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Welcome to the forest theatre: Unveiling a Balkan refugium through paleoart

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ABSTRACT

This paper presents an artistic paleolandscape experiment based primarily on recent palynological data from the Paleolithic site of Pešturina, in the Central Balkans of Serbia. These data are integrated into the general knowledge of flora and vegetation changes in the Balkans and southern Carpathians obtained through other paleobotanical sequences, especially pollen records from lake sediments. The paleoartistic proposal includes several drawing attempts at different geographic scales with an emphasis on plant taxa and their position within glacial refugia. The contrast with the interglacial situation is also illustrated, but the work especially focuses on the concept of long-term refugia and the altitudinal shifts of steppes, conifers, and broad-leaf trees. An ecological and biogeographical discussion accompanies the illustrations, highlighting the insurmountable methodological limitations and the challenges that pose obstacles to the progress of palynology as a technique for paleoenvironmental reconstruction at the spatial scale. The structure of the paper aims to serve as a guiding example for the teaching and scientific dissemination of paleosciences, from a conservationist perspective that is much needed in the current scenario of global change and biodiversity crisis.

1. “Blindness of plants” in Paleoart

We live in a social context where the visual is conceived as culture. Paleoart can thus develop a cultural project that serves to interpret and depict in images the scientific positions on past life. It does so, on the one hand, by giving rise to aesthetic experiences and, on the other hand, evolutionary icons derived from fossil discoveries. These icons, if the paleoartist works vividly enough, can penetrate popular culture, becoming plausible and familiar (Amorós, 2023). However, it is regrettable that the taxonomic details of the plant landscape have been so systematically disregarded in the history of paleoart, which is clearly zoocentric (Buscalioni, 2016; Lescaze and Ford, 2017). In fact, the botanical approach constitutes only a few exceptions, which, moreover, date back to the works of illustrators from the 18th and 19th centuries (e.g., Unger, 1851; Ludwig, 1861; Figuier, 1872; Bressan, 2012).

Hence, the history of plants resembles a silent narrative, often overlooked in the predominantly zoocentric field of paleontology. According to Vujakovic (2019), one of the reasons, if not the most important one, for the "blindness of plants" seems to be their static nature, the lack of animation, and the apparent movement of the plant world, which has led to a rejection of the global narrative about prehistory. Representations, both iconographic and cinematographic, have traditionally focused on preserving living beings with which we could move ourselves in the realm of human emotions. Given all of the above,

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the history of the vegetational landscape will always contain essential information for reconstructing past ecosystems, so artistic representation with attention to plants is a fundamental and indicative task of the main events of geobiological history and, ultimately, of our origin and evolution.

2. More blind spots: Pollen diagrams

Metaphorically, we might still consider an additional blind spot when it comes to using the palynological method. This visual deficit arises from the conjunction of two obstacles. The first is that palynologists have long understood from their foundational principles that pollen spectra are not particularly designed to geolocate the populations of

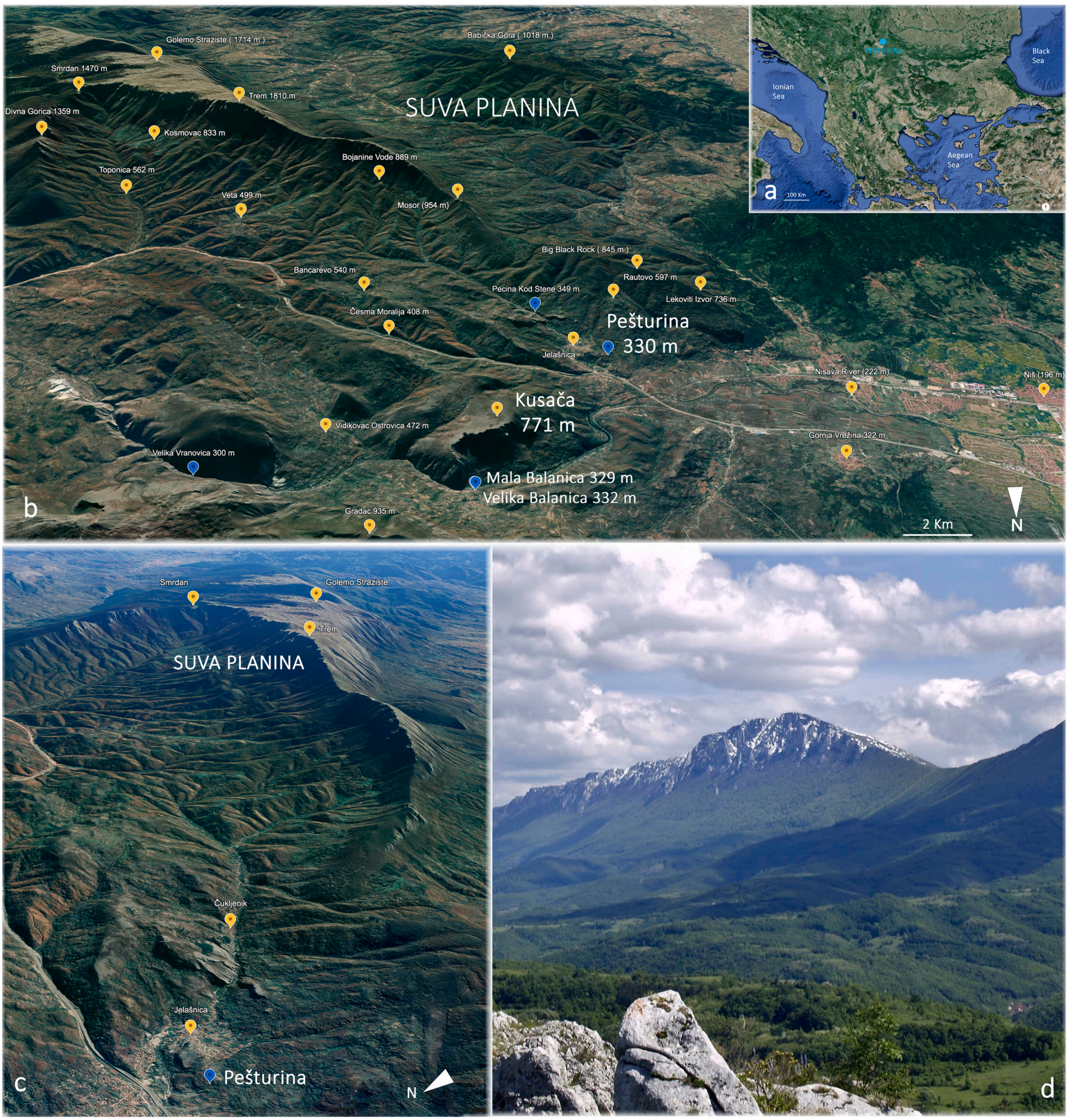

Fig. 1. a. Position of Pešturina in the Balkan Peninsula (Google Earth 10.52.0.0 2023, retrieved April 12, 2024). **b.** Physical setting of Pešturina, in the context of other archaeological sites (blue), Nišava Valley, Suva Planina range, Mount Kusača and other prominent peaks in the surrounding mountains (Google Earth 10.52.0.0, 2023, retrieved March 20, 2024, tilt 65%). **c.** Enlarged and rotated perspective (tilt 70%) to the north of the previous image showing the location of Pešturina looking towards the amphitheatre of Suva Planina **d.** View of the Suva Mountain from the highest peak of the Jelašnička Klisura, Radovanjski Kamen (580 m). Photo by: Una Marinković, Niš, May 12, 2014. Source: *Wikimedia Commons*. Retrieved 15:55, April 1, 2024 from https://commons.wikimedia.org/w/index.php?title=File:Suva_planina_UM.jpg&oldid=477550250.

pollen-producing plants (Ritchie, 1986). Thus, any attempt to spatially arrange these spectra will inherently contain a significant degree of ecological actualism (Anderson et al., 1989; Romano, 2018). In theory, by correcting the biases of pollen production, dispersal, transport, and preservation, the palynological abundance of each taxon would enable the estimation of its abundance in the vegetation, especially if an additional record of macrofossils is available or there is a high density of pollen records in the study region (Birks, 1989, 1993; Fyfe et al., 2015; Giesecke et al., 2019; Liu et al., 2022). However, in practice, this scenario is exceedingly rare outside the temperate latitudes of the Northern Hemisphere (https://www.neotomadb.org/). In the absence of spatial models of pollen-vegetation relationships applicable to a broader geographic cohort, and given the temporal impermanence of plant species communities during the Quaternary (Davis, 1981; Birks, 2023), we must rely on general knowledge about the geological affinities of plant species, which, in any case, are traits forged over deep time and, therefore, relatively stable and reliable (Carrión, 2003).

The second obstacle lies in the representation of the results: the pollen diagram. This is not visually intuitive for the layperson, and it also does not provide precise geographic information. In summary, producing an artistic work placing the identified taxa and their abundances in a paleolandscape framework is akin to cataract surgery, with its obvious advantages and hidden "iatrogenesis" (harmful complication of medical activity). The advantages relate to the suitability for democratizing science (Amorós, 2023). The hazards would come with the temptation to slide from the confidence of scientific data to the liberty of speculation. It is, therefore, essential to delineate which aspects of the artistic endeavor stem from assumptions grounded in certain principles.

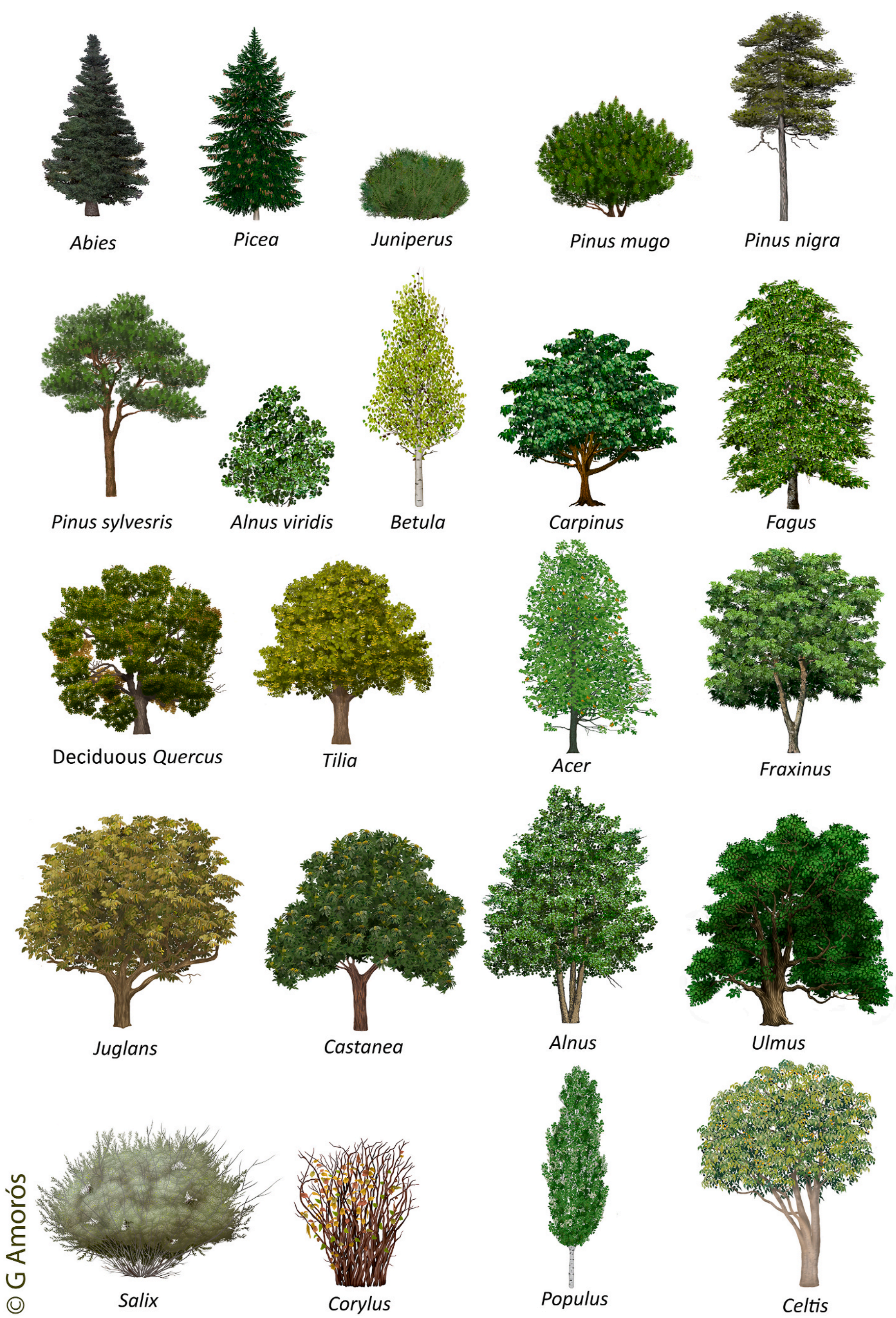

Fig. 2. Original digitised drawings depicting the primary taxa of the paleoartistic reconstruction are displayed in Figs. 4–7 (part 1).

3. Goal and scientific source

With this creative spirit and identical precautions, we follow here the trail of some recent papers (Amorós et al., 2021; Carrión et al., 2024) addressing an exercise of paleolandscape art that draws its main source of information from the recent work of Ochando et al. (2024), who have reported pollen analyses of cave infill and hyena coprolites from Pešturina Cave in the Central Balkans of southeastern Serbia (Fig. 1). Methodological details on the artwork can be found in Amorós et al. (2021) (Figs. 2–7) while Ochando et al. (2024) document the floristic composition and vegetation changes during the MIS 5-MIS 3 period. Both in sediment and coprolites, the pollen spectra of Pešturina for a section of the last interglacial (MIS 5) suggest a forest environment with a predominance of deciduous *Quercus* and *Pinus*, and a wide diversity of tree taxa, among which *Tilia* appears as unusually abundant. Overall, the glacial phases (MIS 4-3) show a more open vegetation landscape with lower arboreal cover, but with the same floristic composition (Figs. 4 and 5). Even here, the frequency and diversity of broad-leaf trees are notable, as well as the more sclerophyllous component of Mediterranean affinity. Ochando et al. (2024)′ study includes pollen analysis of 23 stratigraphically controlled sediment samples and 16 samples of *Crocuta* coprolites, 83 palynological types, the counting of a total of 8840 palynomorphs, including 8203 pollen grains and 637 spores. Pollen preservation was relatively good, and the percentage of indeterminate palynomorphs was always less than 7%. We refer to the original paper for further details.

Ochando et al. (2024) is complemented by information from other proxies from the Balkan Peninsula. Among these we could mention Lake Ioannina (Tzedakis et al., 2002), Tenaghi Philippon (Tzedakis et al., 2006; Wulf et al., 2018), Lake Orhid (Sadori et al., 2016; Sinopoli et al., 2019; Wagner et al., 2019; Brechbühl et al., 2024), Lake Prespa (Panagiotopoulos et al., 2014), Lake Dojran (Masi et al., 2018), and Lake Kopais (Okuda et al., 2001; Lang et al., 2023). For the purpose of artwork, these investigations bolster the floristic findings and inferred

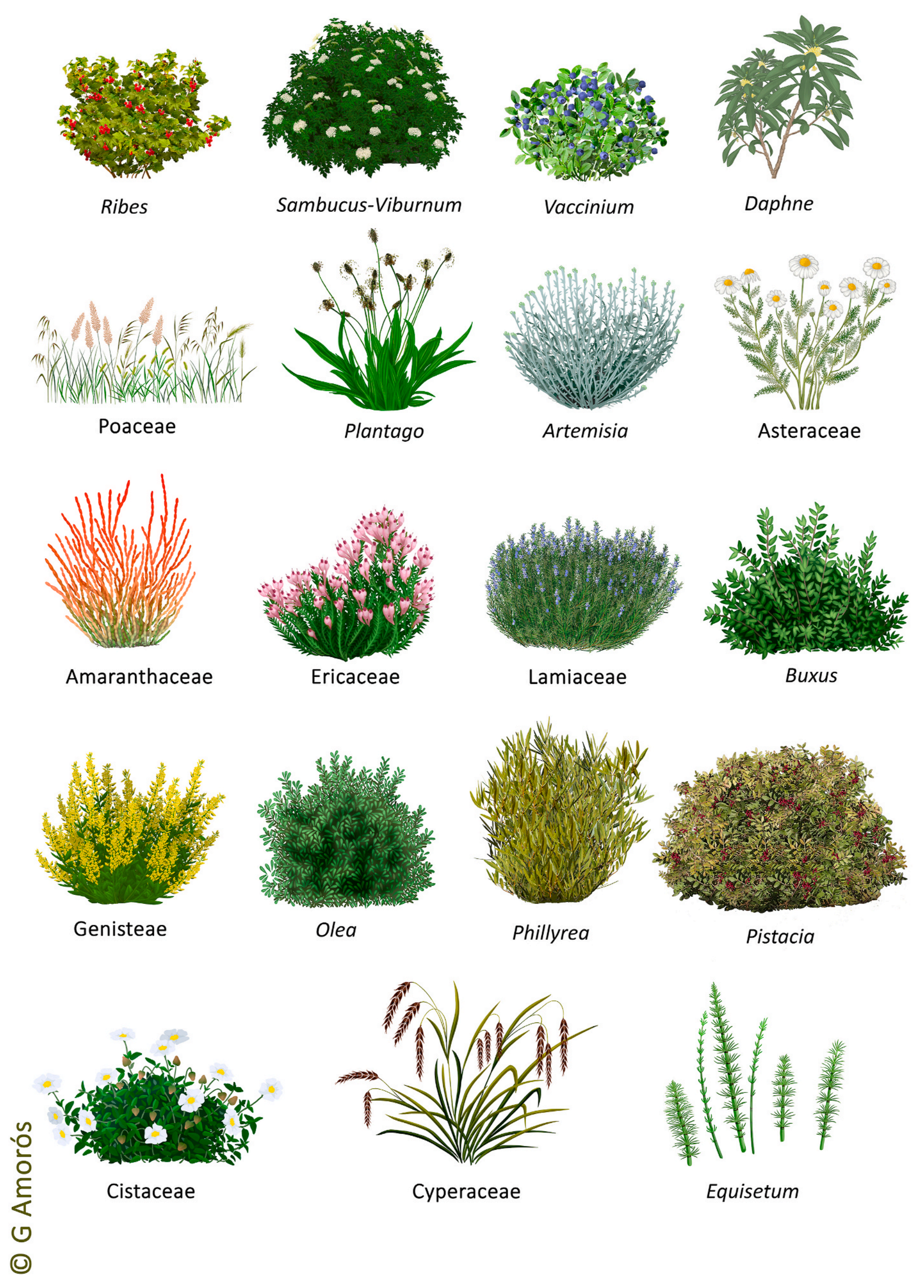

Fig. 3. Original digitised drawings depicting the primary taxa of the paleoartistic reconstruction are displayed in Figs. 4–7 (part 2).

Fig. 4. Artistic paleo-reconstruction of vegetation during the last Interglacial (MIS 5) in a mountain with an altitude close to 1700–2000 m in the Central Balkans. The alder on the right symbolizes the general dominance of angiosperm forests during the warm and humid phases of the Pleistocene. The upper altitudinal zone is dominated by herbaceous and shrubby plants with cushion stands of *Pinus mugo, Juniperus*, and *Alnus viridis*. The zone marking the treeline is dominated by conifers, especially *Pinus sylvestris, P. nigra, Abies, Picea*, and *Juniperus*, along with *Betula, Carpinus*, and *Fagus*. The highest concentration of trees is found in the mixed forests dominated by oaks with a wide diversity of deciduous trees and heliophytes in areas cleared by the nature of the substrate (lithosols) or herbivory, where moist grasslands would prevail and Mediterranean elements (e.g., *Pistacia, Olea,* Cistaceae) would be present.

Fig. 5. Artistic paleo-reconstruction of vegetation during a glacial phase in the MIS 4-3 interval in a comparative context with Fig. 4. The pine (*Pinus nigra*) on the right symbolizes the importance of gymnosperms during these generally cold and arid episodes in the Balkans. There is no reduction in plant diversity compared to the warm phase (Fig. 4), but the vegetation belts are compressed due to the climatically inhospitable nature of both the highlands (periglacial environments with tundra-like vegetation) and the lowlands (aridity, steppes-dominated by *Artemisia*). Conifers, including *P. mugo* and beeches and firs, have descended to mid-altitudes, even into the valleys. The refugia are situated at mid-altitudes, favored by the microclimate with less thermic contrast and the influence of orographic rainfall.

Fig. 6. Reconstruction of glacial-phase paleovegetation in an area of Mount Kusača (771 m, a few kilometers from Pešturina) on the north-northwest slope. With the observer facing south-southeast, we propose an image of what Mala Balanica and Velika Balanica inhabitants might have seen near the cave entrances. The presence of linden trees in the foreground indicates the unusual local abundance suggested by the pollen spectra from Pešturina (Ochando et al., 2024). Although the foreground features deciduous trees, and shade-tolerant shrubs (e.g., *Daphne*), the abundance of conifers is evident in the distance.

Fig. 7. Reconstruction of glacial paleovegetation on the northern slope of Mount Kusača (771 m) from a broader perspective than Fig. 6. Note the predominance of deciduous trees in the lowest elevations.

palaeoecosystem patterns of Pešturina. Furthermore, these pollen records provide confidence by incorporating taxa absent in the Pešturina cave record, such as *Picea abies*. A common observation in these lake and peat sequences is the presence of fluctuations during glacial phases. These fluctuations alternate between open steppe formations, conifer communities featuring *Pinus, Abies*, and *Picea*, and environments dominated by mixed forests containing *Abies, Fagus, Pinus, Betula, Alnus, Corylus, Quercus, Tilia, Ulmus, Acer, Salix,* and *Juglans,* among others. Notably, even during the most open landscape stages, characterized by the coldest and driest conditions, the presence of trees remains continuous.

4. Pollen catchment and taphonomy

In the case of Pešturina Cave (43°17′42'' N, 22°02′48'' E, 330 m a.s.l.), it is probable that there is a predominant pollen influx from the Nišava River valley (with the cave entrance facing west), the Niš Basin, and a network of small depressions, hills, and ravines that extend southeastward towards the expansive amphitheater of Suva Planina Mountain, whose impact on the pollen deposition should also be considered (Fig. 1b–d). This geographical context encompasses other Paleolithic sites: Pećina kod stene to the southeast and Mala Balanica and Velika Balanica near Sićevo Gorge to the north. These archaeological sites are encircled by medium-altitude mountains, including notable peaks such as Kusača (771 m), Lekoviti Izvor (736 m), Rautovo (597 m), and Big Black Rock (845 m) (Fig. 1b).

In cave palynology, there is a distinction in the pollen catchment area between sediment and coprolites. Ochando et al. (2024) observed greater variability in the inferred landscape mosaic from coprolite data, likely due to differing pollen taphonomy. When dealing with entrance facies in large cavities, such as in this instance, models suggest that airborne pollen deposited in cave sediment can originate from a radius of tens of kilometers, with a prevailing local component (Navarro et al., 2000, 2001a, 2001b, 2002; Carrión, 2002a; Ermolli et al., 2022). It is noteworthy that sampling in Pešturina encompassed the entrance area (Ochando et al., 2024) because wind-pollinated species representation diminishes with distance into cave of simple morphology (Prieto and Carrión, 1999; Navarro et al., 2002; Hunt and Fiacconi, 2018). Some cave studies have identified a clear regional flora signal in sediment pollen spectra (e.g., Carrión et al., 1999; Messager et al., 2011; Burjachs et al., 2012; Revelles et al., 2016). For hyena coprolites, the radius has been estimated at no more than 50 km, often exceeding 15 km (Scott et al., 2003; Argant, 2004; Carrión et al., 2007, 2018). Taphonomic disparities are even more pronounced between pollen records in caves and those from conventional deposits (lakes, peat bogs) or marine sediments. In these latter cases, anemophilous taxa dominate the pollen spectra, offering a relatively reliable depiction of vegetation in temperate biomes, but less so in tropical, subtropical, desert, or Mediterranean environments, where vegetation may be characterized or dominated by zoophilous plants (Horowitz, 1992; Carrión, 2002a).

In the Balkans, where anemophilous tree species are abundant, the study of lacustrine palynology is crucial for reconstructing Quaternary vegetation dynamics (Lang et al., 2023). However, certain species exhibit limited pollen dispersal abilities, regardless of their primary pollination vectors. Examples include walnut (Carrión and Sánchez-Gómez, 1992), alder (Mudie and McCarthy, 1994), lime (Andersen, 1970), and fir (Poska and Pidek, 2010). Conversely, some species rely entirely, partially, or occasionally on insect pollination, such as *Acer campestre, Sambucus, Viburnum, Tilia, Salix, Fraxinus, Ilex, Myrtus*, Genisteae, and *Buxus* (Heim, 1970; Gutiérrez-González, 2008; van der Pijl, 2012). In sediments predominantly composed of airborne pollen and transported via aquatic means, strictly entomophilous pollen types are seldom encountered (Carrión et al., 2022). Therefore, it is noteworthy to underscore the agreement between data obtained from sediment and coprolites at Pešturina (Ochando et al., 2024), as described in previous studies (e.g., Scott, 1987; Horwitz and Goldberg, 1989; Carrión et al., 2004; Gatta et al., 2016; Djamali et al., 2020; Ochando et al., 2020). Indeed, to accurately depict both zoophilous and anemophilous plant species, integrating information from cave pollen sequences and conventional deposits is essential. Additionally, the presence of taxa with limited pollen dispersal in Pešturina can be interpreted as indicative of local presence or even local abundance.

5. The eye-catching power of the Balkans (for paleoartistic exploration)

Given that paleoart is particularly time-consuming in its production, it is often imperative to select the sources of inspiration and pictorial purposes; what concepts, or findings are intended to be visualized, and what are the dissemination, educational, or research objectives (Amorós, 2023). Thus, for artistic drive, the Balkan Peninsula presents itself as a seductive setting due to its undisputed role as a bastion of European biodiversity, likely in coherence with its turbulent geotectonic heritage, and great physiographic heterogeneity (Španiel and Rešetnik, 2022). It is also so due to its high endemism levels within the Mediterranean Basin's hotspot (Stevanović et al., 2007; Ranđelović et al., 2008; Matevski et al., 2021). It should be noted that the floristic history of Europe during the Neogene underwent significant taxonomic amputation, with substantial extinction rates during the Pleistocene (Svenning, 2003; Carrión and Fernández, 2009; Magri et al., 2017; Behre and van der Knaap, 2023).

With this background, and considering the expected shifts in species distribution boundaries with Quaternary climate changes, the new sequence from Pešturina stands as phytogeographic sensor at a crossroads between what are now the Pannonian, Alpine, Continental, and to a lesser extent, Mediterranean regions. Paleoecological studies to which Ochando et al. (2024) now add, suggest that the region has been a long-term refugium for temperate trees over the Quaternary and a corridor for faunal and floral exchange with Central Europe and Western Asia (Bennett et al., 1991; Willis, 1994; Tzedakis et al., 2003, 2006; Griffiths et al., 2004; Magri, 2010; Tonkov et al., 2014; Pross et al., 2015; Sadori et al., 2016; Magri et al., 2006, 2017; Zhelev, 2017; Donders et al., 2021; Lang et al., 2023). Intriguingly, the latitudinal position of Pešturina (43°N) is so northern, lying close to colder mountain ranges such as the Carpathians: the presence of relatively cool interglacial conditions could promote the survival of cold-adapted plants between glacial phases (Donders et al., 2021). This stronghold role is supported by genetic diversity studies, which is higher here than elsewhere in Europe (Gómez and Lunt, 2007; Gömöri et al., 2020).

Another catalyst for artwork stems from the fact that the Central Balkans contain an indispensable paleoanthropological and archaeological record for understanding *Homo* evolution and biogeography in Eurasia (Mihailović, 2009, 2020; Roksandic et al., 2011, 2018, 2022; Mihailović et al., 2011, 2022a, 2022b; Marín-Arroyo, 2014; Harvati and Roksandic, 2017; Marín-Arroyo and Mihailović, 2017; Alex et al., 2019; Dogandžić, 2023; Marín-Arroyo et al., 2023). In particular, Pešturina Cave includes Neanderthal and Anatomically Modern Humans fossils, lithic artifacts, and faunal remains, allowing to identify a stratigraphic sequence that includes the Late Pleistocene and Holocene (Mihailović et al., 2022a).

6. Long-term Refugia for scientific outreach

The concept of glacial refugium (Hewitt, 1996, 2000; Comes and Kadereit, 1998), despite its ambiguities and a plethora of terms, such as macrorefugia, microrefugia, paleorefugia, neorefugia, *in situ* refugia, *ex situ* refugia, nunatak, and peripheral (Cruzan and Templeton, 2000; Gómez and Lunt, 2007; Bennett and Provan, 2008; Birks and Willis, 2008; Svenning et al., 2008; Rull, 2009; Stewart et al., 2010; Nieto Feliner, 2011), holds significant educational value. It implies the existence of a specific territory that has served as a refuge for species under abiotic stress conditions for tens or hundreds of thousands of years, and even millions, while also acting as an evolutionary laboratory for complex ecological networks (Thompson, 2005; Stewart et al., 2010; Carrión et al., 2011; Dufresnes et al., 2020). Following Stewart et al. (2010) Tzedakis et al. (2013), we find it useful to use the term "long-term refugia" for cases like the Balkans, where a significant volume of taxonomic and ecological persistence has been demonstrated over multiple Quaternary glacial cycles, extending back into the Tertiary period. This territory has maintained enough biogeographical and evolutionary elasticity to prevent the extinction of its occupying species, making it a priority for conservation efforts (Carrión, 2003; Vajana et al., 2024).

Not coincidentally, as detailed by Birks (2023), one of the "singularities" of the Quaternary is the evolutionary stasis of plants, both at the genealogical and adaptive levels. In this sense, the presence of long-term refugia may have been decisive, as the genetic changes accumulated through geographic isolation, while generating neoendemisms, infraspecific taxa, or adaptations, may not have been sufficient to provoke a phenotypic or genetic disparity leading to the emergence of new species. Conversely, the changes during glacials would gradually dilute after each population regrouping during interstadials and interglacials (Bennett, 1997). The significance of the Balkan Peninsula in this complex ecological and evolutionary scenario is of such magnitude that it has attained a prominent role in the Rewilding Europe initiative (https://rewildingeurope.com/). Given all the above, translating the prehistoric plant landscape of the Balkans into artistic form presents a unique opportunity for scientific outreach, with social value lying in its potential to inspire future naturalist vocations amidst the urgent need to address global ecological degradation (Williams et al., 2021).

7. Mountain belts in full-glacial times

In our visual interpretation of a mountain refugium during a glacial phase, we conceive that along the slopes, the vegetation belts would compress due to the severe cold at higher altitudes and the arid conditions below (Carrión, 2002b) (Figs. 4 and 5). Glacial, periglacial, and permanent snow environments would leave less forested territory available in the high mountains, but there would also be limitations for tree life in some of the lower areas, as they would be more exposed to general aridity. Although around 60% of the Balkan region is above 1000 m a.s.l. (Willis, 1994), we know that there were extensive low-lying areas occupied by xerophytic steppes and semideserts with *Artemisia*, Amaranthaceae, Asteraceae, Poaceae, and other shrubs and herbs, while tundra-like vegetation would dominate the higher altitudes (Birks and Willis, 2008; Masi et al., 2018; Gömöri et al., 2020; Ochando et al., 2024) (Figs. 5 and 8). Paleobotanical information from the high-elevation sites also suggests that *Artemisia* was part of the alpine meadows in the Balkans (Donders et al., 2021), Carpathians (Magyari et al., 2018) and southern slopes of the Alps (Boltshauser-Kaltenrieder and Tinner, 2024). There are not many species of *Artemisia* that behave as orophytes, but there are still some in southern Europe, such as *Artemisia atrata, A. umbelliformis*, or *A. eriantha* (Roskov et al., 2018). Modern analogues for this cold-adapted, *Artemisia*-dominated communities have been suggested in the intermountain systems of the Altai-Sayan-Mongolian border (Magyari et al., 2014; Makunina, 2016).

Establishing with scientific rigor the altitudinal limit of each species, genus, or plant community in the study area is not possible with the

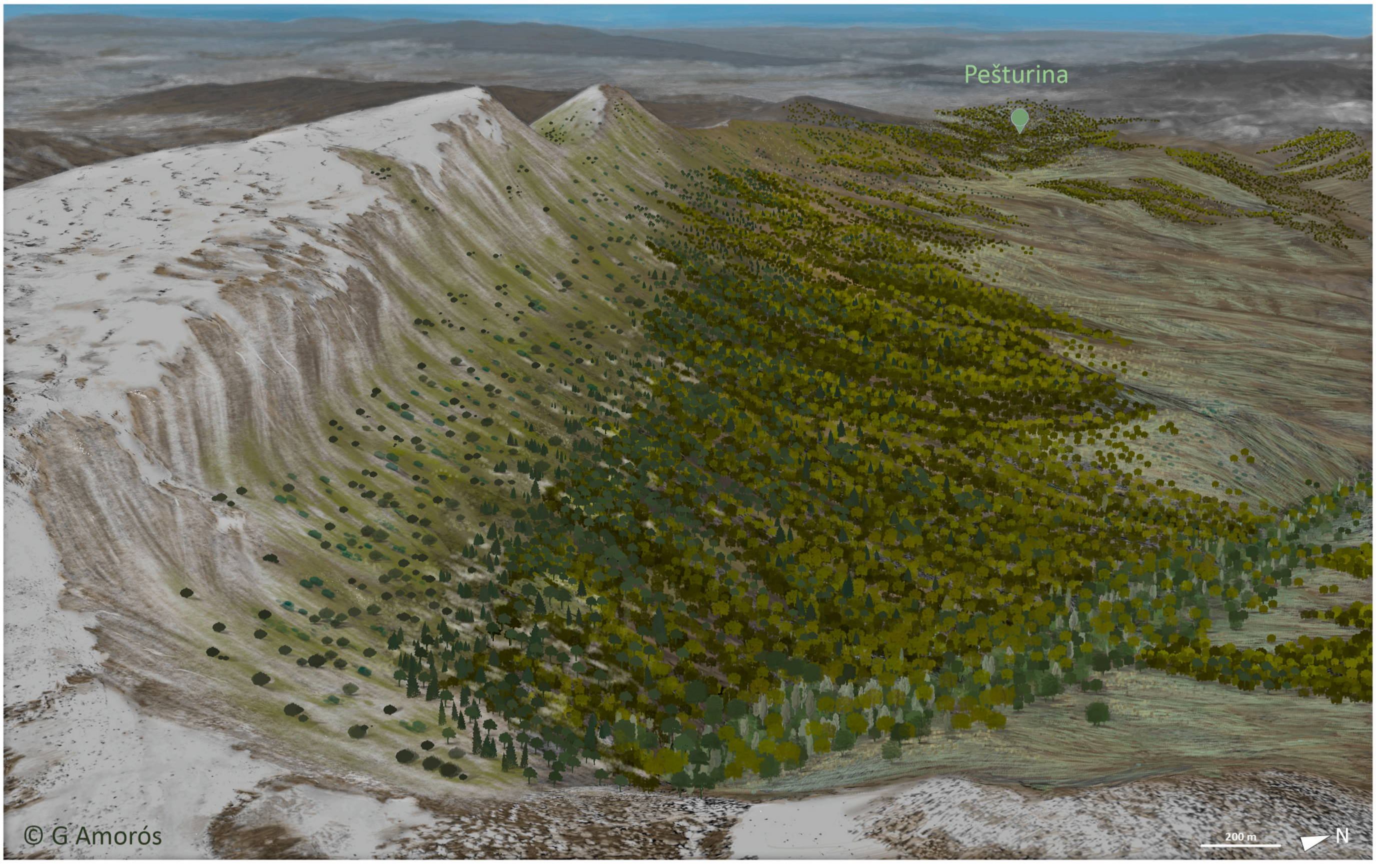

Fig. 8. Vegetation paleolandscape reconstruction of Suva Planina during a glacial phase (MIS 4-3) based on paleobotanical literature from the Balkans, with emphasis on data from Ochando et al. (2024) for Pešturina, located to the west-northwest. Vegetated environments would be below the periglacial summits. We postulate that between approximately 600 and 900 m a.s.l., there would be a mix of broadleaf forest (light green) and needleleaf forest (dark green, except for junipers at higher altitudes), including in the latter both *Pinus mugo* and *P. sylvestris* and *P. nigra*. Only coniferous forests would be found above about 900 m a.s.l., along with *Abies, Picea* (triangular profiles), and perhaps the presence of *Betula*. Between 900 and 1200–1300 m a.s.l., we would mostly find scattered populations of *Pinus mugo* (dark shrubs at the upper level), possibly as the last arboreal element alongside *Juniperus communis*. The cold-adapted conifers would descend to mid and low altitudes during glacial phases. The lower slopes would feature a competitive scenario between forests on one hand, and xerophytic steppes with grasses, *Artemisia*, Asteraceae, Amaranthaceae, and other shrubs (grayish and reddish areas on the right) on the other. This mosaic-like environmental context would characterize the vicinity of the archaeological sites of Pešturina, Mala Balanica, and Velika Balanica, with forests in the mountains and open formations on the plateaus, denuded ravines, and lithosols. Gallery forests with phreatophytes (whitish green) and deciduous trees would be found along river edges. This visual experiment uses a Google Earth snapshot from the northeastern summits above the Golemo Stražište peak (1714 m). In general, the Balkan refugia at these latitudes must have been located in sheltered positions and mid-altitudes of mountains with favorable microclimates, being small in extent but sufficiently dense to enable long-term survival through sufficiently high population sizes.

available information, and we can only make some inferences from Balkan records and those of nearby regions, typically limited to the end of the Last Glacial Maximum (LGM) and especially the Late Glacial period (Fig. 8). The data, in any case, are inconclusive. Although most of the Balkan Peninsula was free of glaciation during the Quaternary, evidence at high altitudes is now common above 2100 m a.s.l. Cirques and moraines have been described from c. 2900 to 1800 m a.s.l., and at least 16 small glaciers still exist in the mountains of the Balkan Peninsula, with the current position of the climatic snow line between 2700 m in the Western Balkans and 3200 m in the Eastern Balkans (Gachev, 2016). It is worth noting that unlike the Alps or the mountains of Turkey and Lebanon, where glaciers reached their maximum extent during the LGM, in the Balkans, this occurred during MIS 12 and MIS 6 (Leontaritis et al., 2020). During the LGM, only the highest elevations of the Balkans and Carpathians were glaciated, with data suggesting that the mean temperature in July was approximately 5 °C lower than today, while the snow line could be up to 1000 m lower (Bognar and Prugovečki, 1997; Španiel and Rešetnik, 2022). In Croatia, the snow limit during glacial phases was around 1150 m a.s.l. in the Risnjak Mountains (1528 m) and 1500 m a.s.l. in the Velebit Mountains (1757 m) (Bognar and Prugovečki, 1997).

Vincze et al. (2017) and Orbán et al. (2018) have reported macro- and microfossils of *Pinus mugo, P. cembra, Picea abies*, and *Juniperus communis* around 1700–1900 m a.s.l. during the Late Glacial period in the Retezat Mountains, southern Carpathians of Romania. Still in the Carpathian Late Glacial, palaeobotanical records from Taul dintre Brazi (1740 m) and Lacul Galeş (2040 m) suggest an uppermost timberline at 1750–1800 m a.s.l. (Magyari et al., 2012). We infer that *Pinus mugo* stands should be located at 1700–1800 m a.s.l. during glacial stages, or even lower (Fig. 5). Below the mugo-juniper grassland zone, the coniferous and deciduous forest belts would stratify and interconnect in mid-altitude areas, where there would be greater orographic precipitation and simultaneously the highest biodiversity peaks (Bennett et al., 1991; Zhelev, 2017). The Lake Prespa basin, situated at an elevation of 849 m a.s.l., maintained temperate tree communities during the last glacial period (Panagiotopoulos et al., 2014). However, the sporadic occurrence and notably low pollen counts of certain drought-sensitive taxa, including *Fagus, Ulmus*, and *Tilia*, from MIS 4 to MIS 2, suggest that environmental conditions posed challenges for growth at such high altitudes. Panagiotopoulos et al. (2014) postulated that the current location of Lake Prespa could therefore mark an upper boundary for the distribution of mesophilous trees at these latitudes in the Balkans.

Regarding the lower forest limit, it might have been diffuse (Figs. 5 and 8). It is clear from the data of Pešturina that there were populations of deciduous trees and mesothermic scrub at around 400-200 m a.s.l. However, during MIS 4-3, there is also an abundance of xerophytes such as *Artemisia*, Amaranthaceae, Asteraceae, Lamiaceae, and several other shrubs and herbs (Ochando et al., 2024), suggesting a mosaic landscape with heliophytic grassland-steppe, mixed forest, and riparian gallery forest (*Fraxinus, Populus, Salix, Ulmus, Alnus*).

8. High-altitude interglacial strongholds: Conifers matter

The cold stadials of the Pleistocene, with their extended temporal duration, have presented opportunities for species that had "refuged" in high mountains during interglacial periods (Fig. 4). The paleobotanical data presented here suggest that the generalization of high mountain conditions in lower areas would enable the downward displacement of conifers and the merging of populations, resulting in the dilution of previously accumulated genetic disparity. In our record, this could affect conifers near the modern treeline such as *Pinus mugo, Pinus sylvestris, Pinus nigra, Abies alba, Picea abies,* and xerocryophilous species of *Juniperus* (Fig. 4). A well-documented example comes from the macrofossils of various conifer species identified during the LGM in the Carpathians at altitudes of approximately 600 m (Obidowicz, 1996). Although pollen of *Pinus mugo* is mostly indistinguishable from that of *P. sylvestris*, the high percentages of *Pinus* pollen categorized as "sylvestris" or "diploxylon" type have frequently been interpreted as evidence of *P. mugo* presence in regions beyond the geographical range of *P. sylvestris* (Ali et al., 2006). This suggests a broader distribution of *P. mugo* during cold Pleistocene periods, similar to the proposed distribution of the closely related *P. uncinata* in the Iberian Peninsula (Benito Garzón et al., 2007). This phenomenon of glacial expansion of cold-adapted conifers is well-documented (Willis, 1994; Cheddadi et al., 2009; Alba-Sánchez et al., 2010; Di Pasquale et al., 2020). Interglacial periods would have resulted in population fragmentation and genetic differentiation for these cold-adapted conifers, similar to how glacial phases affect temperate trees and Mediterranean scrub species (Rodríguez-Sánchez et al., 2010; González-Hernández et al., 2022). Over the past millennia, much of the Mediterranean Basin's mountains have acted as climatic refuges for many plant species, not only due to climatic determinism but also because high-altitude areas have been less impacted by human activity (López-Tirado and Hidalgo, 2014). What is at stake is the extinction of the species (González-Sampériz et al., 2010; Magri et al., 2017). It is well known that the Quaternary survival of a species in the European continent has depended on both its glacial persistence, sometimes under population fragmentation, and interglacial survival (Bennett, 1997; Carrión, 2003), lately under the disruptive influence of human activities (Alba-Sánchez et al., 2018).

Indeed, it is true that many conifers have limited interglacial distribution due to their lack of competitiveness against broad-leaved species at mid-altitudes where abiotic stress is reduced. However, it is important to avoid over-generalization. The idea of the widespread ecological subordination of gymnosperms to angiosperms is part of an old paradigm in evolutionary botany and forest ecology (Arber and Parkin, 1907; Bond, 1989) that, although fading in scientific forums throughout the 20th century (Meeuse, 1987; Becker, 2000; Carrión, 2003; Brodribb et al., 2012), still seems to underlie the collective subconscious of much of the scientific community. This notion may have arisen when it became reported that the radiation of flowering plants during the Cretaceous led to a decrease in the diversity and abundance of gymnosperms (Lidgard and Crane, 1988). Conifers are undoubtedly magnificent at occupying disturbed habitats, but they do not necessarily have to be competitively inferior under more stable edaphoclimatic conditions. For example, over ecological time, in mature stands (home-field advantage), pine forests can be very resilient, suppressing the growth of neighbouring angiosperms (Coates et al., 2009). In paleoecological time, there is evidence that pine forests, even at low altitudes and occupying deep soils, prove to be extremely inertial on centennial to millennial scales, being displaced by oak-dominated forests after disturbance phenomena such as fire (Carrión and van Geel, 1999; Carrión et al., 2000). The ecological and evolutionary history is crucial in this regard, and we must not forget that the gymnosperms displaced at the end of the Cretaceous are not the same species as those existing today. In this sense, our artistic work advocates for the coexistence of conifers with broad-leaved species in the Balkans, especially during cold phases (Figs. 5–8).

9. Strolling through the Paleolithic of Kusača

We have chosen Mount Kusača (771 m) here to artistically project the paleobotanical findings of Ochando et al. (2024) as it lies between Pešturina and other significant Paleolithic sites in the region, such as Mala Balanica and Velika Balanica (Fig. 1). It is highly likely that the inhabitants of these caves frequented these environments. Today, this mountain is on the northwestern edge of Suva Planina and has little altitudinal stratification in vegetation today, which is mainly forested and dominated by *Quercus cerris, Quercus frainetto, Quercus robur, Quercus petraea, Quercus polycarpa*, and *Carpinus betulus*. The main accompanying tree species are *Fagus sylvatica, Ulmus minor, Ulmus glabra, Prunus avium, Acer campestre, Acer platanoides, Acer pseudoplatanus, Tilia tomentosa, Tilia cordata, Fraxinus excelsior*, and *Juglans regia*. Among the shrubby plants are *Corylus avellana, Corylus colurna, Crataegus monogyna, Prunus spinosa, Frangula alnus, Cornus sanguinea, Cornus mas, Lonicera caprifolium, Sambucus nigra*, and *Viburnum tinus*.

Two perspectives have been drawn for the northern slope of Kusača (Figs. 6 and 7). In both cases, we consider it to be a glacial or stadial situation, with conifers having descended considerably from their position in interglacial phases. However, the differences in vegetation between climatic phases at these altitudes should not have been pronounced given the refuge nature of this territory. We, therefore, emphasize the abundance of deciduous and phreatophytic species in the hollows and the prevalence of mixed forests on the slopes, highlighting oaks and beeches.

10. A Bird's-Eye refugium: Suva Planina

Suva Planina is a renowned massif within the Serbian Balkans (Fig. 1b–d). The mountain topography is rugged and although there is localized bedrock diversity, limestones prevail. The chain stretches for about 45 km in length and 12 km in width, oriented northwest-southeast, separating the valleys of Sićevo (northeast) and Zaplanje (east) and covering approximately 250 km^2 with a height difference ranging from 250 to 1810 m. The northern face of the mountain exhibits pronounced karst features. Since 2015, an area of 181 km^2 within Suva Planina has been designated as a Special Nature Reserve, part of the EMERALD Network, and recognized as a Geoheritage Site of Serbia (Decree on the Preliminary Protection of 'Suva Planina', 2008). The highest protection levels are concentrated on the summits ranging from Mosor (985 m) to the highest peak, Trem (1810 m), and Golemo Stražište (1714 m) (Fig. 1).

Indeed, Suva Planina holds immense appeal for any naturalist. Around 1261 plant species (6 gymnosperms, 1232 angiosperms, 3 lycopods, 4 horsetails, 18 ferns), including 128 endemics, have been documented on Suva Planina, representing more than one-third of the Serbian flora (Tutin et al., 1964–1980; Jovanović, 1980). High mountain pastures and deciduous forests of oaks and beech are widespread, while the coniferous forest belt (*Abies alba, Picea abies, Pinus nigra, P. sylvestris, P. mugo*) culminates with a zone of mugo pine. Animal species include 259 species of insects, 14 species of amphibians and reptiles, 13 species of fish, 139 species of birds, and 25 species of mammals. Among these are the golden eagle, European snow vole, wolf, roe deer, and wild boar, among others (Special Nature Reserve Suva Planina, Institute for Nature Conservation of Serbia: https://zzps.rs/). Although snowfall is frequent during winters, the inner valleys provide microclimates protected from wind and cold fronts. Notably, vineyards and other mesothermic species are successfully cultivated, alongside extensive livestock activities (Jarić et al., 2015).

Suva Planina, as discussed above, falls within the expected pollen catchment area of Pešturina. The morphology of this mountain, with its inner valleys open to the Nisava valley, would facilitate the SW-NE movement of descending atmospheric currents, bringing pollen from different vegetation belts to the cave (Fig. 1c). Although uncertainties are inevitable and their delineation requires considerable analytical effort (Jackson, 2012), there is a substantial body of research on pollen-vegetation relationships that supports this dynamic of dispersion in similar heterogeneous landscapes (Liu et al., 2022). Therefore, we selected Suva Planina for a visual experiment using a *Google Earth* snapshot from the northeastern slope, taken from above the peak of Golemo Stražište (Fig. 8). With this perspective, we created an illustration incorporating the observations developed above about the configuration of vegetation belts in the Balkan Mountains.

We argue that refuges in these latitudes must have been of a small spatial extent, presumably in sheltered positions such as the inner valleys of Suva Planina (Tinner et al., 2023). However, we note a significant forest density (Fig. 8). Although, to avoid extinction, plants tolerate population size reduction much better than animals (Traverse, 1988), it seems probable that in the case at hand ("refugia within refugia" as per Gómez and Lunt, 2007), long-term survival was accompanied by relatively high population sizes to promote genetic variability and niche differentiation (Willis and Whittaker, 2000).

11. Humans in the forest theatre

The Paleolithic occupation of the Balkans and adjacent areas has been the subject of much discussion, suggesting a spatially and temporally heterogeneous framework in which topography and climatic conditions influenced human habitat choice (Dogandžić, 2023). The Middle Paleolithic seems to be associated with regular habitation of mountainous areas at medium and low altitudes, often in sites lacking previous (Lower Paleolithic) and subsequent (Upper Paleolithic) occupations (Mihailović et al., 2011). Pešturina, Velika Balanica (MIS 9-7: Mihailović et al., 2022b; Roksandic et al., 2022), and Mala Balanica (>400 ka: Roksandic et al., 2011; Mihailović et al., 2022b) are located where mountains meet valleys, hills, and rivers, sheltered from the rigors of climate near forested areas and not far from what must have been an important refuge of forests, edible and medicinal plants. The forest would also provide additional options for hunting in open spaces, especially for Neanderthals, who appear to have been sprinters (Stewart et al., 2019) and accustomed to making tools for hunting at short distances and by stealth (Finlayson and Carrión, 2007).

The variety of edible plants is extensive: hazelnut (*Corylus avellana*), walnut (*Juglans regia*), chestnut (*Castanea sativa*), nettle tree (*Celtis australis*), rowan trees (*Sorbus aucuparia, S. torminalis*), wild cherry (*Prunus avium*), blackthorn (*P. spinosa*), elderberry (*Sambucus nigra*), raspberry (*Rubus idaeus*), redcurrant (*Ribes rubrum*), blueberry (*Vaccinium myrtillus*), and probably acorns from some oak species (*Quercus*), among many others (Ochando et al., 2024). Many species that could not be identified using palynological methods might include species from the families Rosaceae, Liliaceae, Apiaceae, Asteraceae, Brassicaceae, and Fabaceae, among others. The archaeological information on mammals processed and consumed by humans in Pešturina includes primarily woolly rhinoceros, mammoth, horse, red deer, bison, wild boar, fallow deer, and roe deer. However, the regional archaeozoological record is much broader (Mihailović and Milosevic, 2012).

During glacial phases, the journey to the first forested hills would not have taken more than an hour. For example, from Pešturina to the base of Mount Kusača (771 m), there is no more than 2 km. Even closer are Mala Balanica and Velika Balanica (Fig. 1b and c). There is a similar distance to Mount Lekoviti Izvor (736 m). The Nišava River is currently about 1.6 km from the cave. A route from present-day Niš city to the end of the valley under Suva Planina includes about 25 km (18 from Pešturina). Nowadays, non-professional hikers take about 6–8 h to climb from Bojanine Bode to the peak Trem. In sum, the humans of Pešturina would have encountered freshwater resources and riparian ecosystems to the northwest, and forested valleys and mountains to the southeast. Definitively, a landscape with a broad diversity of physiographic features.

Let us conclude with a philosophical thought. The original manuscript of "Naturalis Historia" by Pliny the Elder includes drawings attributed to Francesco Petrarca (the "first modern man": Páez de la Cadena, 2017). Among these drawings is a landscape devoid of animal life, portraying the ascent towards a mountain in the French Provence ("Mount Ventoux"), where a cave lies at its feet, from which a spring emerges. Petrarca, with his unique contemplative affinity for landscapes, vividly describes this ascent, imbued with an unparalleled sense of exploration in literature. Remarkably, in the early 14th century, landscape art lacked thematic attribution (Martínez de Pisón, 2019). In essence, paleoart, when it honors the landscape, represents a culmination of modern geography's success, appreciated for its dual role as a spatial structure and a representation of meaning, weaving together aesthetics, culture, and science (Amorós, 2023). Therefore, we cannot limit ourselves to conceiving the environment of the Paleolithic inhabitants of Pešturina solely in utilitarian terms and for survival. They were humans after all. There was, and must have been, an aesthetic enjoyment that is reminiscent of Petrarca's experience on Mount Ventoux. The present work, with its phytocentric approach to paleolandscape, aims to help restore plants to the role of essential travellers in the history of life, and above all "visible" members in paleoart. With all the passion that scientists put into it and all the attention to detail that artists put into it.

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.

Data availability

Data will be made available on request.

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