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Beyond the cold steppes: Neanderthal landscapes and the neglect of flora

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ABSTRACT

Understanding the environmental contexts in which Neanderthals lived is essential for interpreting their behavioral adaptations, resource use, and ecological strategies. These landscapes shaped the availability of plant and animal resources, influencing patterns of mobility, technology, and survival. This article presents an integrative reconstruction of Neanderthal landscapes across the full extent of their Eurasian distribution, combining palaeoecological synthesis, archaeobotanical records, and scientifically grounded palaeoart applied to Iberian case studies with particular emphasis on plant species—traditionally marginalized in a predominantly zoocentric paleoartistic tradition. Building on a sustained review articulated through a series of landscape "chronicles," the study contextualizes palaeovegetation mosaics across stadial and interstadial phases during the Middle and Late Pleistocene. By examining the interplay between vegetation dynamics, climatic oscillations, and human presence, we explore the spatial heterogeneity of Neanderthal environments, the persistence of forest elements in southern glacial refugia, the existence of migratory corridors and coastal platforms, and the shifting expression of the Mediterranean biome under Quaternary rhythms. The palaeoartistic reconstructions are firmly rooted in palaeobotanical evidence and serve as heuristic devices for generating hypotheses about Neanderthal habitat structure, ecological plasticity, and niche breadth. These visualizations move beyond mere illustration to render palaeobiogeographic complexity and to support a broader discussion of Neanderthal eco-evolutionary interactions, including resource use, refugial continuity, and interspecific contact. Importantly, this work seeks to challenge the entrenched popular view that Neanderthals must be associated exclusively with treeless, open glacial landscapes, instead highlighting the diversity of vegetated environments in which they lived.

1. Introduction

1.1. Statement of intent

This article is nurtured deep within a matrix of grand ambitions. First, it aims to provide a comprehensive account of the plant communities across Neanderthal territories, with the goal of deriving palaeoecological and biogeographical conclusions grounded in recent discoveries and refined modeling approaches. Second, to impact collective awareness and overturn the outdated—and incorrect—scientific association of Neanderthals with deforested landscapes. Third, to promote an understanding of the Neanderthal species in terms of their true adaptive diversity and the broad range of vegetation habitats they occupied throughout their extensive evolutionary history, including forests. These two last objectives will be achieved through paleoartistic tools focused on vegetated landscapes. This approach recognizes that paleoart stands at the intersection of two manipulative forces: (i) it is shaped by existing scientific biases and prejudices, and (ii) it, in turn, has the power to shape beliefs through its visual impact, influencing human cognitive structures at the individual, disciplinary, and societal levels. This grants paleoart a power, well-known to art theorists but absent from the everyday scientific imagination: the ability to dismantle a paradigm at a much faster pace than traditional scientific activity. The latter, due to its inherent inertia, can require decades to shift, regardless of the strength of the observations and discoveries. "*Science progresses one funeral at a time*" (Planck, 1950)

1.2. Botanical paleoart

In contemporary society, visual media play a central role in shaping cultural understandings of knowledge. Within this framework, paleoart is key to translating scientific interpretations of prehistoric life into visual form. While it can generate compelling aesthetic experiences and produce evolutionary icons grounded in fossil evidence—capable of

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permeating popular culture when convincingly executed (Amorós, 2023, 2024)—a persistent zoocentric bias remains. With a few historical exceptions (e.g. Ludwig, 1861; Unger, 1851), plants are frequently relegated to a secondary role, often depicted without attention to their taxonomic identity or ecological context (Buscalioni, 2016; Lescaze and Ford, 2017; Amorós and Carrión, 2025). In previous work, we reviewed paleoartistic literature and highlighted this imbalance, noting the marginalization of botanical elements in favor of dynamic animal portrayals (Amorós et al., 2021; Spagnuolo et al., 2024; Carrión et al., 2024a, 2024b; Amorós, 2025). To address this methodological gap, we proposed approaches that center plant life in reconstructions—particularly through paleocatenas and landscape-scale illustrations with scientific, pedagogical, and communicative value. These efforts seek to restore the botanical dimension to paleoecological narratives.

This contribution builds upon that foundation by applying the methodology to ecological and evolutionary themes relevant to Neanderthals. These hominins were once portrayed as inhabitants of persistently harsh, glacial environments—a view shaped by their prolonged presence during cold stages. However, as this article will show, Neanderthals occupied a broad range of bioclimatic zones across their European range and temporal span—including mixed forests, boreal and temperate woodlands, grass steppes, heathlands, Mediterranean scrub, alpine and shrub tundra, semideserts, and transitional ecotones shaped by climatic fluctuations (Allen et al., 1999; Fletcher et al., 2010; Duprat-Oualid et al., 2017; Carrión et al., 2019a, 2019b; Sánchez Goñi, 2022; Vidal-Cordasco et al., 2022, 2023). Paleoartistically, here, we focus on ecosystem responses to climate change in environmentally sensitive regions, the structure and composition of vegetation in glacial refugia, and the resilience strategies of Neanderthal populations inhabiting ecologically constrained yet persistently occupied landscapes. We contend that local-scale reconstructions—particularly paleo-landscape illustrations—are especially effective for conveying Neanderthal lifeways, as they reflect direct access to essential subsistence resources. In contrast, broader approaches such as biogeographic mapping help contextualize these behaviors within macroevolutionary and environmental frameworks. Incorporating detailed vegetation not only enriches the visual language of paleoart, but also enhances our understanding of past ecosystems and hominin–environment interactions.

2. Chronicle of Neanderthal lands

Neanderthals inhabited a vast and topographically diverse territory stretching from the Atlantic shores of Western Europe to the highlands of Central Asia, and from the glacial margins of northern Europe to the semi-arid environments of southeastern Iberia and the Middle East (Finlayson, 2009). Their range encompassed multiple biogeographic zones, including the temperate woodlands and loess plains of Central and Western Europe, the Mediterranean basin with its mosaics of evergreen scrub, mixed and deciduous forests, the mountainous ecotones of the Caucasus and Iranian Plateau, and the arid steppe corridors of the Levant and Central Asia (Carrión et al., 2019a; Yaworsky et al., 2024). Such spatial and ecological diversity invites a region-by-region analysis of the palaeovegetation records and landscape contexts in which Neanderthal populations lived, moved, and ultimately disappeared. Given that the Iberian Peninsula serves here as a central case study for reconstructing Neanderthal landscapes, this region will receive a more nuanced and in-depth treatment than the others.

2.1. Temperate and boreal Europe

Vegetation dynamics across temperate and boreal Europe during the Middle and Late Pleistocene were governed by orbitally paced climatic oscillations. The alternation of glacial and interglacial stages, superimposed by millennial-scale stadials and interstadials, led to repeated reorganizations of plant communities and biome boundaries. These changes are well-documented by high-resolution palynological and macrofossil sequences from lakes, peat bogs, and palaeosols (Birks, 1986; Bennett, 1997; Pini et al., 2022; Tinner et al., 2023a,b; Behre and van der Knaap, 2023; Schläfli et al., 2024), as well as by marine pollen records (Roucoux et al., 2001; Sánchez-Goñi et al., 2017). In some cases, pollen and charcoal data have also been recovered directly from archaeological sites associated with Neanderthal occupation, offering tight paleoecological correlations with lithic industries and faunal remains (Messager et al., 2011; Carrión et al., 2011, 2019b; Carrión and Walker, 2019). Interglacials typically supported the expansion of mixed deciduous forests dominated by thermophilous taxa such as *Quercus*, *Fagus*, *Corylus*, *Ulmus*, *Tilia*, *Abies, Alnus*, *Taxus*, and *Carpinus*, while full glacial phases witnessed the contraction of woodland and the dominance of steppe–tundra assemblages, including *Artemisia*, *Poaceae*, *Chenopodiaceae*, and cold-adapted shrubs. These transitions were rarely uniform or ecologically simple: many regions exhibited complex mosaics of forest patches, grasslands, and boreal elements (*Betula*, *Pinus*, *Juniperus*, *Picea*), particularly during interstadials and glacial onsets.

Numerous cases demonstrate long-term Neanderthal persistence through time and across environmental cycles in many regions of Europe. For example, Weiss et al. (2022) present a high-resolution reconstruction of environmental change in northern Central Europe, showing Neanderthals thriving in temperate forests during the Mid-Eemian Interglacial, enduring boreal conditions in late MIS 5c, and exploiting tundra-like landscapes at the onset of MIS 4. However, their responses to climate change were not uniform across space and time. While adaptive persistence characterized some regions, others saw episodic migratory movements, particularly northward incursions into Central Europe during relatively temperate phases of the Late Pleistocene. This dynamic is explored by Skrzypek et al. (2011), who reconstructed climatic conditions at key Neanderthal sites using oxygen isotope ratios from bioapatite in faunal remains. Their analysis suggests that mean annual temperatures (MATs) during such incursions were relatively mild—around 6.8 °C prior to MIS 4 and approximately 6.3 °C during early MIS 3—comparable to or slightly above present-day MATs in cities such as Stockholm or Riga. These warmer-than-expected conditions likely facilitated temporary Neanderthal expansion into Central Europe, illustrating how even subtle shifts in climate thresholds could open or constrain windows of habitability for Pleistocene hominin populations.

It is also worth mentioning the alleged absence of temperate forest north of the Alps during glacial episodes. While some interstadials were long enough to promote arboreal recolonization, vegetation in regions such as the Baltic States, the Netherlands, Scotland, Germany, and northern Russia generally consisted of conifers like *Larix* and *Picea*, and in some cases pioneer taxa such as *Betula* and *Alnus* (Behre and van der Knaap, 2023). The biogeographic and evolutionary significance of these prolonged periods of deforestation lies in the fact that Neanderthal populations in colder regions were likely forced to migrate, which may explain the higher frequency of long-term or recurrent occupations in southern latitudes or Atlantic-influenced areas (Stringer, 2006). If the majority of their evolutionary history unfolded during glacial times, it follows logically that a significant portion of their occupation time was likely concentrated in low latitudes or settings with favorable microclimates and wooded environments with sufficient water availability (Vidal-Cordasco et al., 2022).

In fact, if we adopt a generous chronological model for the Neanderthal lineage—extending from around 430,000 to 35,000 years ago, thus encompassing both classic Neanderthals and their possible precursors—the total span is approximately 395,000 years. Based on paleoclimatic reconstructions, roughly 72 % of this interval corresponds to glacial or stadial phases, while only 28 % reflects interglacial or interstadial conditions. In absolute terms, this equates to about 284,000 years of predominantly cold environments, and just over 110,000 years of more temperate or fluctuating regimes. These figures underscore the evolutionary persistence of Neanderthals within mostly harsh and unstable climatic settings, and further support the idea that favorable refugial zones were critical to their long-term survival.

This latitudinal pattern in Neanderthal settlement—favoring long-term occupations in southern and Atlantic-influenced regions—should be contextualized within a broader biogeographic –and evolutionary-dynamic of occupation and abandonment across Pleistocene Europe (Stringer, 2012b). As Dennell et al. (2011) emphasize, the archaeological record in high-latitude areas such as the British Isles reflects episodic hominin presence, marked by repeated cycles of colonization and withdrawal rather than continuous occupation. These patterns are strongly linked to climatic oscillations and ecological thresholds: regions like southern Britain were periodically abandoned during colder phases and reoccupied during temperate windows such as MIS 11, MIS 9, and MIS 5e. Supporting this view, Stringer (2006) notes that "Britain in the Middle Pleistocene was more often abandoned than occupied," with evidence indicating that Neanderthals and earlier hominins were "extremely sensitive to climatic shifts" in northern environments. In contrast, southern Europe offered greater ecological stability, allowing for longer-term persistence (Bermúdez de Castro et al., 2019). From a broader perspective, vegetation structure would have directly influenced human hunting opportunities, a factor that has been linked to episodes of human population extinction (Allen et al., 2019).

Despite their known adaptability, the apparent absence of Neanderthals in the far north during interglacial phases remains a debated issue. Given their ecological versatility, it is highly unlikely that a species as widespread as the Neanderthal would have been constrained to the areas currently represented in the fossil record. Their apparent absence north of 55°N during the Last Interglacial Complex—including the Eemian and Early Weichselian—has prompted competing hypotheses. Nielsen et al. (2017), combining species distribution models (SDM) with archaeological and paleoenvironmental data, explore two scenarios: one posits that environmental barriers and dispersal limitations defined the northern range boundary; the other suggests that their absence reflects archaeological invisibility or taphonomic bias. Palynological data from the Oerel core (Northern Germany) offer critical insight: during the Eemian, the region supported mixed deciduous forests dominated by *Quercus*, *Corylus*, *Ulmus*, and *Carpinus*, indicating a mild and moist climate. These conditions extended into southern Jutland, suggesting that areas north of 55°N were not as climatically prohibitive as often assumed. With the progression of the Weichselian Glaciation, these forests gave way to boreal assemblages (*Betula*, *Pinus*, *Picea*), reflecting gradual cooling. Still, Nielsen et al. (2017) find no definitive evidence that climate alone prevented Neanderthal occupation. Instead, they emphasize the need to consider alternative factors—such as physical barriers or gaps in the archaeological record—as plausible explanations for their apparent absence in the far north.

In general, the European record—enriched by dense palaeoecological datasets—supports the existence of non-analogue plant communities during periods such as MIS 3, a time marked by exceptional climatic instability. Neanderthals likely inhabited dynamic landscapes shaped by such non-analogue conditions, a concept initially applied to Pleistocene faunal assemblages where cold- and temperate-adapted species coexisted (Stewart, 2005), but equally pertinent to palaeobotanical scenarios. Although spatial reconstructions remain limited by the inherent constraints of palynological data, multiple lines of evidence point to the existence of floristic combinations without direct modern counterparts. These transient communities, composed of taxa with divergent ecological requirements, challenge the applicability of modern geobotanical analogies (Lang et al., 2023). The impermanence of vegetation—even during the Holocene—has been well documented through pollen, plant macrofossils, and charcoal analyses (Bennett, 1997; Davis et al., 2005; Carrión et al., 2006). As such, Neanderthal habitats should not be interpreted using present-day vegetation patterns as a fixed template. Instead, Pleistocene ecosystems—particularly glacial refugia—likely supported species with varying thermal, hydric, and altitudinal preferences, forming mosaic landscapes that defy uniformitarian assumptions and underscore the singularity of past ecological configurations.

Many European Neanderthal occupations are found in areas with readily available freshwater, often near rivers and fluvial valleys. In this context, Guillaud et al. (2021) revisit the question of Neanderthal interaction with freshwater ecosystems by analyzing ichthyofaunal remains from eleven Middle Paleolithic sites distributed across Belgium, France, and Spain, dating from Marine Isotope Stage MIS 11 to MIS 3. Their study aims to assess whether Neanderthals practiced fishing as a consistent subsistence strategy or exploited aquatic resources opportunistically. Although unequivocal evidence of systematic fishing remains limited, the presence of sizeable fish bones—particularly in contexts showing signs of anthropogenic modification—raises the possibility of deliberate capture or exploitation. The identified taxa originate from diverse freshwater settings, ranging from cold, fast-flowing streams to more temperate, slow-moving rivers. The spatial distribution and taphonomic condition of the remains suggest that Neanderthals may have selectively targeted larger fish, such as salmonids, especially in major riverine corridors where these resources were visible, accessible, and abundant.

It is worth noting that the vegetation ecosystems during the period in which the most characteristically Neanderthal morphology was emerging in Europe from Heidelberg ancestors (MIS 11–MIS 6) were physiognomically similar to those of the later Neanderthal interval (MIS 5–MIS 3), and similarly shaped by orbital-scale climatic forcing over multi-millennial timescales. However, during the Middle Pleistocene, the floristic composition of plant communities was considerably different, as several taxa still present during that time ultimately went extinct during the Late Pleistocene. These include *Celtis*, *Eucommia*, *Juglans*, *Castanea*, and *Carya* (Magri, 2010; Magri et al., 2017). This pattern is evident, for instance, in pollen sequences from Germany, Poland, Lithuania, Latvia, France, Great Britain, Ireland, and Greece (Behre and van der Knaap, 2023).

2.2. Balkan Peninsula

The refugial situation of angiosperm trees has been well documented across various geographic locations within the Balkans, with particularly strong evidence in the southernmost, coastal, and Mediterranean-influenced areas (Willis, 1994; Tzedakis et al., 2002, 2003; Panagiotopoulos et al., 2014). The Tenaghi Philippon record stands as one of the most continuous and detailed archives of Quaternary vegetation dynamics in Europe (Tzedakis et al., 2003; Pross et al., 2015). During the last interglacial complex (MIS 5e–5a), pollen data reveal alternating phases of oak–pine forests enriched with Mediterranean elements and periods dominated by xerophytic steppe vegetation. Similarly, the Ioannina basin (northwestern Greece), a sequence extending back approximately 430,000 years, documents the predominance of deciduous *Quercus*, *Carpinus betulus*, *Pinus*, *Ulmus/Zelkova*, *Abies*, and *Fagus*, with notable increases in *Artemisia* and *Poaceae* during MIS 5 d (Tzedakis et al., 2003; Lawson et al., 2004). Further east, the Lake Ohrid sequence, which spans 1.36 million years, offers high-resolution pollen data from MIS 6 to MIS 4 (~160–70 ka). This interval is characterized by sustained presence of *Pinus*, *Quercus*, *Abies*, *Betula*, *Carpinus betulus*, *Corylus*, *Tilia*, and *Ulmus*, alongside Mediterranean taxa such as *Cistus*, *Fraxinus ornus*, *Olea*, *Phillyrea*, and *Pistacia* during the last interglacial complex (Sinopoli et al., 2018, 2019). Complementary insights from Lake Kopais (extending from the Holocene back to MIS 11; Okuda et al., 2001) and Lake Prespa (covering the last ~92 ka; Panagiotopoulos et al., 2014), even the Lesvos Island record (Margari et al., 2009), reinforce a coherent pattern of climatic and vegetational shifts in the southern Balkans, supporting the region's role as a key glacial refugium.

The Middle Palaeolithic record of Greece reveals widespread Neanderthal presence between ~100 and 40 ka BP (Tourloukis and Harvati, 2018). Most sites are located in caves and rockshelters situated at low elevations in the well-watered western regions of the peninsula, particularly west of the Pindus Mountains—areas that received higher precipitation and likely acted as ecological refugia during glacial phases. This spatial clustering suggests a hominin preference for environments that maintained vegetation biomass and game availability throughout climatic fluctuations (Harvati and Roksandic, 2017). Microwear and dental calculus analyses indicate that Greek Neanderthals exploited a broad array of plant resources—including fruits, seeds, grasses, and sedges—reflecting considerable dietary flexibility (Henry et al., 2014). The rugged, tectonically complex terrain of western Greece offered topographic diversity and migration corridors that buffered ecological impacts. In particular, karstic water sources in Mani and Epirus played a key role in sustaining occupation, especially during glacial sea-level lows when new coastal springs and plains were exposed (Tourloukis and Harvati, 2018).

Recent palynological research by Kyrikou et al. (2025) offers compelling evidence for the ecological complexity and resilience of the Megalopolis Basin (southern Greece) during MIS 12. Their findings reveal a persistent mosaic of open vegetation interspersed with mesophilous trees and aquatic taxa, suggesting the existence of microhabitats with sufficient moisture — a key factor for the survival of both flora and fauna in otherwise harsh climatic conditions. Of particular relevance to this study is their documentation of intensified herbivore presence between ~435 and 423 ka, within the archaeological horizon, which coincides with wetter intervals and increased habitat diversity. These conditions would have offered both food and shelter to large mammals and hominins, reinforcing the idea of the Megalopolis Basin as a viable ecological refuge.

However, Neanderthal forest refugia were not limited to low-latitude regions; they also extended into more northerly areas such as the Central Balkans, particularly in the transitional zone bordering the Carpathians. Carrión et al. (2024b) and Ochando et al. (2024) investigate the Late Pleistocene paleoecology of Pešturina Cave, located near Niš in present-day Serbia, providing valuable insight into the environments inhabited by both Neanderthals and early modern humans. Utilizing detailed pollen analysis from cave sediments and hyena coprolites, the study reconstructs vegetation dynamics in the region from MIS 5e through MIS 3. The results indicate that Neanderthals occupied varied, semi-wooded landscapes rich in arboreal species — among them deciduous *Quercus*, *Pinus*, *Juniperus*, *Abies*, *Fagus*, *Carpinus*, *Ulmus-Zelkova*, *Tilia*, *Corylus*, *Castanea*, *Juglans*, *Fraxinus*, *Celtis*, *Ilex*, *Ligustrum*, *Acer*, *Betula*, and others, including a wide diversity of shrubs.

Faunal evidence from the Late Pleistocene deposits of Kiliite Cave, located in the central Stara Planina Mountains of northern Bulgaria (ca. 548 m a.s.l.), points to the coexistence of open and wooded habitats within a forest–steppe mosaic. The avian assemblage includes both light forests with scattered trees (*Sturnus vulgaris*, *Curruca nisoria*, *Pica*), together with broad-leaved deciduous stands (*Turdus viscivorus*, *Garrulus glandarius*) and possible coniferous components. Comparable evidence from the Serbian record further supports the persistence of wooded habitats in high-latitude refugia during the later Pleistocene. Herpetofaunal assemblages from several sites, including Pešturina and other localities in central and southern Serbia, include taxa such as *Bufo*, *Rana temporaria*, and *Anguis fragilis*, which are indicative of temperate, humid, and forested environments (Jovanović et al., 2020). These occurrences are consistent with the presence of woodland or semi-wooded settings throughout MIS 3 and even parts of MIS 2.

2.3. Italian Peninsula

Pollen data from Grotta Guattari have yielded valuable insights into the paleoenvironmental conditions along the Tyrrhenian coast of central Italy during the Middle Paleolithic (ca. 116,000–59,000 years ago) (Rolfo et al., 2023). The evidence points to a landscape primarily dominated by cold, open grassland environments, interspersed with forest and Mediterranean elements. Taxa such as *Fagus*, *Fraxinus*, *Ulmus*, *Pistacia*, *Juniperus*, *Olea*, and *Quercus* suggest the persistence of mixed woodland communities, likely sustained by the buffering climatic influence of the nearby Tyrrhenian Sea. These palynological findings are consistent with the cave's faunal assemblage, which includes species adapted to open, rocky, and wooded habitats. This is just one among numerous paleoecological records—most of them derived from lake sediment sequences—that highlight the crucial role of the Italian Peninsula as a glacial refugium for flora and vegetation (Follieri et al., 1998; Magri and Sadori, 1999; Magri et al., 2006, 2017; Pini et al., 2010; Di Pasquale et al., 2020; Vera-Polo et al., 2024).

The pollen record from Lago Grande di Monticchio provides a high-resolution reconstruction of vegetation dynamics in southern Italy across the last interglacial (MIS 5e) and into the early phases of the last glacial period, offering context for Neanderthal populations (Brauer et al., 2007). During MIS 5e, mixed deciduous and temperate forests—*Quercus*, *Carpinus*, *Fagus*, *Abies*, and *Ulmus*—expanded rapidly under warm and humid conditions. Toward MIS 5 d and MIS 5 b–a, declining arboreal pollen percentages indicate forest fragmentation and the rise of open vegetation dominated by *Artemisia*, Poaceae, *Juniperus*, and *Chenopodiaceae*, reflecting cooler, drier conditions. By the onset of MIS 4 (~71 ka BP), the Monticchio region had transitioned to a steppe-like landscape with scattered woodland patches, signaling a major climatic deterioration that likely shaped Neanderthal subsistence and mobility. These patterns are consistent with other long pollen sequences from the Italian Peninsula, particularly Valle di Castiglione and Lago di Lagaccione in central Italy (Follieri et al., 1998).

Other lines of evidence for past vegetation derive from faunal-based paleoenvironmental inferences, which are equally informative. The paleoenvironmental reconstruction from Fumane Cave—located at 350 m a.s.l. In the Monti Lessini range, northeastern Italy—based on small-mammal assemblages, reveals a dynamic MIS 3 landscape shaped by alternating cold stadials and temperate interstadials, which structured the ecological context for Neanderthal occupation (López-García et al., 2015). The Mousterian units A11 to A9 reflect relatively temperate and humid conditions, with dominance of open woodland habitats, as indicated by forest-adapted micromammals. These findings are supported by medium-mammal taxa such as *Cervus elaphus* and *Capreolus*, diverse avifauna associated with high-elevation forests and cliffs, and anthracological data indicating mountain vegetation dominated by *Larix decidua*, *Pinus*, *Betula*, and *Picea abies*. More recently, dental wear and cementochronological analyses on ungulates from the same site have refined this picture, revealing consistent browsing signals in *Cervus elaphus*, *Capreolus*, and *Megaloceros giganteus* that point to temperate and humid woodland formations, persisting even during episodes of climatic deterioration (Livraghi et al., 2025). These results further support the role of the Italian pre-Alps as a glacial refugium sustaining arboreal and mixed habitats conducive to recurrent Neanderthal occupations and adaptive flexibility (Peresani, 2023). Together, these fossil records illustrate not only the strong climatic forcing on vegetation structure across the Middle and Late Pleistocene, but also the buffering role of the Italian Peninsula's physiographic complexity.

2.4. Iberian Peninsula

Palaeoecological and palynological data consistently reveal that Neanderthals inhabited a strikingly diverse range of ecological settings across the Iberian Peninsula during both glacial and interglacial stages (Carrión, 2002; González-Sampériz et al., 2010, 2010, 2020, 2024c; Carrión et al., 2003; Aranbarri et al., 2014; Ochando et al., 2019, 2022). In the southeast, sites such as Sima de las Palomas reflect a mosaic of Upper Pleistocene plant formations (Carrión et al., 2003) (see below). Further south, in Málaga and the Gibraltar sites of Gorham's and Vanguard Caves, palynological and charcoal data point to the persistence of *Pinus pinea–pinaster* forests interspersed with *Juniperus* and thermophilous shrubland (López-Sáez et al., 2007; Carrión et al., 2008). In these coastal regions, the role of exposed continental shelves was particularly significant, as they hosted frost-sensitive, hyper-thermophilic species such as *Periploca angustifolia* and *Maytenus senegalensis* (Carrión et al., 2018).

This diversity is further underscored by evidence positioning the southernmost Iberian Peninsula as a major glacial refugium. The high-resolution pollen record from Los Tollos, for instance, indicates consistently elevated levels of *Quercus* and other angiosperm pollen even during full-glacial conditions, pointing to forest persistence in topographically sheltered microenvironments near the Strait of Gibraltar and in river valleys and coastal zones (Carrión et al., 2024d). These thermic refugia supported taxa such as *Olea*, *Pistacia*, *Chamaerops*, *Maytenus*, *Myrtus*, *Osyris*, *Ruscus*, *Myrica*, *Alnus*, *Corylus*, *Castanea*, *Juglans*, *Salix*, *Taxus*, and *Fraxinus*. Contemporary floristic inventories strengthen these inferences, with the survival of several subtropical and Tertiary relict species including *Rhododendron ponticum*, *Laurus nobilis*, *Myrica gale*, *Frangula alnus*, *Prunus lusitanica*, *Drosophyllum lusitanicum*, and *Culcita macrocarpa* (Ojeda et al., 1996; Rodríguez-Sánchez and Arroyo, 2008; Verdú et al., 2020). Phylogeographic evidence also supports the persistence of these taxa in long-term refugial contexts (Martín-Rodríguez et al., 2020). Comparable, albeit more attenuated, signals have been documented at inland sites such as Padul (Camuera et al., 2018, 2019) and Siles (Carrión, 2002), which exhibit glacial persistence of temperate taxa despite increased continentality.

The Middle Pleistocene refugia in the eastern Neanderthal occupation zone of Iberia is exemplified by the Bolomor Cave sequence (Ochando et al., 2019), later brought into paleoart by Amorós et al. (2021). The local vegetation reflects essentially forested communities dominated by oaks, holm oaks, and pines, which persisted over an extended period of study (MIS 9–5). This ecological context, beyond the prevalence of *Quercus* and *Pinus*, includes a wide diversity of woody spermatophytes such as *Castanea*, *Olea*, *Corylus*, *Juniperus*, *Alnus*, *Ulmus*, *Populus*, *Salix*, *Celtis*, *Betula*, *Fraxinus*, *Ceratonia*, *Rhododendron*, *Arbutus*, *Sambucus*, *Pistacia*, *Phillyrea*, *Myrtus*, *Myrica*, *Ligustrum*, *Jasminum*, and *Prunus*, among others. A comparable scenario may be proposed for the Late Pleistocene in the northeastern Mediterranean slope of Iberia, specifically in Catalonia, based on pollen analyses from two nearby Paleolithic caves: Teixoneres and Toll. Teixoneres shows the long-term persistence of a relatively dense forest ecosystem dominated again by oaks and pines, accompanied by a similar variety of woody taxa, with notable occurrences of *Abies* and *Fagus* (Ochando et al., 2020a). The pollen record from Cova del Toll, showing similar results, reinforces this idea of a Neanderthal forest refuge (Ochando et al., 2020b).

Palaeoenvironmental reconstructions are not solely grounded in floral data. Sánchez-Hernández et al. (2020) integrated palaeoecological and zooarchaeological approaches by analyzing dental wear patterns in primary prey species (*Cervus elaphus*, *Equus ferus*, *Capra pyrenaica*) from key Mediterranean sites including Arbreda, Teixoneres, Abric Romaní, and El Salt. Their results depict Neanderthal settlement strategies oriented toward ecologically diverse landscapes shaped by Mediterranean climatic variability and altitudinal gradients. These settings encompassed forests, grasslands, and transitional woodlands, creating favorable conditions for broad-spectrum subsistence strategies. The prevalence of *Cervus elaphus* and *Bos primigenius* remains suggests a preference for semi-open environments that offered both protective cover and open foraging areas. Stable plant communities across seasonal cycles likely reduced interspecies competition and enhanced food security for Neanderthal groups. The persistence of taxa such as *Quercus*, *Pinus*, and sclerophyllous shrubs in localized microclimates further underscores the ecological richness of their territories, which provided not only abundant hunting grounds but also potential sources of plant-based nutrition.

2.5. The Levantine Corridor

The Levantine Corridor presents a complex ecological backdrop for understanding Neanderthal occupation in the eastern Mediterranean, marked by steep climatic gradients and pronounced environmental heterogeneity during the Late Pleistocene. The pollen record from Lake Lisan (southern Levant) reveals pronounced vegetation shifts linked to millennial-scale climatic oscillations (Miebach et al., 2019). Arid phases were characterized by the dominance of Irano-Turanian steppe and Saharo-Arabian desert elements, with high frequencies of xerophytic taxa such as *Artemisia*, *Chenopodiaceae*, and drought-adapted Asteraceae (*Centaurea*, *Achillea*), reflecting widespread semi-desert environments. However, despite the prevailing aridity, the record shows the periodic presence of Mediterranean woodland taxa—including *Quercus calliprinos*, *Pistacia palaestina*, and *Olea europaea*—indicating intermittent increases in moisture and the persistence of refugial tree cover. Critically, the presence—albeit in low percentages—of mesic and riverine taxa such as *Platanus*, *Tamarix*, and *Vitis* points to the existence of localized hydrological niches and riparian corridors, which may have served as key microhabitats for both plant and animal life.

Marine pollen records are abundant offshore Israel. A particularly relevant case study is core 9509, which provides a high-resolution archive of environmental dynamics over the past 86,000 years (Langgut et al., 2011). Glacial and stadial phases were dominated by Irano-Turanian steppe elements and Saharo-Arabian desert taxa, including trees (*Acacia, Tamarix*), and Amaranthaceae-Chenopodiaceae, *Ephedra*, and *Zygophyllum*-type pollen, reflecting cold, dry, and windy conditions that supported open vegetation and semi-desert landscapes. Conversely, interstadial and more humid intervals witnessed the expansion of broad-leaf trees and Mediterranean woodland components, with significant representation of *Olea, Phyllirea*, *Pistacia, Ceratonia, Cupressus, Arbutus, Acer, Corylus, Betula, Alnus*, and both evergreen (*Quercus calliprinos*) and deciduous (*Quercus ithaburensis*) oaks. The presence of evergreen *Quercus* is often associated with persistent, drought-resistant woodland refugia, whereas the appearance of deciduous oak signals more temperate and mesic conditions, possibly linked to transient climatic amelioration. Altogether, the record reflects a high degree of climatic instability, with rapid biome turnovers that would have dramatically reshaped Neanderthal ecological niches, influencing settlement duration, resource availability, and mobility strategies.

Palynological analysis at the Late Middle Paleolithic open-air site of Nahal Mahanayeem Outlet (NMO), dated to approximately 65–51 ka, provides a detailed reconstruction of the vegetation associated with Neanderthal occupation in the northern Jordan Rift Valley. The pollen record indicates the presence of Mediterranean maquis woodlands in mosaic with steppe-like vegetation. The sequence also documents two humid episodes—one notably cooler and wetter—evidenced by increased arboreal pollen and the presence of taxa such as *Cedrus libani*, *Abies*, and *Alnus*, indicating the temporary development of moist forests on surrounding uplands. Importantly, the detection of riparian elements such as *Typha*, *Carex*, *Scirpus*, and occasional *Platanus* and *Tamarix* points to the existence of wetland habitats and riverine vegetation along the Jordan River. These findings portray a complex landscape comprising wooded slopes, freshwater corridors, and open plant communities, offering Neanderthal groups a variety of ecological resources even within a generally arid climatic backdrop. Comparable pollen sequences from the Hula Basin (e.g., core L07) support the presence of humid conditions during the same timeframe, with Mediterranean maquis vegetation dominating upland slopes, and marshy elements along basin margins (Weinstein-Evron, 1983; Weinstein-Evron et al., 2001).

Palynological and multi-proxy analyses from the Mount Carmel caves—especially Tabun—reveal a complex Middle–Late Pleistocene vegetation mosaic associated with repeated Neanderthal occupations. Sedimentary pollen traces, alongside herpetofauna-based palaeoenvironmental reconstructions (Lev et al., 2023), indicate alternating phases of Mediterranean woodland and open vegetation. During humid interstadials, groves of *Quercus*, *Pistacia*, *Olea*, and even riparian species such as *Platanus* and *Tamarix* colonized the slopes and canyon corridors. In contrast, colder and drier stadials saw a shift to shrubby and semi-open woodlands, with *Ceratonia*, *Rhamnus*, and drought-tolerant taxa expanding across the landscape. The presence of amphibians and reptiles in Tabun layers further confirms periodic increases in moisture and habitat diversity during Neanderthal occupation phases (Lev et al., 2023). On the other hand, the macrofaunal diversity is significant, with large (rhinoceros, hippopotamus, horse, aurochs, camel), medium (red deer, capra, fallow deer and wild boar), and small ungulates (gazella, roe deer) Marín-Arroyo, 2013) Overall, the evidence portrays a dynamic environment, where shifting water availability and vegetation structure created a resilient mosaic—perhaps explaining the long-term stability and eventual ritual behaviors (e.g., fire use, burials) observed at the site.

Palaeoenvironmental reconstructions from Amud and Kebara Caves offer complementary insights into the range of habitats occupied by Neanderthals in the region during MIS 4 and early MIS 3. At Amud Cave, phytolith and stable isotope analyses suggest that Neanderthals inhabited a mosaic landscape characterized by open woodlands, herbaceous vegetation, and microhabitats shaped by local edaphic and hydrological conditions (Madella et al., 2002). Phytolith assemblages were dominated by grasses, sedges, and dicot herbs, with sporadic arboreal indicators such as *Quercus* and *Olea*, suggesting patchy woodland sustained by ephemeral or permanent water sources. Additional paleoecological evidence based on micromammal remains from Amud indicates environmental stability during the MIS 4/3 transition, with only subtle shifts in rodent communities despite changes in vegetation cover (Belmaker and Hovers, 2011). This period saw a reduction in grassland habitats and a modest expansion of woodland areas, yet the persistence of a Mediterranean biome—even under increasingly arid conditions—challenges models that attribute Neanderthal disappearance in the region solely to climatic deterioration. Kebara Cave, with one of the most detailed phytolith records in the region, corroborates this scenario: the assemblages include abundant Panicoideae and Pooideae grasses, Cyperaceae, and shrubby dicots, alongside evidence for fire use and woody plant exploitation, particularly of *Pistacia, Tamarix*, *Quercus*, and other sclerophyllous taxa (Albert et al., 2012). The recurring presence of riparian and disturbance-adapted species in both cave contexts underscores the ecological complexity of Neanderthal landscapes in northern Israel and demonstrates their adaptability to dryland conditions interspersed with localized water-rich refugia.

These millennial-scale vegetation dynamics are independently corroborated by speleothem-based isotope records from the eastern Mediterranean (Bar-Matthews et al., 1999, 2003), which show cyclic fluctuations in precipitation and humidity closely aligned with the palynological phases described. Earlier syntheses by Horowitz (1979, 1989) had already outlined the responsiveness of Levantine floristic provinces to glacial-interglacial variability, laying the groundwork for interpreting current findings in terms of biome contraction, woodland refugia, and ecological corridors critical to hominin persistence.

The northern and central sectors of the Levantine Corridor—including present-day Syria, Lebanon, and Jordan—host a series of important, albeit unevenly studied, Middle Paleolithic sites that expand our understanding of Neanderthal ecological breadth in the eastern Mediterranean. In Syria, key cave sites such as Dederiyeh and Yabroud have yielded Mousterian lithics, faunal remains, and in the case of Dederiyeh, a well-preserved Neanderthal child burial (Nishiaki et al., 2022). While detailed palynological records are lacking, associated fauna—including cervids, wild boar, and goats—suggest a heterogeneous landscape combining open steppe and woodland habitats, possibly sustained by orographic moisture along the Jebel Druz and Anti-Lebanon ranges. In Lebanon, sites such as Ksar ‘Akil and Ras el-Kelb, though better known for their later Paleolithic sequences, also contain Mousterian layers associated with Mediterranean woodland taxa (El Zaatari, 2018). The region’s steep climatic gradients and coastal refugia likely sustained localized forest patches during glacial phases, potentially offering continuity of occupation. Finally, Jordan is represented by sites such as Wadi Zarqa, Tor Faraj, and Tor Sabiha in the southern basin, which indicate ephemeral Middle Paleolithic occupations under increasingly arid conditions. Micromammal data and lithic techno-complexes suggest adaptation to steppe-desert environments with access to seasonal water sources and patchy vegetation cover (Neeley and Clark, 2024). Collectively, these records underscore the ecological diversity and geographical variability of the northern Levant during Neanderthal times.

2.6. Pontic region and the Caucasus

The Pontic region, surrounding the Black Sea and spanning parts of northeastern Turkey, Georgia, southern Russia, Ukraine, and eastern Romania and Bulgaria, features a mosaic of coastal, steppe, and mountainous environments. It is significant for studies in biogeography, paleoclimate, and human prehistory. Layer 4 at Molodova I, located in the Dniester basin of southwestern Ukraine and attributed to Neanderthal occupation during MIS 3, presents a well-preserved faunal assemblage that offers valuable insights into the site’s paleoenvironmental context. The presence of cold-adapted taxa such as *Rangifer tarandus*, *Bison priscus*, *Coelodonta antiquitatis*, and *Mammuthus primigenius* suggests a dry, cold open landscape, while *Cervus elaphus* indicates the development of sporadic forest patches, likely along riverine corridors (Demay et al., 2012). Carnivores such as *Alopex lagopus*, *Vulpes*, *Panthera pardus*, and *Canis lupus* reflect ecological flexibility, pointing to a mosaic of plains and wooded margins. The small mammal record, which includes steppe and tundra species such as *Marmota bobac*, *Lagurus lagurus*, *Dicrostonyx henseli*, and several *Microtus* species, further supports the reconstruction of a mixed environment combining cold steppe, bushy zones, and coniferous forest strips (Demay et al., 2012). These paleoecological signals converge on the reconstruction of a wide-open plain landscape with localized forest habitats under cold and dry conditions, consistent with Neanderthal adaptation to steppe-like ecosystems in Eastern Europe.

Palynological and pedosedimentary data from the Crimean Mountains’ foothills—an ecotonal region between the Eastern European steppes and Mediterranean-influenced refugia—reveal a complex sequence of climatic oscillations throughout the Late Pleistocene (Gerasimenko, 2007). The base of the Upper Pleistocene sequence records forested conditions during the final stages of the last interglacial, followed by Early Glacial transitions marked by colluviation and the development of luvisol and rendzina-derived soils under forest–steppe and boreal environments. These interstadials, dated by ESR to between ~85,000 and 74,000 years ago, reflect changing moisture regimes, from warmer and wetter to cooler and drier. During the Early and Middle Pleniglacial (~60,000 to 30,000 BP), alternating phases of tundra–-steppe and boreal forest–steppe prevailed, with an increasing trend toward aridity. Climate reconstructions from Kabazi II and Buran-Kaya III suggest that broad-leaved taxa persisted in western refugial zones of Crimea during interstadials, while stadials were dominated by dry steppe.

These data place Neanderthal occupations in Crimea—such as those in Zaskalnaya and Kiik-Koba—within dynamic ecotonal landscapes that oscillated between forest–steppe and open grassland under varying cold stress. Overall, multi-proxy analyses from the Crimean Peninsula—including pollen, soils, geomorphology, and archaeological stratigraphy—indicate that the region underwent marked climatic oscillations over the past 130,000 years (Cordova et al., 2011). During the Eemian interglacial (MIS 5e), warm and humid conditions favored the expansion of temperate forests. Throughout the last glacial cycle (MIS 5d–2), the peninsula alternated between open steppe vegetation during colder stadials and forest–steppe mosaics during interstadials, with wooded refugia likely persisting in sheltered or lowland areas.

Key Neanderthal sites in the western Caucasus have yielded well-preserved fossils, long stratigraphic sequences, and essential genetic data, offering insights into Neanderthal adaptation and survival. Radiometric data place the Middle Paleolithic in the Caucasus between ~260 and 210 ka and 40 ka. Doronicheva et al. (2023) report evidence from Mezmaiskaya Cave and Saradj-Chuko Grotto for two culturally distinct Neanderthal populations: western assemblages linked to the Eastern Micoquian, and eastern ones associated with the Zagros Mousterian, suggesting separate origins in Central/Eastern Europe and the Armenian Highlands. This implies that the North Caucasus functioned as a contact zone for divergent Neanderthal groups during the Late Pleistocene. Palynological data from Mezmaiskaya Cave (~70–40 ka), a key Middle Paleolithic site in the northwestern Caucasus, reveal Mousterian-associated environments characterized by a mosaic of coniferous and broad-leaved trees (*Pinus*, *Betula*, *Alnus*, *Quercus*) alongside herbaceous taxa (Poaceae, *Artemisia*, Amaranthaceae), consistent with open steppe and forest–steppe settings. Fluctuations in mesothermal species (*Carpinus*, *Ulmus*) suggest brief temperate interstadials within an overall cold sequence, pointing to repeated Neanderthal occupation of an unstable ecotone between montane forest and lowland vegetation.

The southern Caucasus, particularly the Lesser Caucasus range and adjacent intermontane basins of Georgia, likely functioned as a crucial biogeographical refugium during glacial phases of the Pleistocene. This region's rugged topography, varied elevation, and complex climatic gradients fostered the persistence of temperate deciduous and Pontic–Hyrcanian elements even during the coldest stadials, contributing to its current designation as a biodiversity hotspot. This refugial capacity is supported by the survival of several Tertiary relict taxa—such as *Fagus orientalis*, *Carpinus betulus*, *Tilia*, *Juglans regia*, *Zelkova carpinifolia*, *Parrotia persica*, *Pterocarya fraxinifolia*, *Taxus baccata*, and *Corylus colurna*—which are still present in the region today and whose ecological requirements suggest long-term climatic buffering during glacial episodes. The ecological continuity implied by these species may have supported viable Neanderthal and possibly pre-Neanderthal populations throughout the Pleistocene, offering stable woodland, riparian, and ecotonal habitats within a climatically unstable continent. Recent paleoenvironmental studies from sites such as Ortvale Klde and Sakajia Cave in western Georgia, both situated in montane and piedmont zones, confirm Neanderthal presence during MIS 5–3 under a regime of fluctuating temperature and moisture (Adler et al., 2006). Archaeological and faunal data from Ortvale suggest a mosaic of steppe, open woodland, and forest patches, conducive to diverse ungulate populations and foraging opportunities in a corridor linking the Near East and Eurasian steppes. These conditions would have been reinforced by the presence of relic forest patches harboring the above-mentioned taxa, indicating that the Lesser Caucasus played not only a role in preserving floristic diversity, but also in maintaining ecological niches critical to Late Pleistocene hominin survival.

Recent modeling work has emphasized the role of the Caucasus not only as a refugial zone but also as a dynamic corridor facilitating Neanderthal dispersals toward the east. Ghasidian et al. (2024) employed topographic cost-surface analysis to reconstruct likely movement pathways across the region, revealing that Neanderthals may have avoided the highest mountain barriers of the Central Caucasus, instead utilizing mid-altitude passes and riverine corridors connecting the Black Sea and Caspian basins. Their results also suggest cultural differentiation between western (Micoquian) and eastern (Mousterian) assemblages, consistent with the idea that the North Caucasus served as a contact zone between distinct Neanderthal populations. This supports the view that the region offered both ecological stability in its southern forests and strategic connectivity across diverse Late Pleistocene landscapes.

Saradj-Chuko Grotto provides another remarkable case. Located in the Elbrus region of the North-Central Caucasus (Kabardino-Balkaria, Russia) at ~934 m a.s.l., the site lies in a river valley, tributary of the Baksan River. During MIS 5, the landscape supported mixed deciduous forests dominated by *Quercus*, *Carpinus caucasica*, *Juglans regia*, *Tilia*, *Ulmus*, and *Fagus orientalis*, with thermophilous and relict taxa such as *Carya ovata*, *Castanea sativa*, *Corylus colurna*, *Tsuga canadensis*, *Magnolia*, and *Ephedra*, reflecting a warm, humid interglacial climate with dense woodland and sparse herb cover. MIS 4 saw the emergence of cooler, unstable conditions, though arboreal taxa like *Carpinus*, *Ulmus*, *Tilia*, *Alnus*, *Acer*, and *Juglans* persisted in reduced abundance. An increase in Poaceae, Cyperaceae, and hygrophilous species (*Beckmannia eruciformis*, *Osmunda regalis*) suggests expanding wetlands and decreasing forest density. During MIS 3, pollen spectra indicate continued climatic oscillations, with *Betula* and *Alnus* expanding during stadials and temperate taxa (*Pinus*, *Carpinus orientalis*) returning during interstadials. Despite forest fragmentation, consistent arboreal pollen percentages suggest persistent patchy woodland or open forest–steppe throughout glacial phases.

Finally, palynological records from Lake Van in eastern Anatolia—a dry, mountainous region—offer detailed insights into MIS 7 and MIS 6 environments, potentially relevant to early Neanderthal populations (Pickarski and Litt, 2017). MIS 7 saw the development of closed-canopy temperate forests dominated by *Quercus*, *Juniperus*, *Ostrya–Carpinus orientalis*, *Fagus*, and *Betula*, consistent with humid interglacial conditions. In contrast, MIS 6 was marked by sharp climatic and vegetational shifts: forest taxa declined steeply, replaced by steppe and semi-desert elements (*Artemisia*, Amaranthaceae, Poaceae), reflecting colder and drier climates. These trends were punctuated by short-lived woodland recoveries, with taxa such as *Juniperus* and *Betula*. The resulting patchwork of open steppe, shrubland, riparian corridors, and forest patches generated diverse ecological niches over short timescales, posing both challenges and adaptive opportunities for Middle Paleolithic hominins in eastern Anatolia.

2.7. *Zagros Mountains*

Although Shanidar Cave remains one of the most emblematic Neanderthal sites in the Zagros Mountains—yielding important osteological finds and refined chronological frameworks—its potential for paleoenvironmental reconstruction has been historically limited. Early palynological interpretations by Leroi-Gourhan (1975) were critically reassessed by Fiacconi and Hunt (2015), who demonstrated that the pollen spectra were compromised by modern contamination, thereby invalidating earlier assumptions about vegetation and climate. However, microfossil analyses of dental calculus from Shanidar III have provided alternative ecological signals: starches and phytoliths derived from wild cereals (*Triticeae*), legumes, and date palms (*Phoenix*) suggest access to a mosaic landscape combining open woodland, grassland, and riparian components (Henry et al., 2011). These dietary residues—some altered by heating—support the inference of a seasonally productive environment offering diverse plant resources and cooking opportunities, despite the absence of robust palynological records.

Kaldar Cave, located in the western Zagros of Iran, preserves a stratified Paleolithic sequence that provides important insights into environmental variability and human adaptation in semi-arid mountain zones. Layer 4, attributed to the Middle Paleolithic and tentatively associated with Neanderthals based on its Levallois-dominated lithic industry, is dated between ~54,400 and 36,750 cal BP. This layer is overlain by Layer 3, assigned to the early Upper Paleolithic and associated with anatomically modern humans, indicating a local Middle to Upper Paleolithic transition (Bazgir et al., 2017; Djamali et al., 2023). Although no pollen data are available, paleoenvironmental reconstructions based on faunal and charcoal evidence suggest a dry, variably wooded forest-steppe landscape. The large mammal assemblage includes wild caprines (*Capra* sp.), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), and smaller carnivores, along with micromammals such as *Meriones*, *Microtus*, *Cricetulus*, *Apodemus*, and *Mus*. These faunal indicators point to a cold and arid steppe-like environment interspersed with patches of woodland or dense shrubland, likely concentrated near water sources. The dominance of *Prunus*, *Amygdalus*, and other Rosaceae in the charcoal record supports the presence of xerophytic shrub communities adapted to semi-arid montane conditions. Together, these data suggest that both Neanderthals and modern humans inhabited a dynamic ecotonal setting.

There is strong evidence that Neanderthals in these territories adapted successfully to the environmental challenges of arid lands. They appear to have preferentially settled in mountainous ecosystems, where orographic rainfall likely enhanced plant productivity and increased prey availability. Yousefi et al. (2020) applied species distribution models (SDMs) to reconstruct the paleoecology of Neanderthals on the Iranian Plateau—a region still underexplored in hominin ecological studies. By examining the modeled past distributions of Neanderthals and their key prey species—wild goat (*Capra aegagrus*), wild sheep (*Ovis orientalis*), and Persian gazelle (*Gazella subgutturosa*)—the study identifies the Zagros Mountains as the most suitable area for Neanderthal settlement in southwestern Asia. These mountainous zones offered ecological resilience, while high summer temperatures constrained their range further south, leaving only isolated pockets of potential habitat in central Iran.

2.8. Altai and Central Asian highlands

The Altai Mountains, situated at the intersection of Russia, Mongolia, China, and Kazakhstan, form a biogeographical crossroads between Europe, Central Asia, and Siberia. Ecologically, the region lies within the boreo-montane Asian zone, a transitional belt between the Siberian taiga (boreal biome), the Asian steppe (cold grasslands), and montane tundras. From a biogeographical standpoint, it is analogous to the European alpine region, and from a paleoecological one, it represents the easternmost margin of confirmed Neanderthal occupation. Palynological records from Chagyrskaya Cave (Russia) reveal valuable insights into local environmental conditions during Neanderthal presence (Rudaya et al., 2017; Salazar-García et al., 2021). During the late MIS 4 period, open steppe landscapes dominated the Charysh River valley, with pollen assemblages composed primarily of grasses, *Artemisia*, Asteraceae, Caryophyllaceae, Cyperaceae, and other herbaceous taxa. Associated faunal remains—*Bison priscus*, *Equus ferus*, *Coelodonta antiquitatis*, and *Ovis ammon*—support the interpretation of a cold, arid steppe ecosystem, corroborated by loess accumulation. With the onset of MIS 3 interstadials, vegetation shifted toward a mosaic of steppe and forest-steppe habitats, marked by the expansion of coniferous species such as *Pinus sibirica*, *Picea*, and *Larix* into riparian zones.

Further north, new palynological research from key Middle Paleolithic sites—Okladnikov and Verkhnyaya Sibiryachikha caves—confirms that Neanderthals endured persistently cold and dry conditions in mostly treeless landscapes (Alekseitseva et al., 2025). At Okladnikov Cave (ca. 44–40 ka BP), vegetation consisted of steppe, dwarf tundra, and temperate xerophytic shrubland dominated by *Artemisia*, Poaceae, and Fabaceae, with tree pollen restricted to *Pinus*, *Salix*, and *Betula* in moist microhabitats. At Verkhnyaya Sibiryachikha (ca. 48–28 ka BP), steppe vegetation—comprising Poaceae, Ranunculaceae, and Rosaceae—remained stable, with only sporadic arboreal elements like *Ulmus* and *Tilia*, suggesting isolated forest patches in wetter niches.

Denisova Cave, occupying a higher-altitude montane taiga zone, records a more dynamic sequence. Neanderthal-associated layers (MIS 4–early MIS 3) reflect transitions from closed coniferous forests (*Picea*, *Larix*, *Abies*) to increasingly open steppe and tundra communities (Alekseitseva et al., 2025). This environmental heterogeneity, possibly linked to microclimatic buffering, distinguishes Denisova from more arid neighboring sites. Meanwhile, Strashnaya Cave further exemplifies xeric Middle Paleolithic habitats: its pollen spectra (ca. 50 ka BP) are dominated by *Artemisia*, Asteraceae, and Amaranthaceae, with no arboreal presence, pointing to dry grasslands, tundra, salt-marshes, and semi-desert mosaics in periglacial conditions.

Southward, the highlands of Central Asia—particularly Uzbekistan—preserve sparse but significant evidence of Middle Paleolithic Neanderthal presence. At Teshik-Tash Cave (Machay Valley), faunal remains dominated by *Capra sibirica*, *Ovis ammon*, and *Equus hemionus*, along with *Bos/Bison*, *Marmota*, and *Canis lupus*, suggest a cold, rugged, and arid steppe-mountain environment with minimal forest cover (Okladnikov, 1949). Avifaunal remains, including falcons, owls, and chukar partridges, support this reconstruction. Other sites in Uzbekistan—Obi-Rakhmat, Sel'Ungur, Aman-Kutan, and Kulbulak—are under active investigation and offer promising contexts for future paleoenvironmental research (Nishiaki and Aripdjanov, 2021).

Beeton et al. (2013) propose a preliminary ecological niche model for late Pleistocene hominins in Central Asia, a region they define broadly to include Kazakhstan, Uzbekistan, Turkmenistan, and parts of northern Afghanistan. Using ecological niche modeling, they assess the spatial distribution of archaeological sites in relation to climatic and topographic variables during the last glacial cycle. The results suggest that hominins in this region occupied a more flexible and expansive range of environments than previously assumed. A persistent association with hydrological features—particularly terminal lakes, spring-fed systems, and riparian corridors—is evident across climatic phases. Yet, the spatial footprint of suitable habitat varied markedly: interglacial periods enabled occupation of broader lowland zones, while glacial conditions restricted habitability to environmentally buffered refugia. This indicates a capacity for ecological plasticity, with freshwater access acting as a critical constraint structuring hominin land use.

Recent paleoclimatic and dispersal modeling studies suggest that the broader landscapes of Central and Eastern Asia—traditionally viewed as arid and ecologically limiting—periodically provided viable corridors for hominin movement during humid phases of the Late Pleistocene. Least-cost path analyses by Li et al. (2019), informed by paleohydrological and climatic datasets, identified potential eastward dispersal routes across regions such as the Gobi Desert, the Altai Mountains, and associated fluvial systems. Their results highlight the importance of episodically wetter conditions in transforming otherwise inhospitable areas into transit zones, reinforcing the idea that hominin groups—including Neanderthals—may have exploited ecological windows of opportunity across the steppic and montane belts of Central Asia. Adding further resolution to this picture, Coco and Iovita (2025) used agent-based least-cost simulations to model specific Neanderthal movements across southern Siberia and the Urals. Their results show a strong preference for major river corridors such as the Volga–Kama and Ob–Irtysh systems, allowing for relatively rapid eastward dispersals even under stadial conditions. These simulations underscore freshwater availability and hydrological connectivity as key constraints shaping Neanderthal land use and dispersal strategies. Together, these modeling efforts align with paleoecological data from the Altai and surrounding highlands, where riparian zones and forest-steppe mosaics provided persistent ecological niches within a climatically unstable landscape.

Despite clear Neanderthal signals in the Altai and Uzbekistan, fossil evidence across Asia remains highly uneven. Many regions—including Tajikistan, Kazakhstan, Kyrgyzstan, Turkmenistan, Afghanistan, Pakistan, India, and Mongolia—lack hominin fossils, despite the presence of Middle Paleolithic lithic industries (Dennell, 2009). This distributional gap reflects not only preservation biases and research access but also broader structural asymmetries in global archaeological knowledge.

2.9. Arctic Neanderthals?

A particularly provocative case in the debate over potential late Neanderthal survival is the site of Byzovaya, located near the Arctic Circle, where Slimak et al. (2011) reported a Mousterian lithic industry dated between ~34,000 and 31,000 cal yr BP. Although no human remains were found, the authors argue that, given the strong association of Mousterian technologies with Neanderthals in Eurasia up to that point, the most parsimonious explanation is that the assemblage was produced by a late Neanderthal population. This interpretation would imply not only a significantly later survival than generally accepted but also the capacity for ecological adaptation to subarctic environments. In his critical assessment of the find, Hawks (2011) emphasized that while a Neanderthal attribution cannot be confirmed in the absence of osteological evidence, there are no compelling reasons to reject the stratigraphic integrity or chronological validity of the site. Hawks frames the dilemma clearly: either Neanderthals persisted in northern Eurasia well beyond 31 ka cal BP, or we must entertain the possibility that *Homo sapiens* groups maintained Mousterian technological traditions far longer than previously assumed. As he notes, the site "may be the most recent known [Neandertal] population" if the cultural attribution holds. This case illustrates the importance of remaining open to alternative extinction scenarios, particularly in peripheral or ecologically marginal zones, and of critically engaging with outlier evidence that may reflect underrepresented demographic realities or cultural refugia in the Late Pleistocene.

3. Perspectives on Neanderthal evolutionary ecology and biogeography

3.1. *Neanderthals: Chronospecies in shifting ecosystems*

The origin and demise of the Neanderthal chronospecies is best understood as a protracted, non-linear evolutionary process rather than a discrete taxonomic event. Morphologically derived Neanderthal features begin to emerge in the Middle Pleistocene, particularly from around 430 ka, as exemplified by the fossil assemblage from Sima de los Huesos (Atapuerca, Spain), which shows synapomorphies in the midface, dentition, and mandible, despite lacking the full suite of traits associated with later Neanderthals (Arsuaga et al., 2014; Meyer et al., 2016). Other Middle Pleistocene fossils from European sites similarly exhibit a mosaic of archaic and derived traits, suggesting a gradual emergence of Neanderthal morphology across western Eurasia between MIS 11 and MIS 7 (~400–250 ka) (Dennell and Roebroeks, 2005; Stringer, 2012a; Bermúdez de Castro et al., 2019; Rosas et al., 2022a,b; Sala et al., 2025). By the Late Pleistocene (MIS 5–3), classical Neanderthal morphology is fully expressed across Europe and the Near East (Herrera and Garcia-Bertrand, 2023). The terminal phase of the species is best documented in southern and western Iberia, providing evidence of Neanderthal presence as late as 40–37 ka BP, perhaps, although not clearly, overlapping with early *Homo sapiens* (Finlayson et al., 2006; Higham et al., 2014; Zilhão et al., 2017; Carrión et al., 2019b; Vidal-Cordasco et al., 2022). Plausibly, Iberia may have served both as an early locus of Neanderthal anatomical emergence and as a biogeographic refuge during their final millennia.

Throughout their evolutionary trajectory, Neanderthals experienced at least five major glacial periods (MIS 12, 10, 8, 6, and 4), four interglacials (MIS 11, 9, 7, and 5), and the highly unstable MIS 3, which alone encompassed over 25 abrupt stadial–interstadial oscillations, commonly known as Dansgaard–Oeschger (D–O) events (Rasmussen et al., 2014). These oscillations, recorded in Greenland ice cores and North Atlantic marine sediments, reflect temperature shifts of up to 10–15 °C occurring within a few centuries or less (Capron et al., 2021). At least six major Heinrich events—massive iceberg discharges into the North Atlantic—also punctuated this period, further amplifying ecological disruption. In total, the Neanderthal lineage may have endured over 30 cold phases, including long glacial maxima and short stadials, and a comparable number of temperate intervals, whether full interglacials or brief interstadials. Some of the most climatically severe episodes included MIS 12 and MIS 6—major glacial periods marked by widespread cold and aridity—as well as MIS 4, a particularly abrupt cooling phase following the last interglacial optimum (MIS 5e). In addition, Heinrich Event 4 (~39 ka) stands out as one of the most abrupt cold episodes of the Late Pleistocene (Hemming, 2004). Many of these transitions occurred on sub-millennial timescales, producing rapid and pronounced variability in temperature, humidity, seasonality, and ecosystem structure.

As we have discussed, these climatic extremes profoundly affected Eurasian vegetation, driving repeated contractions and expansions of forest biomes, fragmenting woodland habitats, and promoting the dominance of steppe, tundra, and open shrubland communities during glacial phases (e.g. Lang et al., 2023). Rapid transitions often led to unstable ecotonal mosaics, with shifting boundaries between forested and treeless environments, reducing biome continuity and altering resource landscapes for primary consumers and critical for hominin survival. This long-term exposure to highly dynamic environmental conditions shaped not only Neanderthal ecological niches but also their behavioral and cultural adaptations (Finlayson and Carrión, 2007). In contrast, anatomically modern humans (*Homo sapiens*) emerged in Africa under comparatively more stable climatic regimes during the later Middle Pleistocene, likely between 300 and 200 ka (Scerri et al., 2019). Although they too experienced significant environmental fluctuations—particularly during phases of aridification linked to glacial maxima—the amplitude and frequency of abrupt climatic shifts in tropical and subtropical Africa were generally lower than those affecting mid- and high-latitude EurasiaIt was only during their later expansions into Eurasia, from ~70 ka onwards, that *H. sapiens* populations began to encounter the full intensity of rapid stadial–interstadial cycling, including Heinrich events and D–O oscillations (Timmermann and Friedrich, 2016). Thus, unlike Neanderthals—who evolved and persisted entirely within the heart of Pleistocene climatic volatility—modern humans initially developed under less extreme conditions, only later confronting and adapting to northern climatic unpredictability as part of their global dispersal (Mylopotamitaki et al., 2024).

3.2. *Born of disruption*

High-resolution carbon isotope records from loess deposits in Central Asia and Northwest China indicate that the Mid-Pleistocene Climate Transition (MPCT), spanning approximately 1.2 to 0.7 million years ago, intensified aridification and increased climatic instability across the Palearctic (Zan et al., 2024). This climatic shift restructured continental landscapes, driving the expansion of loess plains, desert belts, and episodic freshwater systems, while disrupting ecological continuity on a broad scale. The authors argue that such environmental changes affected the timing and routes of hominin dispersals, underscoring a strong link between climatic instability and evolutionary processes. Importantly, the MPCT predates the emergence of *Homo neanderthalensis* and instead aligns with the rise of *Homo heidelbergensis*, widely considered the last common ancestor of Neanderthals and modern humans. In this light, Middle Pleistocene hominins—including early Neanderthals and coeval populations—should be viewed as evolutionary responses to mounting ecological stress (Trajer, 2022). They were not passive inhabitants, but adaptive agents shaped by an increasingly unpredictable world.

Neanderthals, in particular, appear as hominins forged by instability—ecological heirs to environmental disruption, whose behavioral and physiological adaptations reflect landscapes in flux. However, biome-scale patterns are only part of the story: patchy steppe environments, when adjacent to forested refugia or permanent water sources, could still offer viable niches for hominin occupation. This suggests that local ecological structure, rather than generalized biome classification, is crucial to understanding hominin survival and dispersal dynamics.

3.3. *Evolutionary hotspots in the Neanderthal range*

The widespread and long-lasting presence of Neanderthals across the Mediterranean Basin is hardly surprising, considering this region's longstanding role as a biodiversity reservoir during the most climatically challenging phases of the Pleistocene. The Mediterranean is globally recognized as a biodiversity hotspot, and its ecological richness appears to have played a crucial role in hominin evolutionary dynamics. Carrión et al. (2011) noted that the emergence and persistence of evolutionary novelties among hominins often coincided with zones of high biological diversity—so-called evolutionary hotspots. These are typically relict landscapes: remnants of formerly broader ecosystems that have served as long-term reservoirs of both plant and animal diversity throughout the Cenozoic. The most prominent example is the Horn of Africa and its southern margins, particularly in Kenya and Tanzania, where the earliest fossil appearances of hominin genera—including *Ardipithecus*, *Orrorin*, *Australopithecus*, *Kenyanthropus*, *Paranthropus*, and *Homo*—have been recorded. Yet, parallel processes of evolutionary significance can also be observed within Eurasia, influenced by factors such as intra-continental diversification (Martinón-Torres et al., 2011), tectonic and topographic complexity, habitat mosaicism, ecological interaction intensity (Finlayson et al., 2011), and overall biotic complexity (Carrión et al., 2011). In this context, the idea that a Neanderthal hotspot corresponds to the Eurasian mid-latitude belt appears well supported—an ecologically rich corridor that may have offered both evolutionary opportunities and demographic refugia (Finlayson, 2009; Dennell et al., 2011; Carrión et al., 2019c).

3.4. *Revisiting the breadth of the Neanderthal niche*

Recent species distribution modeling approaches have begun to overcome limitations imposed by taphonomic bias and the fragmentary nature of the Neanderthal archaeological record. Henry et al. (2017), focusing on the Levant, found that Neanderthal sites consistently clustered in areas with moderate slopes, low terrain ruggedness, and proximity to reliable water sources. These locations often lay within ecotonal zones, where environmental variability and accessibility were optimal for repeated occupation. Yaworsky et al. (2024) developed a spatiotemporal species distribution model using the Maximum Entropy (MaxEnt) algorithm, combining millennial-scale paleoclimate reconstructions with georeferenced, chronologically constrained Neanderthal sites across Western Eurasia. Their results allowed the estimation of the Neanderthals' fundamental climatic niche between 145 and 30 ka ago. A key finding is that, despite the extended temporal framework, Neanderthals occupied a relatively narrow climatic niche, consistently favoring temperate, humid, and moderately productive environments, while avoiding more extreme climatic conditions. Moreover, the study indicates that Eastern Europe was generally climatically unsuitable for Neanderthals during stadial phases of the Late Pleistocene, reflecting long-standing climatic contrasts with Western Europe. Although the mammoth steppe in Eastern Europe supported abundant megafauna, this does not appear to have attracted Neanderthal populations—possibly due to the availability of higher-ranked prey, such as reindeer, in other regions. Similarly, Zeller et al. (2023) used global biome modeling to show that Neanderthals favored temperate forest environments and were largely absent from the most open and extreme biomes, such as deserts or tundras. Their ecological niche appears narrower than that of other hominins, with contractions into forested refugia during colder phases of the Pleistocene. Nevertheless, the spatial scale of biome distribution is a key consideration: even in landscapes dominated by open steppe, the local proximity of forested patches or freshwater sources may have made such environments attractive and suitable for Neanderthal occupation. This suggests again that ecological structure at the landscape level, rather than biome type alone, played a critical role in shaping patterns of Neanderthal land use.

Trájer (2023) offers a detailed ecological reconstruction of the habitats occupied by Neanderthals and their ancestors in Western Eurasia from approximately MIS 20 to MIS 4. By integrating biome classification, climate zone mapping, wind exposure, cave orientation, karst typologies, and solar irradiation data, the study reconstructs the ecological niche breadth of these hominin groups over time. The results show a progressive niche shift from woodland-shrubland and temperate forests to colder environments, particularly boreal forests, reflecting a long-term trend toward greater climatic tolerance and ecological plasticity. During MIS 4, over half of the Neanderthal sites were located in boreal zones, though populations in southern areas such as Iberia and the Levant remained within temperate or semi-arid environments. No populations are recorded directly within tundra biomes, but some groups appear to have lived near its boundaries. A key insight from the study is the close ecological overlap between Neanderthals and their primary prey species (e.g., *Cervus elaphus*, *Sus scrofa*, *Capra ibex*, *Rangifer tarandus*), highlighting the strong trophic dependence that shaped Neanderthal settlement patterns. This reinforces the image of a flexible yet ecologically constrained Neanderthal niche—capable of significant adaptation, yet sensitive to environmental and demographic pressures. Although Neanderthals demonstrated increasing resilience through time, their dependence on energetically demanding hunting strategies, low demographic density, and vulnerability to prey scarcity may have limited their capacity to respond to abrupt environmental change. As discussed above, Neanderthals—despite being one of the most intensively modeled Paleolithic populations—lived through a vast span of ecological and climatic shifts. Any reconstruction of their behavior must acknowledge the deep time scale of their evolutionary trajectory and the adaptive challenges it entailed. Far from being static, their niche evolved alongside changing biomes and climates, pointing to a species that was both resilient and vulnerable in equal measure.

3.5. *Open spaces in interglacial forests: Herbivory and fire*

Pearce et al. (2025) challenge the traditional view of densely closed Last Interglacial forests by reconstructing temperate European vegetation using scale-explicit models (LOVE and REVEALS). Their results reveal a predominantly light woodland mosaic (63 %), interspersed with lower proportions of open (17 %) and closed (21 %) forest vegetation. The weak correlation between local and regional vegetation patterns suggests that local disturbance regimes—rather than climatic forcing—were the primary drivers of landscape structure. The prevalence of disturbance-adapted taxa and the inferred role of large and medium herbivores in maintaining openness point to inherently dynamic and heterogeneous ecosystems. These findings not only refine our understanding of pre-anthropogenic biodiversity but also underscore the ecological role of megafauna, with implications for present-day conservation and rewilding strategies.

Complementary evidence is provided by Roebroeks et al. (2021), who argue that Neanderthals were active landscape agents, not passive dwellers. Drawing on multiproxy data from the Last Interglacial site of Neumark-Nord (Germany), they demonstrate that Neanderthal occupation coincided with persistent open spaces within otherwise wooded environments—openings that may have endured for centuries. Archaeological layers at the site align with declines in arboreal pollen and increases in herbaceous taxa, suggesting deliberate or incidental modification of vegetation. A likely mechanism behind these changes is fire—used to manage hunting grounds, encourage edible plant resources, or maintain landscape openness. This interpretation is consistent with ecological models that depict Pleistocene landscapes as mosaics of open and semi-open habitats, shaped by the combined actions of herbivores and fire regimes. Palaeoecological data from Iberian sites such as Los Tollos (Carrión et al., 2024d) reinforce this perspective, pointing to the recurrent presence of natural fires in Quaternary ecosystems. The work by Kyrikou et al. (2025) in Megalopolis also shows natural fire activity linked to vegetation biomass and climatic transitions during the middle Pleistocene. Together, these lines of evidence suggest that Neanderthal landscapes were more open, varied, and actively maintained than traditionally assumed—sculpted by both human and non-human ecological agents.

4. Paleoartistic narratives of Neanderthal plant environments

The visual representation of Neanderthal landscapes—much like the evolving iconography of their facial and bodily morphology—has undergone a transformation driven by scientific discoveries that, over time, gave rise to entrenched assumptions and were eventually overturned through paradigm shifts that define the current state of the art (Gurche, 2013; Amorós, 2023). Nevertheless, this shift in scientific perspective has not always permeated the popular imagination. Neanderthals are still frequently envisioned through the lens of early misconceptions, often portrayed in glacial or steppe environments—at best, within sparse wooded tundra, but more commonly in entirely or nearly treeless landscapes. These representations can be seen in the works of artists such as František Kupka, Zdenek Burian, Benoît Clarys, Randii Oliver, and Tom Ungemach (Fig. 1). Over time, this stereotype has weakened, and Neanderthals have increasingly been depicted within taiga, temperate forest, or Mediterranean woodland settings, as exemplified in the work of Mauricio Antón (https://mauricioanton.wordpress.com/) and Raúl Martín (https://www.raulmartin-paleoart.com/), and more recently by Gabriela Amorós (Amorós et al., 2021). Still, traces of the older cold-adapted ecological framing persist—for instance, in the otherwise outstanding paleoart of Tom Björklund (https://www.tombjorklund.fi/), which sometimes continues to place Neanderthals predominantly in cryophilic settings.

However, it is now well established that Neanderthals possessed extraordinary adaptive capacities. Their long evolutionary trajectory—across vast spatial and temporal scales—enabled them not only to colonize and persist, but also to disappear, within floristically and ecologically diverse environments. In the following section, we present paleoenvironmental reconstructions that highlight this diversity, using the Iberian Peninsula as a case study.

Two particularly relevant factors make the Iberian Peninsula especially suitable for this investigation. First, it hosted important glacial refugia for woody angiosperms during the studied period. Second, we have access to paleobotanical records from Neanderthal sites in which climate-driven changes significantly reshaped the landscape—without necessarily leading to Neanderthal depopulation. In line with these premises, the paleoartistic study is developed around three working scenarios: (i) visualizing vegetation changes in the Cantabrian coastal region, northern Iberia, in response to stadial–interstadial climatic dynamics; (ii) providing comparative imagery showing how similar climatic shifts did not affect flora and vegetation in southern localities; and (iii) illustrating a continental Neanderthal territory, where vegetation landscapes underwent marked transformations from the Last Interglacial to the eventual disappearance of Neanderthal populations.

This approach allows us to integrate continental, interregional, and local perspectives through drawing-based reconstructions. Following the same order as above, the illustrations aim to depict: (i) shifting conditions in ecotonal zones; (ii) long-term survival in physiographically buffered environments—often stabilized by microclimatic effects; and (iii) millennia-long persistence within floristic and vegetational settings highly sensitive to climatic change.

4.1. Paleoecological dynamics of ecotones in Cantabrian Iberia

A first paleoartistic attempt is grounded in a geobotanical comparison between a stadial and an interstadial period in the Cantabrian region of Iberia during the Late Pleistocene. Climatic fluctuations during this time appear to have profoundly shaped evolutionary, ecological, and biogeographic processes affecting both flora and fauna—including *Homo neanderthalensis* and *H. sapiens* (Vidal-Cordasco et al., 2022; Marín-Arroyo and Sanz-Royo, 2021; Férnandez-García et al., 2023).

Fig. 1. Reconstructions of Neanderthal vegetation landscapes in the literature, showing a prevailing emphasis on shrubby or graminoid steppe-tundra, with or without coniferous elements. (a) Artwork by Zdeněk Burian for the cover of *Prehistoric Man* (Augusta et al., 1960); source: http://zburian.blogspot.com/. (b) *Chasse aux chevaux* (2005) by Benoît Clarys; source: https://www.penserletravailautrement.fr/. (c) *Neanderthal family around 60,000 years ago* by Randii Oliver; source: http://timoneandertal.blogspot.com/. (d) *Neanderthals hunting bison* by Grégoire Cirade; source: https://www.sciencephoto.com/.

Stadials in this region conform to the broader Atlantic-influenced temperate European pattern, characterized by open landscapes dominated by grasses, heaths (*Erica*), *Artemisia*, other Asteraceae, *Ephedra*, Cyperaceae, *Plantago*, and a range of herbaceous and shrubby species. Scattered tree populations—primarily *Pinus* (likely *P. sylvestris*), *Betula*, and *Juniperus*—also punctuate these open environments (Fig. 2). In striking contrast, interstadials witnessed relatively rapid reforestation (within centuries or even decades) by mesophilous taxa, notably oaks and other deciduous broadleaf species such as willows, hazels, birches, alders, elms, ashes, maples, walnuts, and chestnuts, alongside diverse shrub and herbaceous components—again with heaths playing a significant role (Fig. 3). To symbolically represent faunal associations with these contrasting climatic phases, we illustrated stadials with the reindeer (*Rangifer tarandus*) and woolly rhinoceros (*Coelodonta antiquitatis*), and interstadials with red deer (*Cervus elaphus*), roe deer (*Capreolus*), and red fox (*Vulpes*). These depictions are intentionally simplified and non-exhaustive, aiming to support paleoenvironmental reconstruction rather than provide a comprehensive faunal inventory.

The palynological and anthracological data underlying this reconstruction have been synthesized in Carrión et al. (2024c), drawing on a range of cave, lacustrine, and marine records. These include both direct evidence from Mousterian contexts and paleoenvironmental inferences from earlier (pre-Neanderthal) or later (sapiens-associated) periods sharing similar stadial/interstadial dynamics. Relevant sequences span sites such as El Castillo (Uzquiano, 2007), Covalejos (Uzquiano, 2008; Ruiz-Zapata and Gil-García, 2005), Altamira (Carrión and Dupré, 2002), Lago de Ajo (Allen et al., 1996), Lago de Sanabria (Muñoz-Sobrino et al., 2004), Laguna de la Roya (Muñoz-Sobrino et al., 2013), Area Longa (Gómez-Orellana et al., 2007), and Lagoa de Lucenza (Iriarte-Chiapusso et al., 2016), as well as marine cores MD99-2331 and MD03-2697, which jointly span the last three glacial–interglacial cycles (Naughton et al., 2009; Sánchez Goñi et al., 2008).

Like our own species, Neanderthals were compelled to adapt to these shifting ecotones. These adaptive responses likely entailed technological and cultural changes independent of species-specific trajectories (Finlayson and Carrión, 2007; Pederzani et al., 2023; Gómez-Olivencia et al., 2018). As discussed above, Neanderthals exhibited remarkable plasticity in response to both short- and long-term climatic variability, employing strategies such as resource optimization, seasonal mobility, and cultural innovations that facilitated survival in often challenging environments (Roebroeks and Soressi, 2016; Albert et al., 2012). During shorter-term climatic oscillations—particularly those occurring in MIS 3—Neanderthals adjusted by managing resources efficiently and modifying mobility patterns.

Within this broader context, Cantabrian Iberia must be viewed as part of a southwestern European refugial network (Carrión et al., 2011; González-Sampériz et al., 2010; Magri et al., 2017). This included primary habitats for Neanderthals alongside secondary refugia such as Liguria, the Balkans, the Peloponnese, and the Rhône Valley (Vidal-Cordasco et al., 2023). These landscapes underwent progressive fragmentation during stadials, followed by expansion during interstadials—dynamics that likely influenced Neanderthal population fluctuations. Their ability to reoccupy these habitats during interstadial phases suggests a robust degree of climatic resilience, one that appears to have persisted until the Greenland Interstadial 12 (GI-12), a period associated with demographic decline and the eventual disappearance of Neanderthal populations from Iberia (Vidal-Cordasco et al., 2022, 2023). At this terminal stage, it is plausible that the last Neanderthal groups encountered reduced interspecific competition, at least temporarily, from expanding *Homo sapiens* populations arriving from the East (Paquin et al., 2024).

Fig. 2. Palaeolandscape reconstruction of a pre-coastal Cantabrian valley during a stadial phase of the Neanderthal period. This composite image represents average vegetation patterns derived from multiple regional archaeobiological studies, with a focus on pollen and anthracological data (see Carrión et al., 2024c, for compilation). The landscape is dominated by heliophilous, graminoid vegetation with abundant *Artemisia*, *Ericaceae*, *Asteraceae*, and *Cyperaceae*. Woody elements include birch trees (foreground and lower slopes) and scattered pines and junipers in the background. Two species of the Pleistocene cold-adapted fauna, *Coelodonta antiquitatis* and *Rangifer tarandus*, are depicted grazing. See Supplementary Information for taxonomic details and Section 4.1 for further discussion, data, and concepts. Artwork: G. Amorós.

Fig. 3. Palaeolandscape reconstruction of a pre-coastal Cantabrian valley during an interstadial phase of the Neanderthal period. This composite image integrates regional data from multiple archaeobiological studies, with an emphasis on pollen and charcoal records (see Carrión et al., 2024c, for compilation). Warmer and moister interstadial conditions favor forest expansion, with broad-leaved trees (mostly deciduous oaks, but also groundwater-fed vegetation) in deeper soils, and conifers and birches in montane zones. Shrub and herbaceous diversity is greater than during the stadial phase. Deer, fallow deer, and foxes complement the scene. See Supplementary Information for taxonomic details and Section 4.1 for further discussion, data, and concepts. Artwork: G. Amorós.

4.2. Refugial settings for Neanderthals in southeastern Iberia

A second paleo-landscape study is based on Mousterian and Neanderthal-associated palynological findings from the southeastern Iberian coastal shelves, with particular attention to Sima de las Palomas (Carrión et al., 2003). The site holds one of the most important late Neanderthal fossil assemblages in the region, with remains from at least 14 individuals identified to date (Trinkaus and Walker, 2017; Walker et al., 2008, 2017). The pollen sequence at Sima de las Palomas likely covers a significant portion of MIS 4 and MIS 3. The pollen record is dominated by *Quercus*—likely including *Q. faginea*, *Q. ilex-rotundifolia*, *Q. coccifera*, and *Q. suber*—along with various species of *Pinus* (*P. nigra*, *P. halepensis*, *P. pinea*) and *Juniperus* (*J. phoenicea*, *J. oxycedrus*), with possible presence of *Tetraclinis articulata*. Several taxa currently absent from the region are also represented, such as hazel (*Corylus avellana*), ash (*Fraxinus*), strawberry tree (*Arbutus unedo*), boxwood (*Buxus*), and birch (*Betula* cf. *celtiberica*) (Carrión et al., 2003). Additional palynological evidence includes *Olea europaea*, *Phillyrea*, *Chamaerops humilis*, *Rhamnus*, *Maytenus europaeus*, *Withania frutescens*, *Smilax aspera*, *Pistacia lentiscus*, *Periploca angustifolia*, *Osyris quadripartita*, *Asphodelus*, and representatives of Lamiaceae, Asteraceae, Cistaceae, *Thymelaea*, and *Calicotome intermedia,* among other legumes. The pollen spectra at Sima de las Palomas show little variation throughout the sequence, which supports its interpretation as a glacial refugium for a diversity of plant species (Figs. 4 and 5). This interpretation is further reinforced by complementary sequences from other sites in southern Spain, including Gorham's and Vanguard Caves in Gibraltar (Carrión et al., 2008, 2018), Bajondillo (López-Sáez et al., 2007), and Abrigo del Humo in Málaga (Ochando et al., 2020c).

These ecosystems are ecologically distinctive. Alongside the dominance of pines and oaks in a savanna-like mosaic, a key feature is the coexistence of deciduous trees with cold-adapted pines, drought-tolerant conifers, Mediterranean shrubland, Iberian-North African xerothermophilous species, grasslands, and elements typical of Irano-Turanian steppe environments. These coastal areas may have functioned as ecological corridors, facilitating human dispersal routes during favorable phases where the climatic changes were less sharp and abrupt, providing a more stable environment for animals and humans (Bailey et al., 2008; Vidal-Cordasco et al., 2023). Indeed, the spatial architecture of these paleoecosystems merits dedicated paleoecological investigation. Based on current pollen rain data, they have no direct modern analogues (Carrión et al., 2024c).

One working hypothesis envisions arboreal metapopulations forming regional networks within local climatic microrefugia, often in montane areas near the coast. In such settings, forested vegetation could have buffered climatic oscillations, helping to mitigate the generally arid conditions that prevailed across broader platforms during MIS 4–2 stadials. These glacial refugia, while perhaps functioning as "local anomalies," held broader ecological significance as biodiversity reservoirs. This view challenges a long-standing assumption: that regional vegetation states are primarily governed by large-scale climatic trends. Instead, it argues for the pivotal role of local microclimates and topography in shaping ecological persistence and human resilience. This perspective counters traditional frameworks that attribute ecological and human evolutionary outcomes chiefly to astronomical-scale climatic drivers (Behre and van der Knaap, 2023). In support of this view, the record from Los Tollos in the southernmost Iberian margin—derived from a long lacustrine sequence spanning the past 40,000 years—offers further insight. Here, montane forest vegetation appears to have withstood cold and arid climatic pulses that severely impacted the more continental sectors of Andalusia (Carrión et al., 2024d).

Fig. 4. Palaeolandscape reconstruction of the southeastern Iberian coastal mountains during a Neanderthal stadial phase. Based on a synthesis of data by Carrión et al. (2024c), with emphasis on pollen data from Sima de las Palomas (Carrión et al., 2003). The landscape is dominated by woody plants, including trees such as *Quercus faginea*, *Q. ilex*, *Q. suber*, *Q. coccifera*, *Pinus pinaster*, *P. nigra*, *Fraxinus*, *Corylus*, and *Juniperus* species. The thermophilous Mediterranean scrub shows high diversity, including Ibero-North African taxa like *Periploca angustifolia* (foreground, left). Representative fauna includes goats, deer, rabbits, and foxes. See Supplementary Information for taxonomic details and Section 4.2 for further discussion. Artwork: G. Amorós.

Fig. 5. Palaeolandscape reconstruction of the southeastern Iberian coastal mountains during a Neanderthal interstadial phase. The similarity to Fig. 4 reinforces the concept of glacial refugia as ecologically resilient structures under favorable microclimatic and topographic conditions. Deer, lynx, and rabbits are depicted. See Supplementary Information for taxonomic details and Section 4.2 for further discussion. Artwork: G. Amorós.

4.3. Four vegetation worlds: Climatic landscapes of Mediterranean Neanderthals

Here we present a paleoartistic experiment based on four defining phases of vegetational change (Figs. 6–9) inferred from the pollen record of Carihuela Cave, a Paleolithic site located on the northern cliffs of Monte del Castillo, south of Píñar in inland Granada (southern Spain), at 1020 m asl. This record was chosen due to the direct involvement of the authors in its study (Carrión, 1992; Carrión et al., 1999, 2019b; Fernández et al., 2007; Jiménez-Arenas et al., 2019).

From the standpoint of paleovegetation and paleoflora, the Carihuela sequence documents marked changes throughout a prolonged human occupation, extending from at least MIS 6 (~145 ka; Riquelme-Cantal et al., 2024) to around 1250 years BP. The Pleistocene vegetation is generally dominated by Pinus, Poaceae, and *Artemisia*, with a notable presence of Quercus and Olea around 127 ka cal BP (Fig. 6). Peaks in steppe elements often correlate with declines or disappearances of mesothermophilous taxa, a recurring pattern especially during MIS 4 and MIS 2 (Figs. 7 and 9). These phases also coincide with increased frost-shattered sediment particles, indicating severe climatic deterioration. There is good palynological correspondence between Carihuela and the nearby Padul peatland (Camuera et al., 2018, 2019), although the sites now occupy ecologically distinct environments—Carihuela being more continental. Notably, *Pinus* maxima in Carihuela correspond to *Quercus* peaks in Padul, and xerophyte increases suggest a parsimonious correlation model (Carrión et al., 2019b) (Fig. 8).

Carihuela gained prominence in the 1970s with the discovery of anatomically modern human remains associated with Mousterian lithics in Unit IV. Later interpretations proposed the site as a potential Neanderthal refugium in the Iberian Peninsula (Vega-Toscano, 1988, 2005), within the broader "southern Iberian refuge" model (Finlayson et al., 2006). Excavated since the 1950s, the cave contains a deep stratigraphic record encompassing Paleolithic to post-Neolithic phases. The most extensive project (1979–1992) identified twelve stratigraphic units: Units XII–III span the Pleistocene and II–I the Holocene (Vega-Toscano, 1988). Neanderthal skeletal remains have been found in Units VIII–V and the basal part of Unit IV, which also contains a rich Mousterian lithic assemblage dated between ~44 and 25 cal ka BP. These controversial dates are addressed in Carrión et al. (2019b). Modern human remains appear in Units III–I and in the uppermost layers of Unit IV.

Of particular note is the presence of *Crocuta* coprolites at Carihuela, which were analyzed for pollen and radiocarbon dated alongside those from the adjacent Las Ventanas Cave (Carrión et al., 2001; Ochando et al., 2020d). While Las Ventanas coprolites span from ~43 ka BP, those at Carihuela begin at ~31 ka BP, in sedimentary contexts lacking both Mousterian industry and Neanderthal fossils. This suggests that hyenas occupied the cave after Neanderthals had vacated it, though both likely shared territory over millennia. In sum, multiple scenarios remain plausible: a conventional or delayed Neanderthal disappearance, Mousterian production by early modern humans, immediate or delayed arrival of *H. sapiens* after Neanderthal abandonment, or even coexistence of Neanderthals, *sapiens*, and carnivores within the Monte del Castillo karst system. Given these uncertainties—and considering current evidence of interaction between the two human species across Europe—we offer a speculative illustration depicting a shared moment in time: one Neanderthal and three *sapiens* engaged in daily activities in the Río Píñar valley, beneath the escarpments of Carihuela and Las Ventanas, quietly observed by a group of hyenas (Fig. 9).

5. Final remarks. The end of Neanderthals? A view from southern Iberia

Charton et al. (2025) provide a high-resolution palaeoecological reconstruction from marine core ODP Site 976 in the Alboran Sea, shedding light on vegetation and climate dynamics in the southwestern Mediterranean between 41 and 34 ka BP, with special attention to Heinrich Stadial 4 (HS4, ~39 ka BP). This stadial, characterized by severe winter cooling and a sharp reduction in precipitation, triggered the rapid spread of steppe and semi-desert vegetation across southeastern Iberia. The study identifies a three-phase environmental trajectory during GS9/HS4, revealing the intensity and pace of ecological disruption and its likely consequences for human populations during the Middle to Upper Palaeolithic transition (MUPT). Notably, the data show that HS4 disrupted the region's typical Mediterranean precipitation

Fig. 6. Artistic rendering of the Last Interglacial (Unit VIIa: Vega-Toscano, 1988) in the Piñar River Valley and Monte del Castillo, where the Neanderthal site of Carihuela and Las Ventanas Cave (left cliffs) are located. The landscape features forests dominated by *Quercus* and *Olea*, and a riparian gallery (center) with willows, ashes, alders, and elms. Pines appear on more exposed and rocky biotopes. These forests may have been partially cleared by megaherbivore activity (Pearce et al., 2023, 2025). The Holocene sequence from the same site lacks dominant *Olea*, being instead characterized by both deciduous and evergreen *Quercus* (Fernández et al., 2007). See Supplementary Information for taxonomic details and Section 4.3 for further discussion (Carrión, 1992; Carrión et al., 1998, 2019b). Artwork: G. and A. Amorós.

Fig. 7. Palaeoartistic approximation of grassland phases at Carihuela, likely corresponding to parts of Units X, VIIb, VI, and IV, within the MIS 5–MIS 3 interval. Grazing pressure is assumed to have been high, consistent with the presence of vertebrate remains (e.g., *Bos*, *Cervus*, *Equus*). Water-table-associated flora on the river margins. See Supplementary Information for taxonomic details and Section 4.3 for data and interpretations (Carrión, 1992; Carrión et al., 2019b). Artwork: G. and A. Amorós.

Fig. 8. Interstadial conditions at Neanderthal Carihuela, with prevalence of conifers (e.g., *Pinus nigra*, *Juniperus*) and temperate trees (largely oaks) in areas with greater edaphic water availability (e.g., Units VIII, VI). *Dicerorhinus kirchbergensis* is depicted in the foreground. See Supplementary Information for taxonomic details and Section 4.3 for data and interpretations (Carrión, 1992; Carrión et al., 2019b). Artwork: G. and A. Amorós.

regime, generating conditions of extreme aridity that likely compromised the ecological viability of Neanderthal habitation in the area. While precise archaeological correlations remain elusive due to dating limitations, the authors propose that Neanderthal populations in southeastern Iberia were already demographically diminished and ecologically fragmented before HS4. The onset of this stadial likely intensified those pressures, potentially accelerating local population decline or prompting site abandonment. Spatial analyses show a significant reduction in evidence for human presence in the region during and immediately following HS4, supporting the idea that environmental thresholds were crossed during this period. In this dynamic landscape, southwestern Europe may have functioned as a climatic refugium. Simultaneously, evidence suggests that *Homo sapiens* may already have been present in parts of southern Iberia during HS4 (Cortés-Sánchez et al., 2019; Paquin et al., 2024), complicating narratives of clear biogeographic separation between the two species (Finlayson et al., 2023).

Despite growing consensus on a relatively early Neanderthal disappearance around 40 ka cal BP, scattered yet persistent archaeological signals raise the possibility of extended survival in ecological refugia across southern Iberia. Simulation-based studies by Vidal-Cordasco et al. (2022) support this view, indicating that certain chronometric datasets from Iberian Middle Palaeolithic sites permit survival probabilities slightly beyond 40 ka cal BP, especially in Meso and Thermomediterranean regions. Similarly, Zilhão et al. (2017) have defended Mousterian occupations at Cueva Antón until ∼38.5 ka cal BP. Other

Fig. 9. Full-glacial phase of MIS 3 at Carihuela (Unit V), with dominance of *Artemisia*, grasses, *Ephedra*, composites, and other herbaceous and small shrub species, along with scattered pines. This represents the most coldest dry phase in the sequence, with the disappearance of thermophilous taxa. Reedbeds and willows are present along the Piñar River course. A group of hyenas (*Crocuta*) observe a departing group of humans composed of three *sapiens* and one Neanderthal (left, with feathers). This is a speculative inclusion not meant to imply direct evidence from Carihuela, though competition between humans and hyenas for karstic shelter sites in the Monte del Castillo is well-documented (Carrión et al., 2019b; Ochando et al., 2020d). The co-occurrence of Neanderthals and *sapiens* is intended to reflect likely gene flow events (Reilly et al., 2022; Rosas et al., 2022a,b) which in the Iberian Peninsula, are supported by the Lagar Velho child (Linscott et al., 2025). See Supplementary Information for taxonomic details and Section 4.3 for data and interpretations (Carrión, 1992; Carrión et al., 2019b). Artwork: G. and A. Amorós.

sites—such as Gorham's Cave in Gibraltar (Finlayson et al., 2006) and Carihuela in southern Spain (Carrión et al., 2019b)—have yielded both late Middle Palaeolithic assemblages and environmental proxies compatible with ongoing Neanderthal presence into the mid-30s ka BP. These examples, however, are often excluded from broader extinction models due to methodological concerns (e.g., dating resolution, stratigraphic ambiguity), raising the possibility that simplification and confirmation bias have influenced dominant narratives of rapid replacement.

This tension is further underscored by the recent re-dating of the Lapedo child from Abrigo do Lagar Velho, Portugal. Using hydroxyproline radiocarbon techniques, Linscott et al. (2025) estimate the burial at approximately 28 ka cal BP—well after the generally accepted Neanderthal extinction threshold. While the child has long been cited as exhibiting possible Neanderthal traits (Duarte et al., 1999), the new chronology makes direct admixture improbable unless Neanderthals survived in western Iberia for much longer than currently acknowledged. More plausibly, these features reflect deeply introgressed traits from earlier admixture events. If not, the case calls for a renewed assessment of contested late Neanderthal sites whose systematic exclusion has shaped prevailing extinction chronologies.

A final reflection concerns the broader implications of the Signor–Lipps effect (Signor and Lipps, 1982), a key concept in paleontology which states that the last appearance of a taxon in the fossil record rarely corresponds to its true time of extinction. Statistically, the probability of recovering remains from the final living population is vanishingly small. Accordingly, even if the latest securely dated Neanderthal fossils cluster around 35–40 ka cal BP, this need not represent the species' biological endpoint. It is entirely plausible that small, low-density groups persisted beyond that temporal horizon, remaining undetected due to the patchy nature of the fossil record. As Finlayson and Carrión (2007) argue, Neanderthal extinction was likely a gradual, regionally heterogeneous process driven by ecological attrition, rather than abrupt replacement. Ultimately, this highlights the importance of distinguishing between the end of archaeological visibility and true extinction (Finlayson et al., 2023). While archaeological narratives must be grounded in available evidence, we should remain cautious about the often-formulaic assertion that Neanderthals disappeared "around 40,000 years ago"—a statement repeated in countless publications. Robust models of Neanderthal disappearance must acknowledge the statistical and evidentiary limitations of the fossil record, and remain open to regional variability and the possibility of extended survival in marginal landscapes.

Author contributions

Conceptualization, Writing – Original Draft, Writing – Review & Editing: José Carrión, Writing – Original Draft, Writing – Review & Editing, Visualization: Gabriela Amorós, Visualization: Gabriela Amorós, Ariadna Amorós, Writing – Review & Editing, Discussion, Supervision: Ana B. Marín-Arroyo, All authors contributed to the discussion of the illustrations and approved the final version of the manuscript.

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.quascirev.2025.109673.

Data availability

All data and/or code is contained within the submission.

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Supplementary Information

Main taxonomic details for FIGURE 2

Main taxonomic details for FIGURE 3

Main taxonomic details for FIGURE 4

Main taxonomic details for FIGURE 5

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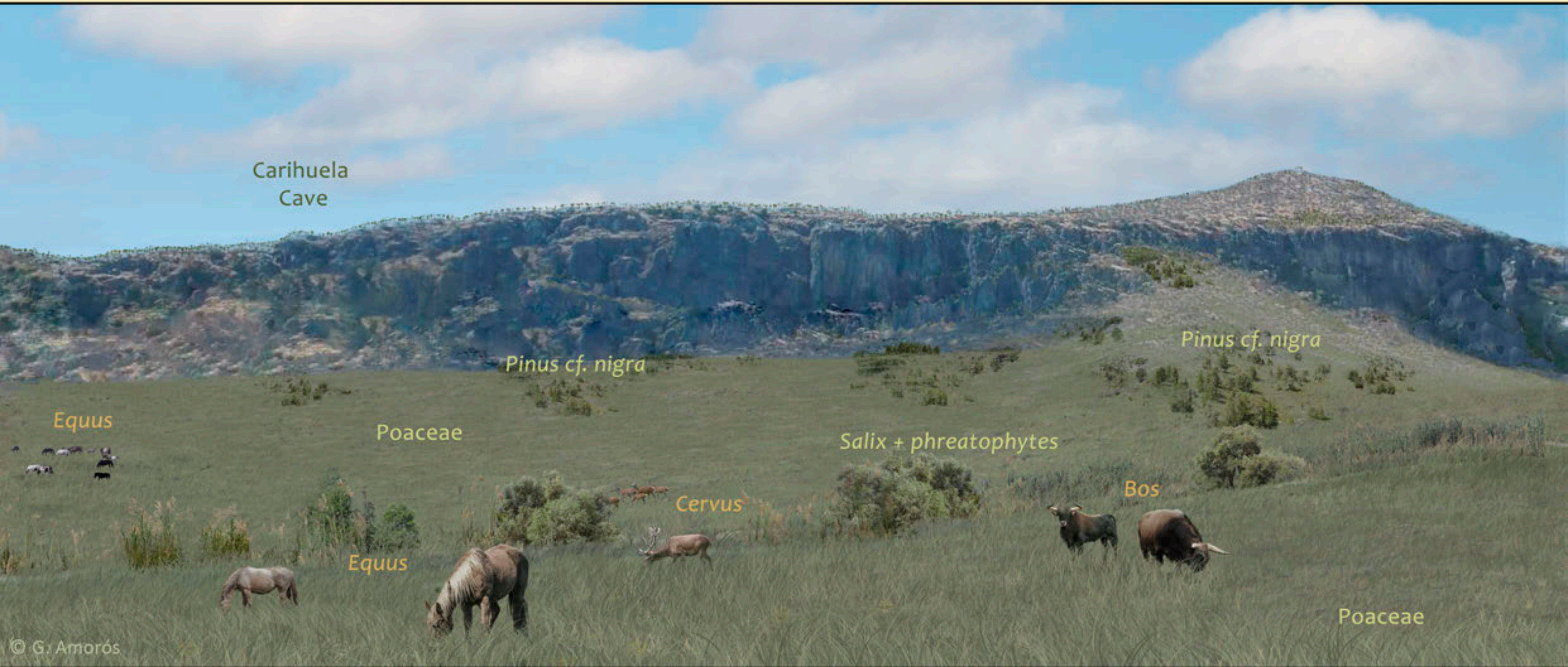
Main taxonomic details for FIGURE 6

Main taxonomic details for FIGURE 7



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Main taxonomic details for FIGURE 8

Main taxonomic details for FIGURE 9