combines exceptional anatomical accuracy with

Fig. 16. Neanderthal scenes at the Rock of Gibraltar, with fauna and flora reconstructed from the excavations of the Gorham's and Vanguard Paleolithic caves. Artwork by Mauricio Antón. The vegetation includes stone pines (*Pinus pinea*), *Juniperus*, *Ephedra*, grasses, *Artemisia*, Amaranthaceae, Asteraceae, among others. (**a**) Hunting scene in the coastal plain. (**b**) A leopard with an ibex on the eastern sand slopes of Gibraltar, being challenged for its prey by a group of Neanderthals. Paleobotanical information based on Carrión et al. (2008, 2018) and Finlayson and Carrión (2007). Images courtesy of Mauricio Antón.

Fig. 17. Quaternary landscapes of Eastern Spain (Valencia Region) illustrated by Carles Puche and based on paleoecological data, mainly archaeological charcoal and pollen (Villaverde, 2001). (**a):** Late Glacial of Cova de les Cendres**. (b):** Cova del Parpalló during the Last Glacial Maximum. (**c):** Full-Glacial Cova Negra. (**d):** Early Holocene from Santa Maira. Courtesy of Valentín Villaverde.

convincing ecological realism. His achievements, recognized by distinctions such as the John J. Lanzendorf PaleoArt Prize for Scientific Illustration (2010), attest to his international standing. Although renowned primarily for reconstructions of vertebrate palaeobiology, he has also produced outstanding depictions of fossil vegetation. In Trümper et al. (2023), for instance, he illustrated the Sinigo fossil forest, a short-lived Kungurian wetland dominated by walchian and voltzialean conifers in a volcanogenic landscape, while in Dal Corso et al. (2020) he rendered a Carnian (Late Triassic) ecosystem under the influence of the Carnian Pluvial Episode, populated by araucariaceous and cheirolepidiaceous conifers, bennettitaleans, cycads, ferns, and sphenophytes together with early archosaurs and dinosaurs (Figs. 13, 14). When Bonadonna turns to vegetation, it is rarely schematic: morphologies and ecological settings are portrayed with unusual taxonomic clarity, an uncommon strength in paleoart that greatly enhances both scientific communication and didactic value.

Although primarily focused on dinosaurs, other major popularizers such as Julius Csotonyi (Csotonyi and White, 2014) demonstrate that traditionally zoocentric paleoart can nevertheless integrate plant taxonomy and diversity in the service of reconstructions that are both ecologically harmonious and scientifically grounded (https://www.csotonyi.com/). Mauricio Antón, in his prolific paleoartistic work (https://mauricioanton.wordpress.com/), has produced countless reconstructions in which the botanical component—though not central to his objectives—is consistently taken into account, especially in its physiognomic dimension, from which emerges an unquestionable paleoecological coherence.

9.3. Resources and challenges

These initiatives run parallel to advances in paleobotany that have made flora increasingly reconstructable. The description of new taxa and enigmatic forms as well as visual explanations of complex ecological processes (Pearce et al., 2023, 2025), show how art supports paleoecological reasoning. Paleobotany itself is detective-like: modular fossils are assembled into whole plants (Herrera, 2009; Carrión and Cabezudo, 2003) of Carboniferous mire ecosystems (DiMichele et al., 2020; Gastaldo et al., 2020) and of lineages with no modern analogues (Barreda et al., 2012; Beans, 2022; Benca, 2022) have expanded the visual palette available to artists. Resources such as the Extinct Plant Paleoart Database (Jud, 2020) provide centralized references, while popular media—video games, documentaries, comics—are becoming increasingly plant-literate (Wings et al., 2023). A recent resource can be found in the work of Julianne Kiely (https://palaeoflora.blogspot.com/). Most of her pieces are examples of scientific illustration, documented from a paleobotanical perspective, but some works could also be perfectly categorized as botanical paleoart. In fact, the production of geobotanical illustrations using fossil data has a long tradition, especially in the form of dioramas representing paleovegetation catenas (e.g., Cúneo et al., 2014; Borruel-Abadía et al., 2014; Marchetti et al., 2015; Altolaguirre et al., 2020, 2021; Spicer et al., 2021; Kustatscher et al., 2014, 2017, 2019, 2024; Matamales-Andreu et al., 2022).

In the field of freelance animators and illustrators specializing in the natural sciences, the monumental work of Walter B. Myers (https://www.arcadiastreet.com/index.html) must be highlighted. With

Fig. 18. Prehistoric habitats of Neanderthals inhabiting Bolomor Cave and the Valldigna Valley in the Mondúver Mountains (eastern Spain) during the Middle and early Upper Pleistocene, reconstructed from paleobotanical data (Amorós et al., 2021). Extensive forest cover is depicted with *Pinus nigra*, *P. pinaster*, and junipers on rocky slopes, while *Quercus ilex*, *Q. faginea*, and other angiosperms dominate deeper soils. In the foreground, *Erica*, *Pistacia*, *Rhododendron*, *Myrtus*, and *Chamaerops* are represented. Ethnographic details include a Neanderthal child playing with tortoises and an adult consuming hazelnuts. Photograph of the original painting by Gabriela Amorós (colored pencils).

many decades of experience producing for books, magazines, museum exhibits, and television, his art strives toward photorealism. Although the majority of his artworks are centered on fauna, the ecosystemic component prevails and there are exceptional works of Paleozoic as well as Mesozoic vegetation (Fig. 15). Walter B. Myers' paleoart is characterized by a cinematic and immersive approach, often resembling digital landscape art more than traditional illustration. His work emphasizes atmospheric realism, with expansive skies, dynamic lighting, and sweeping perspectives setting the stage for ancient worlds. Vegetation and geological settings are carefully reconstructed, though with a slightly idealized, almost photographic clarity that enhances accessibility for general audiences (Fig. 15).

Yet poor practices persist in both amateur and professional paleoart, where vegetation is often left unreviewed by specialists. For example, in a reconstruction of the East Kirkton Quarry (Mississippian, Scotland), certain plants were depicted with palm- or pine-like silhouettes, and even grasses in the herb layer (Garza et al., 2025). These are anachronisms: true palms (Arecaceae) are Late Cretaceous angiosperms, pines (*Pinus*) are much later conifers, and grasses evolved long after the Carboniferous. More plausible candidates include tree ferns such as *Psaronius* or seed ferns with palm-like crowns, and cordaitaleans with conifer-like habits. Such visual ambiguities reveal how iconic but inaccurate morphotypes continue to be projected into deep time, despite paleobotanical evidence. As emphasized by Philippe et al. (2009), the "monkey puzzles and parking lots" reflex remains pervasive, with many reconstructions still recycling early 20th-century templates or morphotaxa such as *Araucarioxylon* and *Brachyphyllum* as if equivalent to living *Araucaria*. Philippe and colleagues explicitly warned that such silhouettes, based on familiar modern conifers, are largely hypothetical and often ignore extinct families or southern taxa documented in the fossil record.

This tension between iconic templates of vegetation and data-driven reconstructions highlights both the persistence of plant blindness in paleoart and the growing opportunities to overcome it. A particularly striking example is the enduring depiction of *Cycadeoidea* (Bennettitales, Cretaceous) with conspicuous, flower-like bisexual cones. This imagery, based on Wieland (1906-1916), was rejected decades ago (Delevoryas, 1968; Crepet, 1972) and reinterpreted as closed reproductive organs adapted to partial self-pollination (Stidd, 1980; Rothwell and Stockey, 2002). Nevertheless, outdated versions persist across toys, posters, and outreach media, revealing how folkloric iconography can outlive scientific correction.

In sum, while paleobotanical research has increasingly informed artistic reconstructions, its penetration into paleoart has been neither firm nor extensive. In the most popular and widely disseminated domains, vegetation often remains marginal, or is portrayed through

Fig. 19. Paleoartistic illustration of Early Pleistocene vegetation (1.6–1.2 Ma) in the Orce Archaeological Zone (OAZ), based on palynological data, by Gabriela Amorós in Carrión et al. (2024b). **(a)** The scene highlights altitudinal gradients, with conifers and birches at higher elevations, deciduous forest belts below, and valleys with deeper soils supporting woody angiosperms. At the lowest levels, lacustrine and riparian habitats appear with sedge meadows and phreatophytic vegetation. The rhinoceros depicted in the foreground (bottom right) alludes to the significant role of herbivory in maintaining heliophytic features of Pleistocene forests in the region. **(b)** Riparian landscape under relatively arid conditions in the OAZ at ca. 1.6 Ma. Tree cover is denser in areas influenced by groundwater, while rocky slopes and marls are dominated by *Ephedra*. Halophytic vegetation occupies the lower zones, whereas *Artemisia* proliferates across open, treeless slopes. Digitally adapted from Carrión et al. (2024b).

Fig. 20. Paleoartistic rendering of environmental conditions in a mountain landscape near Pesturina Cave, Central Balkans, during the Upper Pleistocene (Carrión et al., 2024a). **(a)** Last Interglacial (MIS 5). The scene depicts a mountain rising to 1700–2000 m, where the prevalence of angiosperm forests under warm and humid conditions is symbolized by the alder placed at the right margin. At higher elevations, herbaceous and shrubby vegetation dominates, with cushion stands of *Pinus mugo*, *Juniperus*, and *Alnus viridis*. The treeline is defined by a belt of conifers—*Pinus sylvestris*, *P. nigra*, *Abies*, *Picea*—accompanied by *Juniperus*, *Betula*, *Carpinus*, and *Fagus*. Mixed deciduous forests with oaks and other broadleaves occupy the mid-altitudes, where tree cover is densest. **(b)** Glacial stage (MIS 4–3). A pine (*Pinus nigra*) in the foreground emphasizes the dominance of gymnosperms under cold and arid climates. Mid-elevation refugia are maintained by milder microclimates and the buffering effect of orographic precipitation. Vegetation belts appear compressed: tundra-like periglacial communities at high altitudes and steppe environments dominated by *Artemisia* in the lowlands. Conifers such as *P. mugo*, together with firs and beeches, descend into mid-altitudes and even valley bottoms. Digitally adapted from Carrión et al. (2024a). Artwork Gabriela Amorós.

Fig. 21. Botanical paleoart illustrating vegetation dynamics—and continuity—during stadial and interstadial phases of the Iberian Upper Pleistocene. **(a)** Stadial conditions in a pre-coastal Cantabrian valley show open grasslands with *Artemisia*, sedges, heaths, and composites, together with *Betula* on lower slopes and scattered pines and junipers in the distance, where *Coelodonta antiquitatis* and *Rangifer tarandus* are grazing. **(b)** Interstadial phases depict warmer and more humid climates favouring forest expansion, with broad-leaved trees on deeper soils, birches and conifers at montane elevations, and greater shrub and herb diversity, accompanied by deer, fallow deer, and foxes. **(c)** In the southeastern Iberian coastal region, palaeolandscapes are reconstructed as largely wooded, featuring multiple *Quercus* and *Pinus* species along with *Fraxinus*, *Corylus*, and *Juniperus*, while Mediterranean scrub exhibits high thermophilous diversity including Ibero-North African taxa. **(d)** Interstadial phases in the same area reinforce the role of glacial refugia as resilient ecological structures, with deer, lynx, and rabbits depicted. More taxonomic details in Supplementary Figs. 2–7. Artwork by Gabriela Amorós digitally adapted from Carrión et al. (2026).

conceptual errors that paleobotany corrected decades ago but which still persist in the broader scientific imagination. The "green" dimension of deep-time reconstructions thus continues to suffer from neglect, even as opportunities for a floristically informed paleoart have never been greater.

10. Botanical paleoart and Quaternary paleoecology: precedents

Botanically explicit reconstructions of Quaternary paleolandscapes remain uncommon. As in the Miocene and Pliocene record, much of the available paleoart clusters around hominin contexts (e.g., Turner and Antón, 2007; Agustí and Antón, 2013; Ferrández Verdú et al., 2023). A subset of these works resolves vegetation floristically enough to permit taxon-level identification. Notable examples include Domingo López González's reconstruction of the early Pleistocene Barranc de la Boella (NE Iberia), supervised by Antonio Rosas (Fidalgo et al., 2023), and Mauricio Antón's scenes for the Neanderthal contexts of Gorham's and Vanguard Caves in Gibraltar, informed in part by Carrión et al. (2008, 2018) (Fig. 16).

The advantage of working with paleobotanical records from Quaternary sediments lies in their anchoring to extant species, even when the ranges of those species have since shifted due to climate change or human influence. Yet, in the case of palynology, for instance, the process of translation from pollen diagram to image is far from straightforward. Pollen evidence is fragmentary and scale-dependent (Birks et al., 2016), demanding artistic decisions that privilege taxonomic intelligibility over strict naturalism. Excessive photorealism risks blurring distinctions, whereas a consciously selective visual language—highlighting diagnostic fruits, flowers, leaf habits, or growth forms—can make ecological diversity visible and refugial landscapes legible (Amorós et al., 2021). Moreover, the inherent ambiguity of pollen catchment, with contributions from both local and regional sources (Abraham, 2023), invites rather than hinders creative reconstruction. It allows for the visualization of assemblages where taxa of contrasting ecological affinities coexist, underscoring the multi-scalar role of glacial refugia in shaping Quaternary biotas. Ultimately, paleoart is not simply illustration but a methodological act situated at the intersection of accuracy and narrative. It requires choices that amplify differences, accentuate diagnostic traits, and occasionally orchestrate ecological juxtapositions so that the silent data of pollen counts can be transformed into evocative, scientifically grounded visions of ancient landscapes.

10.1. Paleoartistic reconstructions in Paleolithic and Neolithic Valencia

An early and notable precedent is the volume edited by Villaverde Bonilla (2001), remarkable for its paleoecological rigor. This work synthesizes research on Neanderthals and Cro-Magnons in the eastern Iberian region of Valencia and is richly illustrated by Carles Puche, whose hand-drawn images provide detailed botanical and faunal reconstructions (Fig. 17). Examples include the Late Glacial vegetation of Cova de les Cendres (Badal and Carrión-Marco, 2001), Cova del Parpalló around 18,000 BP (Dupré and Carrión, 2001), the Pleistocene record from Cova Negra (Martínez Valle, 2001), Holocene sequences from Santa Maira (Pérez Ripoll and Martínez Valle, 2001), and Last Interglacial deposits from Cova de Bolomor (Guillem Calatayud, 2001). Together, these examples represent some of the earliest attempts in the Iberian Peninsula to translate anthracological and palynological data into visual paleoartistic reconstructions, highlighting the potential of

Fig. 22. Artistic renderings of two Upper Pleistocene phases in the Píñar Valley, adjacent to Carihuela Cave (cliffs on the left), a classic Neanderthal site in southern Iberia. The area, at ~1000 m a.s.l., is today subject to continental Mediterranean climate. **(a)** Interstadial conditions are represented by extensive woodlands with *Pinus nigra*, *Juniperus*, and diverse oaks thriving where soil moisture was greater; *Dicerorhinus kirchbergensis* occupies the foreground. **(b)** A contrasting stadial landscape shows grass-dominated steppe, with intense herbivory inferred from faunal remains including *Bos*, *Cervus*, and *Equus*. Along the river margins, phreatophytic vegetation is depicted. More taxonomic details in Supplementary Figs. 8–9. Artwork by Gabriela Amorós, digitally adapted from Carrión et al. (2026).

botanical evidence in shaping Quaternary landscapes.

10.2. Iberian Paleofloras Project

The monographs on Iberian paleoflora and paleovegetation covering the Paleocene–Pliocene (Carrión et al., 2024c), the Pleistocene (Carrión et al., 2024d), and the Holocene (Carrión et al., 2024e) compile a broad selection of paleoartistic works (Supplementary Fig. 1). These volumes stand out for explicitly situating faunal material within its floristic and geobotanical context. They feature dioramas conceived as paleovegetation catenas (sequences across topographic gradients), together with a wide range of scientific illustrations. Some Cenozoic catenas derived from pollen diagrams and macrofossil lists of Iberian paleoflora were generated by Amorós (2023). Taken together, these works represent a rare attempt to weave paleobotanical data into visual narratives of long-term landscape history, providing an important precedent for subsequent plant-focused paleoart in the Quaternary.

10.3. Mid-Pleistocene landscapes in Bolomor

The reconstruction of Neanderthal habitats at Bolomor Cave (eastern Spain) (Amorós et al., 2021) is a pioneering example of paleoart explicitly grounded in high-resolution palynological evidence. The pollen record showed that Neanderthals occupied woodlands for hundreds of thousands of years, in contrast to the long-standing image of treeless steppe environments. To reflect this, the artworks were executed in colored pencil with the deliberate aim of maximizing taxonomic legibility and ecological distribution—conifers (*Pinus nigra*, *P. pinaster*, *P. halepensis*) in exposed uplands; mesothermophilous angiosperms (*Quercus*, *Corylus*, *Castanea*, *Pistacia*, *Phyllirea*, *Myrtus*) in sheltered valleys (Fig. 18). Particularly noteworthy is the illustration of genera with biogeographic significance, such as *Rhododendron* cf. *ponticum*, *Betula* cf. *celtiberica*, *Celtis australis*, *Ceratonia siliqua*, *Chamaerops humilis*, and *Taxus baccata*. Ethnographic details—such as hazelnut gathering or the use of bird feathers—further shifted the emphasis away from stereotypical hunting scenes toward broader ecological interactions.

Fig. 23. Last Interglacial vegetation within the European temperate forest biome, consistent with pollen-based reconstructions of vegetation structure (Pearce et al., 2023). Iconic fauna include *Palaeoloxodon antiquus*, *Stephanorhinus kirchbergensis*, and *Bos primigenius*, together with species still extant such as fallow deer (*Dama dama*), great spotted woodpecker (*Dendrocopos major*), European robin (*Erithacus rubecula*), and greylag goose (*Anser anser*). **(a)** Early temperate stage showing light woodland with tall trees and hazel (*Corylus avellana*) transitioning into grassy clearings. **(b)** Another early temperate landscape with open grasslands interspersed with woodland patches alongside closed-canopy stands. **(c)** Late temperate phase dominated by hornbeam (*Carpinus betulus*) woodlands flanked by more open vegetation. **(d)** Late temperate depiction of grass- and sedge-rich habitats containing scattered oaks (*Quercus robur*), backed by continuous deciduous forest. Illustration courtesy of Elena Pearce and artist Brennan Stokkermans.

Paleoecologically, the Bolomor reconstructions highlighted the persistence of forest refugia consistent with faunal, lithic, and fire evidence, emphasizing the resilience of human settlement in a montane–coastal ecotone (Blasco et al., 2016). Didactically, they showed how paleoart can illustrate ecological processes—altitudinal gradients, mixtures of thermophilous, cryophilous, phreatophytic, and xerophytic taxa—without oversimplifying biodiversity.

10.4. Early Pleistocene Orce

The Orce Archaeological Zone (southern Spain), with sites dated between 1.6 and 1.2 million years ago, offers another recent attempt to integrate paleoecological data into visual reconstruction (Carrión et al., 2024a). Four digital paintings were grounded in pollen records from Venta Micena 1 (VM1), Barranco León (BL), and Fuente Nueva 3 (FN3) (Ochando et al., 2022), which are the three sites currently under active excavation within this major project led by J.M. Jiménez-Arenas (Martínez-Navarro et al., 2003; Espigares et al., 2019; Luzón et al., 2021; Yravedra et al., 2024). The team developed a formalized protocol: diagnostic taxa were first drawn with emphasis on fruits, inflorescences, and growth habits, and then assembled into composite landscapes. Conventions and concessions were explicitly stated—for example, chenopods depicted in red hues, overlapping phenological stages, or generic morphotypes within *Juniperus*—so that interpretive choices remained transparent. The resulting images portray an altitudinal mosaic: conifers and birches on uplands, angiosperms in deeper soils, open steppe vegetation on lithosols, and persistent wetlands functioning as hydroclimatic refugia that may have facilitated early human occupation. Particularly striking is the visibility of Tertiary relict taxa such as *Parrotia*, *Zelkova*, *Carya*, *Cathaya*, and *Eucommia*, which survived as evergreen vestiges within Early Pleistocene landscapes, creating plant communities without modern analogues (Fig. 19).

10.5. Balkan plant refugia of Pešturina

A third pilot study addressed paleolandscapes reconstructed from palynological data at the Paleolithic site of Pešturina in the Central Balkans of Serbia. Here, cave pollen records (from sediments and coprolites) were integrated with broader sequences from the Balkans and southern Carpathians, allowing reconstructions to be attempted at

Fig. 24. Surrounding landscape of the Cueva del Arco during the Neanderthal occupation phase (Martín-Lerma et al., 2023; Carrión et al., 2025). Paleoecological information derives from pollen, carpological, anthracological, and archaeozoological analyses, complemented with records from nearby sites in southeastern Iberia (Supplementary Fig. 23). The vegetation shows a coexistence of Mediterranean scrub (*Quercus*, *Phillyrea*, *Olea*, *Myrtus*, *Cistus*), conifers (*Pinus nigra*, *Juniperus*, *Taxus*), mesophilous trees such as deciduous oaks, and xerophytes including *Artemisia*, Amaranthaceae, *Ephedra*, and Lamiaceae. See Supplementary Figs. 10–13, for taxonomic details. Artwork by Gabriela Amorós.

multiple geographic scales (Carrión et al., 2024b). The resulting paleoart contrasted glacial and interglacial conditions, emphasizing the persistence of refugia and the altitudinal shifts of steppes, conifers, and broad-leaved trees between MIS 5 and MIS 3 (Fig. 20).

10.6. Upper Paleolithic French Pyrenees at Isturitz

A fourth and more recent case, distinct in its focus yet complementary to the previous studies, comes from the Aurignacian levels of Isturitz Cave in the French Pyrenees (Berlioz et al., 2025). The research centered on ungulate paleoecology, combining stable isotope analysis of enamel and collagen with dental microwear texture analysis to reconstruct herbivore diets and their ecological responses to MIS 3 climatic oscillations. Paleoart entered as an additional interpretive layer, with reconstructions by Gabriela Amorós depicting the vegetation and faunal communities of the cave surroundings. Unlike the earlier palynology-driven works, the Isturitz imagery was not based directly on pollen diagrams but instead integrated zooarchaeological proxies with regional paleoenvironmental knowledge. The visual strategy emphasized coherence between faunal isotopic signals, vegetation types, and climatic backdrop, rather than fine-grained taxonomic detail. This shift in visual grammar underscores an important methodological point: paleoart can extend beyond palynological constraints and still function as a heuristic bridge, connecting proxy data, ecological modeling, and human behavioral inference.

10.7. Diversity of Neanderthal Vegetation Landscapes

In the broader discussion of Neanderthal landscapes across Eurasia and through the species' evolutionary trajectory, Carrión et al. (submitted) offer a set of botanically oriented reconstructions that develop and expand upon the approaches illustrated in the preceding case studies. Their explicit aim is to counter the persistent stereotype of Neanderthal environments as uniformly cold, treeless steppes. The project restores plants to the center of Pleistocene landscape narratives. The paleoartistic work—primarily by Gabriela Amorós, unfolds as a set of "chronicles" across Iberian regions, each grounded in pollen, charcoal, and macrofossil records (Fig. 21, Supplementary Figs. 2–7). In the Cantabrian Mountains, stadial phases dominated by *Artemisia*, *Ericaceae*, *Asteraceae*, and *Cyperaceae* with sparse conifers are contrasted with interstadials that rapidly reforested into oak- and birch-rich woodlands, depicted alongside emblematic fauna such as *Rangifer tarandus*, *Coelodonta antiquitatis*, *Cervus elaphus*, and *Capreolus capreolus*. In southeastern Iberia, Amorós illustrates stadial and interstadial refugia, highlighting the persistence of *Quercus faginea*, *Q. ilex*, *Q. suber*, *Pinus nigra*, and Mediterranean scrub including *Periploca angustifolia* under favorable microclimates (Carrión et al., 1995, 2003) (Fig. 21, Supplementary Figs. 4–7).

Further reconstructions from the Piñar River Valley (Carihuela and Las Ventanas) contrast Last Interglacial forests of *Quercus* and *Olea* with later grasslands shaped by grazing pressure, and with interstadial mosaics of pines, junipers, and oaks. A striking MIS 3 glacial scene depicts

Fig. 25. Cueva del Arco during the Gravettian (Martínez-Navarro et al., 2003; Carrión et al., 2025), showing the predominance of *Pinus halepensis*, more common here than *P. nigra* as evidenced by archaeological charcoal remains. No substantial changes are observed in the ecological structure compared to the preceding Mousterian phase. See Supplementary Figs. 14–16, for taxonomic details. Artwork by Gabriela Amorós.

Artemisia-dominated steppe punctuated by scattered *Pinus*, riverine reedbeds, and speculative elements such as hyena–human competition in karstic shelters (Carrión et al., 2019). Although Carihuela is located in southern Iberia, its inland position under a continental climate has made it particularly sensitive to stadial–interstadial vegetation shifts. Unlike forest-refugial environments, this site clearly records such fluctuations, as represented in a figure specifically designed to illustrate this dynamic (Fig. 22, Supplementary Figs. 8, 9). By weaving botanical and faunal proxies into coherent visual landscapes, these reconstructions reveal the diversity of habitats, and the ecological plasticity of Neanderthals.

10.8. Paleoart in the Venice Biennale

A Backstory article presents "Out of the Cave", an installation selected for the 2025 Venice Architecture Biennale (Amorós et al., 2025). The work reframes deep-time knowledge through scientifically grounded paleoart, a mode of reconstruction that has been virtually absent from the Biennale's program. Rather than using plants as background décor, the installation foregrounds botanical detail and ecosystem structure, integrating palaeoenvironmental, archaeobotanical, and biogeographical data from a Late Pleistocene Cantabrian context. Its aim is to demonstrate how contemporary paleoart can articulate ecological narratives that challenge entrenched stereotypes—such as the simplistic open-steppe model of Pleistocene Europe—and to show how biodiversity, refugial dynamics, and human–environment interactions can be communicated through evidence-based visual synthesis.

10.9. Last European Interglacial and light woodlands

Although not explicitly conceived as botanical paleoart, several recent studies have nonetheless produced reconstructions with a clear paleobotanical basis. Pearce (2023) and Pearce et al. (2023) applied the REVEALS model to a large set of pollen records from across Europe, reconstructing vegetation structure during the Last Interglacial (MIS 5e). Their results demonstrated that more than half of the temperate biome consisted of light woodland and open habitats, contradicting the long-standing view of Europe as dominated by closed-canopy forests before the arrival of *Homo sapiens*. Disturbance regimes and megafaunal herbivory were identified as key forces maintaining this ecological openness. These findings were translated into paleoartistic reconstructions by Brennan Stokkermans, who depicted heterogeneous mosaics of grassland, shrubland, and woodland populated by characteristic interglacial megafauna such as *Palaeoloxodon antiquus* and *Bos primigenius* (Fig. 23). Pearce et al. (2025) extended this line of work by combining REVEALS with the LOVE model to capture both regional and local vegetation dynamics. The study showed that while light woodland dominated regionally, local landscapes often diverged, forming fine-grained mosaics of open ground, semi-open woodland, and patches of closed forest. Disturbance-adapted taxa and megafaunal activity emerged as central drivers of this heterogeneity, beyond what can be explained by climate alone. These results were accompanied by new paleoart by Hodari Nundu, synthesizing modeled vegetation with ecological proxies of megaherbivore impact.

Fig. 26. Plausible scenario for the vegetation of the riparian canyons adjacent to Cueva del Arco (Segura and Quípar rivers) based on pollen analyses. A proliferation of trees and shrubs behaving as phreatophytic species is interpreted under generally arid conditions. The surrounding environment was largely dominated by *Artemisia* and grass steppes, with scattered pines and junipers on exposed lithosols. In contrast, the canyon bottoms and rocky walls hosted ash, elm, willow, poplar, alder, strawberry tree, maple, and yew, among others. This is a pictorial representation of a hydrorefugium during a stadial phase of the Late Pleistocene. See Supplementary Figs. 17 and 18, for taxonomic details. Artwork by Gabriela Amorós.

11. Botanical Paleoart for Pleistocene Ecological Mosaics of the Segura Basin

Within the framework of the ECCE HOMO research group (University of Murcia), we have assembled a digital archive of more than 200 Cenozoic plant taxa represented through multiple morphotypes. This resource provides both an aesthetic toolkit and a taxonomically robust reference for paleoecological reconstruction. Complementing this archive, extensive Iberian paleobotanical datasets (Carrión et al., 2024a, 2024b, 2024d) guide the selection and ecological calibration of the sequences explored here. From recent pilot experiences (Amorós et al., 2021, 2025; Carrión et al., 2024a, 2024b), it has become evident that the most demanding stage of reconstruction is not illustration but the paleoecological investigation that precedes it. Each case becomes a forensic synthesis of diverse proxies—chronology, stratigraphy, palynology, plant macrofossils, phytoliths, charcoal, dendrochronology, ancient DNA, isotopes, biomarkers, paleohydrology, paleoclimate data, archaeology, coprolites, and ecological modeling—whether to update existing studies or to build new ones where gaps remain. In this context, we present four reconstructions for inland southeastern Spain (Figs. 24–27; Supplementary Figs. 10–22), grounded in the available paleoecological evidence for the Quípar–Segura basin (Supplementary Fig. 23). Three correspond to the Upper Pleistocene and are inspired by the sequence from Cueva del Arco: (i) a Mousterian landscape dominated by pine–juniper woodlands; (ii) a Gravettian scenario set in karstic terrain and lithosols; and (iii) a riparian refugium along the river gorges, which—given the stability of pollen spectra—could plausibly represent either cultural phase. A fourth reconstruction reaches back to the late Early Pleistocene, drawing on the palynological record of Cueva Negra del Estrecho del Río Quípar, where the co-occurrence of evergreen and deciduous oaks with conifers and riparian elements underscores the refugial character of the basin (Carrión et al., 2003; Walker et al., 2020).

11.1. A living Mosaic: Late Pleistocene Landscapes of Southeastern Iberia

The Cueva del Arco complex (Cieza, Murcia) overlooks the Segura basin from the cliffs of the Almadenes and Quípar canyons. Its stratified sequence spans the Mousterian to the Neolithic (Martín-Lerma et al., 2023; Román et al., 2024; Carrión et al., 2025, 2026). In this rugged landscape of river gorges, limestone slopes, and upland forests, both Neanderthals and early modern humans found diverse habitats and resources. Faunal assemblages reflect this diversity: rabbits (*Oryctolagus cuniculus*) dominate all occupations, while ungulates such as *Capra pyrenaica*, *Cervus elaphus* and *Bos primigenius* indicate mosaics of rocky terrain, forest margins, and open patches; remains of *Equus ferus* point to nearby steppic or open woodland environments. Carnivores are sporadic (*Canis lupus*, *Felis silvestris*), underscoring the ecological heterogeneity of the area (Martín-Lerma et al., 2023; Román et al., 2024; Carrión et al., 2025, 2026).

Vegetation evidence from charcoal, carpological remains, and pollen (including carnivore coprolites) depicts a compressed landscape where steppe, Mediterranean scrub, and montane conifers coexisted at short distances. Mousterian fires relied mainly on *Pinus nigra*-type and *Juniperus phoenicea* (Fig. 24), while Gravettian hearths show increased use of *Pinus halepensis* (Fig. 25). Plant macroremains—bracts of *Pinus* cf. *halepensis* and *tp. nigra*, rhizomes of *Macrochloa tenacissima*, leafy stems and endocarps of *Juniperus*, drupes of *Celtis*, and seeds of *Buglossoides* cf. *arvensis*, *Galium*, and other Boraginaceae—attest to the exploitation of woodland, scrubland, riparian, and steppe resources. Pollen spectra confirm this mosaic: conifers (*Pinus*, *Juniperus*, *Taxus*) coexist with mesophilous taxa (*Quercus*, *Acer*, *Alnus*, *Betula*, *Corylus*, *Castanea*, *Juglans*, *Fraxinus*, *Ulmus*, *Ilex*) and thermophilous elements (evergreen *Quercus*, *Pistacia*, *Phillyrea*, *Olea*, *Myrtus*, *Buxus*, Cistaceae, Ericaceae), alongside xerophytes such as *Artemisia*, Amaranthaceae, *Ephedra* and *Teucrium*. These archives, together with complementary regional records (Supplementary Fig. 23; Carrión, 1992; Carrión and Munuera, 1997; Carrión-Marco, 2005; Burjachs, 2009; Vidal-Matutano, 2016; Vidal-Matutano et al., 2015, 2017; Badal and Martínez-Varea, 2018; Badal et al., 2019; Martínez Alfaro et al., 2022), portray a heterogeneous environment of coniferous ridges, riverine corridors of *Populus* and *Salix*, juniper–pistachio scrub, and open steppes frequented by ibex and wild horses.

Artistic reconstructions based on these data depict landscapes comparable to modern uplands shaped by long-term grazing (Figs. 24–26). Around the cave, patches of evergreen *Quercus*, *Pistacia*, *Phillyrea* and *Rhamnus* occupy karstic soils, with herbaceous cover dominated by *Artemisia*, Asteraceae, legumes, Lamiaceae, bulbous taxa, *Plantago*, *Erica*, *Papaver*, *Cistus*, *Armeria*, *Helianthemum* and Caryophyllaceae. Gravettian reconstructions emphasize more open grasslands punctuated by Mediterranean pines, while the canyon is rendered as a humid refugium dominated by *Populus*, *Salix*, *Ulmus*, *Fraxinus* and *Alnus*, contrasting with evergreen oak scrub on the slopes. Cooler niches are signalled by *Taxus baccata* and *Acer*, and juniper–pine stands link the canyon to upland forests. This mosaic supported diverse faunas—from waterfowl to large herbivores—and provided hominins with stable water, shelter, plant foods, and raw materials, reinforcing the role of riparian systems as glacial refugia (Carrión et al., 2025, 2026).

Fig. 27. Paleovegetation reconstruction of the late Early Pleistocene archaeological site of Cueva Negra, based on palynological data from Carrión et al. (2003). The reconstruction highlights the local abundance of trees with different ecological requirements, including pines, junipers, oaks, and other broadleaved taxa, as well as shrubs and Mediterranean vegetation in general. Groundwater and local microclimate likely conditioned the surrounding vegetation, while xerophytic steppes extended across the adjacent plateaus. The river corridor is depicted in simplified form, with widened stretches and riparian vegetation, acknowledging that subsequent canyon incision has significantly altered the local geomorphology. The image thus conveys the fluviolacustrine setting inferred for the Pleistocene without attempting a literal reproduction of present-day topography. See Supplementary Figs. 19–22, for taxonomic details. Artwork by Gabriela Amorós.

Some artistic decisions reflect local ecological constraints. Junipers near the cave are depicted as small, consistent with skeletal exokarstic soils and potential wind exposure or wood-gathering disturbance. Woodland clearance by cave occupants remains uncertain, though burning cannot be excluded; nearby Pleistocene sites (e.g., Los Tollos: Carrión et al., 2024f) show recurrent fire use during Neanderthal occupations, while Neumark-Nord (Germany) documents anthropogenic opening of forests through repeated burning (Roebroeks et al., 2021). In the canyon scene, trees are intentionally shown as slightly enlarged relative to scale to convey structural contrast, whereas some herbaceous taxa are drawn directly from pollen and carpological finds (Fig. 26). The inclusion of *Buglossoides* cf. *arvensis*—indicative of nutrient-rich habitats and moderate disturbance—responds to this dual evidence and is placed near the cave entrance. Finally, the portrayal of a Neanderthal youth beside a wildcat, with facial painting echoing the animal's patterning, is an artistic device symbolizing coexistence rather than domestication.

11.2. Arboreal hydro-refugia during the Early–Middle Pleistocene transition

Perched above the gorge of the Quípar River in Murcia, Cueva Negra preserves a sedimentary archive securely dated to the late Early Pleistocene, between the close of the Jaramillo subchron (~0.99 Ma) and the Matuyama–Brunhes boundary (0.772 Ma). Magnetostratigraphic and biochronological constraints place this record between MIS 23 and 21, within the Early–Middle Pleistocene Transition. Global and North Atlantic syntheses identify glacials MIS 24 and particularly MIS 22 as among the most severe of the interval, with major ice-volume peaks and circulation reorganizations. Stadials of LGM-like severity are therefore plausible at the regional scale, though their terrestrial imprint in southeastern Iberia was modulated by latitude and topography. This chronological framework is supported by ESR/U-series assays on *Equus* cf. *altidens*, and by key faunal markers such as *Megaloceros novocarthaginiensis* and *Stephanorhinus etruscus*, consistent with the frameworks proposed by Walker et al. (2013, 2020) and Linares-Matás et al. (2021). Transitional species between the *Iberomys huescarensis* and *Terricola arvalidens* biozones further consolidate the attribution to ~0.9–0.8 Ma (MIS 21–19), as confirmed by Fernández Ruiz (2021). Micromorphological analysis revealed early traces of thermal alteration in deep layers, foreshadowing later discoveries of combustion (Angelucci et al., 2013). Indeed, thermally altered bone and chert dated to ~0.8 Ma constitute some of the earliest evidence of fire in Europe, underscoring the cognitive and adaptive capacities of its hominin occupants (Walker et al., 2020).

The faunal assemblage supports this framework. Large ungulates (*Equus* cf. *altidens*, *Stephanorhinus etruscus*, *Megaloceros novocarthaginiensis*) indicate open woodland and plains, while cervids, suids, and caprines reflect productive ecotones and rugged terrain. Carnivores (*Crocuta, Ursus, Canis*) and primates (*Macaca*) enrich the spectrum, with hyenas central as both competitors and taphonomic agents in interaction

with early humans (Linares-Matás et al., 2021). Leporids (*Oryctolagus* cf. *giberti*), small mammals, and avifauna such as anatids and rallids point to grasslands, riparian cover, and wetlands, reinforced by amphibians, reptiles, and *Testudo hermanni* (Fernández Ruiz, 2021). Together with the adjacent paleolake (Walker et al., 2020), these records portray the Quípar basin as a biodiversity hotspot and ecological refugium nearly one million years ago.

The pollen record complements this picture by revealing a surprisingly wooded landscape despite xerophytic signals (Carrión et al., 2003) (Fig. 27). Arboreal pollen consistently outweighs herbaceous forms, indicating the persistence of mixed and evergreen forests across glacial oscillations. Pines dominate, while *Juniperus* is steady. Oaks are abundant and diverse: evergreen (*Quercus ilex/rotundifolia*, *Q. coccifera*) coexisted with deciduous elements (*Q. faginea*, *Q. pyrenaica*-type), evidencing both sclerophyllous and mesophilous stands. Signals of *Corylus avellana*, *Betula*, *Ulmus minor*, *Fraxinus excelsior/angustifolia*, *Acer*, *Hedera*, *Typha*, Cyperaceae, and *Alnus glutinosa* point to riparian groves and moist niches, while *Taxus baccata* hints at montane refugia. Mediterranean elements—*Olea europaea*, *Pistacia*, *Phillyrea*—are complemented by traces of *Ilex aquifolium*, *Buxus sempervirens*, *Arbutus unedo*, *Cistus*, and Ericaceae (*Erica*, *Calluna*). The result is a patchwork where willow and poplar galleries merged with oak and pine groves, while sun-exposed slopes bore pistachio, mastic, and wild olive (Fig. 27).

In paleoartistic terms, Cueva Negra invites the reconstruction of a mixed, wooded setting associated with a fluviolacustrine wetland on the valley floor adjacent to the Quípar River. Evergreens and deciduous oaks mingled with pines and riparian trees along shallow backwaters and slack-water pools formed behind local bedrock thresholds or colluvial barriers. Large ungulates grazed near these damp clearings, while hyenas and early humans contested the same terrain. The persistence of woodland despite recurrent stadial incursions justified depicting a greener, more wooded environment than might be expected under glacial conditions, highlighting the refugial role of the Quípar basin at the dawn of the Middle Pleistocene.

11.3. Environmental contrasts and Refugia in the Headwaters of the Segura Basin

In order to contextualize the phytosociological reconstructions at Cueva Negra del Estrecho del Río Quípar (Caravaca de la Cruz) and Cueva del Arco (Cieza), it is necessary to outline their physiographic and climatic settings. Cueva Negra lies at ~740 m a.s.l., on Tortonian biocalcarenite cliffs about 40 m above the Quípar River, while Cueva del Arco occupies a lower elevation (~300–400 m a.s.l.) within the Almadenes Canyon, a karstic gorge shaped by the Segura and its confluence with the Quípar. Present conditions highlight these contrasts: Caravaca records ~14.5 °C mean annual temperature, cold winters, and 370–420 mm annual precipitation, within the dry meso-Mediterranean belt; Cieza is warmer (~16.7 °C), drier (~330 mm), and falls in the semi-arid thermo-Mediterranean zone. These gradients delineate distinct ecological mosaics, with Cueva Negra cooler and slightly wetter than the more arid canyon environment of Cueva del Arco.

Paleoclimatic simulations (CHELSA-TraCE21k; Karger et al., 2023) indicate LGM declines of 35–40 % in precipitation and temperature drops of ~6 °C, consistent with Alboran Sea cooling (Martrat et al., 2004, 2007) and regional pollen evidence. Although the LGM is younger than the Early–Middle Pleistocene transition, these data suggest MIS 22 stadials could have approached comparable severities, modulated by latitude and topography. Palynological records reinforce the environmental divergence: Cueva Negra spectra show xerophytes >30 % yet sustained high arboreal pollen, pointing to a resilient refugium buffered by fluviolacustrine settings (Carrión et al., 2003). By contrast, Upper Pleistocene pollen from Cueva del Arco reflects pine–juniper mosaics interspersed with open steppes, evidencing stronger aridity and ecological openness. Hydrological proximity emerges as a decisive factor: Cueva Negra maintained more stable woodland cover, whereas Cueva del Arco exhibited compressed mosaics of riparian, scrub, and steppe communities, offering diverse adaptive opportunities to humans. More broadly, Cueva Negra connects with one of the major biodiversity reservoirs of southern Iberia, the Sierras of Alcaraz, Segura, Cazorla, and Las Villas (Carrión, 2002; Pugnaire et al., 2024), part of the Betic metapopulations of angiosperm forests that extended south to Algeciras and Campo de Gibraltar, as documented at Lake Los Tollos (Cádiz; Carrión et al., 2024f). These landscapes continue to act as biodiversity hotspots, rooted in Pleistocene refugial persistence.

12. Final thoughts

Although paleoart that respectfully incorporates the vegetal component of landscapes—both taxonomic and ecosystemic—is not a recent practice, its trajectory has been fragmentary. As we have seen, nineteenth-century works already displayed remarkable detail, yet botanical paleoart remained scarce and often picturesque, as in Kuwasseg's illustrations. The history of paleoart has largely been shaped by zoocentrism, much as molecular biology dominates contemporary organismal studies. In recent decades, however, a controlled expansion of interest in plants within paleoecosystem reconstructions has taken place. Much remains to be done, particularly at the methodological level and in terms of recruiting new artists, but there are signs of progress and of a gradual departure from the "plant blindness" that has characterized paleoart. With the rise of digital methodologies and an online marketplace where authorship is sometimes opaque, it is unsurprising that scientific communities—rooted in logical positivism and empiricism—remain cautious regarding the scientific status of paleoart products. At present, botanical paleoart should therefore be understood as an embryonic stage in the development of the discipline, with significant potential for growth.

Whether paleoart is "science-informed art" (Witton, 2020) or part of science itself matters less than what it accomplishes. Reconstructions do not merely illustrate; they generate knowledge. Goethe's *Metamorphosis of Plants* (1790) showed how a single archetype could reveal a system, just as a Carboniferous swamp is not "a list of calamites and sigillarias" but an atmosphere. Leonardo's dictum *sapere vedere*—"to know how to see"—points to the same epistemic power: drawing was for him a way of reasoning. In this lineage, paleoart is visual science, comparable to cladograms or climate simulations—provisional yet indispensable models that integrate evidence and make the deep past intelligible.

This epistemic role is also cultural. As Rosenberg and Burke (2022) argue, paleoart chronicles human values as much as extinct life—from mythical griffins to Alexis Rockman's dystopias. It is therefore not ornament but both hypothesis and cultural archive, bridging paleoscience and society. Yet its history has been shaped by zoocentrism. To advance, paleoart must also rescue paleobotany, too often relegated to background. Plants were agents that shaped climates, soils, and evolutionary opportunities. Botanical paleoart goes beyond taxonomy: it reconstructs forests, wetlands, and savannas as living physiognomies, exposing biases and gaps in the fossil record. There is also a need to consolidate a professional space for this practice, still largely unoccupied yet rich in potential—scientific, educational, artistic, and ethical. Its impact extends beyond paleoscience, inspiring new generations and nurturing respect for nature.

Looking forward, paleoart should integrate paleobotanical evidence not as an addendum but as a central axis. Doing so would provide rigorous ecological baselines, counteract plant blindness in education, and foster cultural awareness of the photosynthetic foundations of life. If paleoart is visual science, then botanical paleoart is its ecological conscience—a reminder that every reconstructed dinosaur, mammal, or hominin once lived within a green world whose forms and cycles deserve equal visibility.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.earscirev.2025.105371.

Data availability

No data was used for the research described in the article.

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