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Neanderthal coasteering and the first Portuguese hominin tracksites

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Multiple sources of evidence for the systematic use of coastal ecosystems and resources by Neanderthals are known. Fossil hominin footprints offer direct portraits of individual or social group presence and locomotor behavior, and interspecific interactions, in the coastal ecospace. Here we describe the first two hominin tracksites found in the southwestern most region of Europe. At Monte Clérigo, dated to 78 ± 5 ka, trackways of three individuals demonstrate how Neanderthals navigated dune landscapes. These behaviors suggest route planning, with dune systems serving as advantageous settings for ambush hunting or stalking prey. A single footprint at Praia do Telheiro site, dated to 82 ± 5 ka, sustains the presence of Neanderthals in the dune ecosystem during Marine Isotope Stage (MIS) 5a. Network analysis provided dietary preferences and ecological interactions of Neanderthals in coastal areas. A review of the Neanderthal coastal sites associated with faunal evidence shows that their diet was primarily centered on cervids, horses and hares. The consistent presence of these mammal taxa highlights their role as reliable food sources, irrespective of the varying environments inhabited by Neanderthals. In addition, the Neanderthal diet also incorporated animals from neighboring littoral habitats, indicating a broad foraging strategy that capitalized on local biodiversity.

Keywords Ichnoarcheology, Neanderthals, Coastal habitats, Diet ecology, Eolianite, Portugal, SW Iberia

Understanding the eco-geographical dispersion of distinct hominin groups in the Pleistocene is crucial to our understanding of their abilities for surviving in specific environments. The coast, particularly the Atlantic, is highly important because of the role of coastal habitats in the evolution of human modernity, where coastal adaptations, including the exploitation of marine resources and shoreline settlements, appear to have been pivotal[1–4]. According to Marean[5] the use of marine resources, specifically shellfish, provided predictable high rank dietary resources that allowed a reduction of mobility and an increase in population among Anatomical Modern Humans (AMHs). Coastal habitats are rich in biomass and offer numerous easily accessible and predictable dietary resources for hunter-gatherers. Such coastal occupation and exploitation appear to have had

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similar outcomes for Neanderthals for which there is increasing evidence for their presence in Mediterranean and Atlantic coastal areas of mainly small family-based groups[3,6–13].

The use of coastal environments by Pleistocene humans underscores the importance of these areas in shaping hominin cognitive and social development. However, the postglacial sea level rise has considerably complicated the preservation and detection of Neanderthal evidence along the Atlantic coastline, constraining our understanding of the limits of the Neanderthal ecological niche and the consequent extent of their geographical dispersion[4,14]. During the Pleistocene, sea levels were periodically lower than present levels, particularly during glacial periods, resulting in the substantial expansion of coastal habitats accessible to hominin hunter-gatherers[4]. These expanded coastlines provided rich sedimentary environments for hominin occupation and resource exploitation. Sedimentary environments such as sea caves, dune systems, tidal flats and coastal lagoons have the potential to provide access to a record of millions of footprints and other animal tracks, feeding remains and tools, as these are currently being exposed, and eventually destroyed, by sea level rise[15,16].

The components of Neanderthal behavior include spatial mobility, subsistence strategies, lithic technology and raw material procurement, and demography[17]. Hominin footprints and trackways can be used to trace Neanderthal behaviors. Reconstructing Neanderthal behavioral ecology is essential for understanding their diets and interactions with other animals, as well as social organization and spatial ecological patterns[18]. Footprints can provide valuable data for reconstructing the environment and ecology of the ancient landscape, and the behavior of its inhabitants, including insights into the behavior and biomechanical capabilities of hominins[19]including Neanderthals.

Footprints are the combined result of foot anatomy, gait dynamics, and substrate properties[20]. They reflect the pressure distribution as the foot makes contact with the substrate, but also the sediment geomechanical properties. Therefore, fossil footprints record in vivo the behavior of extinct hominins and they offer a great potential to reveal locomotor patterns at various times and places across the human fossil record[21]. They can also provide direct information on biological characteristics, such as stature and age of hominin groups[14,22,23]. Such information can be obtained from morphometry, either from trackways or isolated footprints[24,25]. When found in the same track-bearing surface outside cave environments, footprints can be used to quantify the size and composition of a Neanderthal social group[26]. In reality, footprints are only preserved if the substrate conditions permit and when rapidly buried, thus representing a snapshot of life. By recording in situ a fleeting biological activity, fossil tracks provide a level of detail that usually escapes other kinds of, more strictly archeological, records. In this way, they differ from most archeological sites which represent palimpsests. Hominin footprints and other animal tracks associations and their interactions with the environment, which may also be identified through spatial analysis and temporal markers (as in the case of overprinting between different trackmakers), can help reconstruct in detail a site's paleobiological context and the chronological dynamics of its frequentation. Intra- and intergroup, and trophic interactions usually occurred over a rather narrow timeframe, that coincided with the last phase of the context's lifetime before it was buried by new sediments[19].

Footprints produced in non-coherent sedimentary substrates are usually ephemeral and degrade very quickly after formation. Exceptional conditions for their preservation include sudden burial episodes or environments with high sedimentary rates, which may inhibit intense trampling; these can be found in coastal areas. The fossil record of hominin footprints, and especially the ones attributed to Neanderthals, is exceedingly rare although increasing rapidly in the last few years with a rise in interest as a source of important ichnoarcheological[27]anthropometric and paleobiological information (for an updated list see[28]). Here we describe and present geochronological data for two new hominin tracksites found in eolianite deposits (dune bioclastic sands cemented by carbonate) in Portugal, from a time when Neanderthals were the only hominin species known in the Iberian Peninsula[29–32]. The findings presented add to previous records from the coast of SW Iberia[33–35]providing a unique opportunity to examine the close ecological interplay between Neanderthals, animals, and their environments.

Review of the coastal hominin track records during the Pleistocene

Hominin presence in coastal habitats can be traced using the fossil record of footprints and trackways. The map in Fig. 1 together with Table S2 synthesize the present location and knowledge about the Pleistocene hominin footprint record in coastal marine environments.

The footprints exposed briefly on the Norfolk coast at Happisburgh, England, provided the oldest hominin tracksite outside of Africa. They were formed on the intertidal mudflat of a river estuary, by *Homo antecessor* based on the geochronology and archeological context[24]. Of 152 footprints recorded briefly before they were eroded, 49 were distinctive enough to indicate the direction of travel (preferentially to SW), and 12 were complete enough for detailed analysis, indicating at least five individuals including adults and children, with foot lengths between 140 and 260 mm[24]. The family group was interpreted by Ashton[36] as resident in the area, without taking into consideration the high mobility of these hominin groups in the search for resources.

Terra Amata is an open-air Lower Paleolithic site near the delta of the Paillon River, SE France. A single hominin footprint found in coastal deposits at Nice was attributed to *Homo heidelbergensis*[37–39]. Meldrum[40] suggests that this footprint lacks a modern medial longitudinal arch, like the ones from Roccamonfina in Italy, dated as slightly younger[41,42].

Most of the sites attributed to early Anatomical Modern Humans (AMHs) are found in the coastal eolianites from South Africa, with single occurrences in North Africa (Morocco) and the Americas (Canada and Argentina). The oldest tracksite thus far attributed to AMHs with an age of 153 ± 10 ka, is located in the Garden Route National Park[43] (Fig. 2A). The first open-air hominin tracksite ever to be described was from Nahoon Point, on South Africa's east coast[52]. It comprises a trackway made of three hominin footprints together with a carnivore trackway and avian tracks. One of the hominin footprints exhibits well-defined digit impressions (Fig. 2B). The tracks were reliably dated to the last interglacial Eemian MIS 5e[53]. Another site is Langebaan

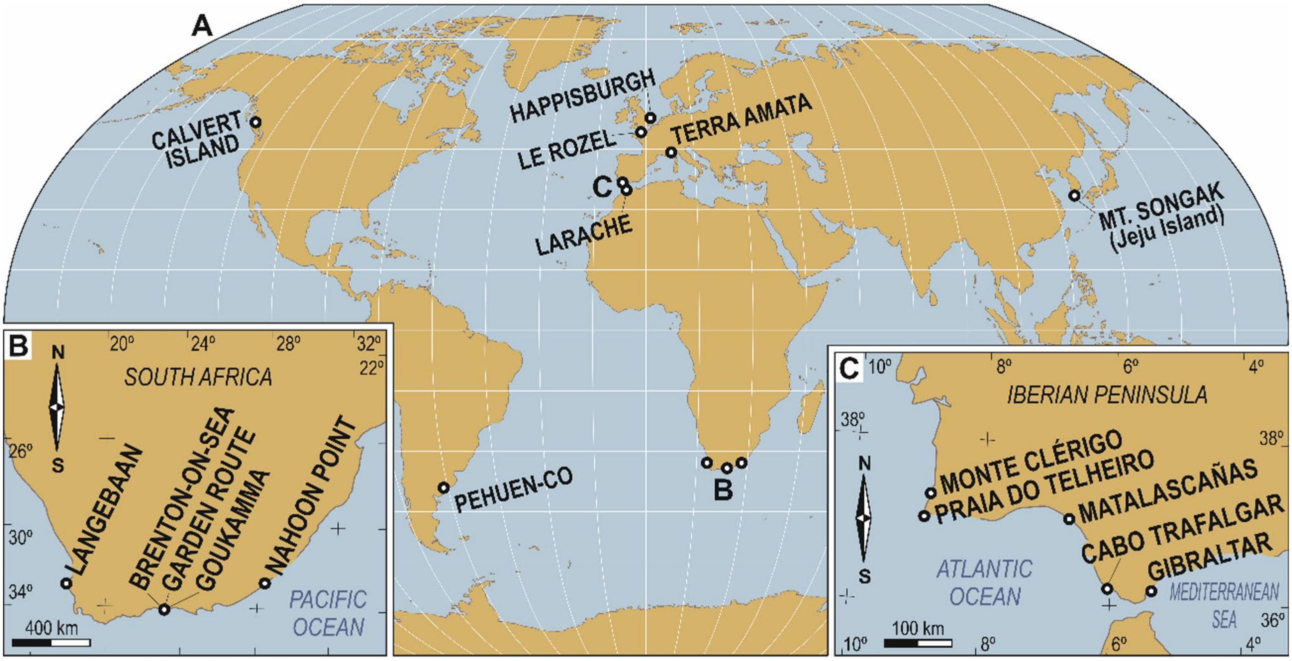

Fig. 1. World map distribution of Pleistocene coastal marine hominin tracksites known to date (**A**), highlighting the main AMHs tracksites known in South Africa, environmental and chronologically correlatives of Iberian Peninsula (**B**), and the two new tracksites in Portugal described in this paper, within the realm of Iberian Peninsula hominin ichnology (**C**); MIS refers to the marine isotope stages and sub-stages: Happisburgh, England (~ 950–850 ka/MIS 25–21) with *Homo antecessor* as likely producers[24,36]; Terra Amata, France (~ 380 ka/MIS 10) with *H. heidelbergensis* as likely producer[39]; Garden Route National Park at Gericke's Point, South Africa (~ 153 ka/MIS 6) with AMHs as producer[43]; Matalascañas, Spain (~ 151 ka/MIS 6) with Neanderthals as producers[33]; Catalan Bay, Gibraltar (late MIS 6-to-MIS 5) with Neanderthals as producers[33]; Nahoon Point, South Africa (~ 127 ka/MIS 5e) with Anatomical Modern Humans (AMHs) as producers[44]; Langebaan, South Africa (~ 117 ka/MIS 5c) with AMHs as producers[44]; Brenton-on-Sea, South Africa (~ 90 ka/MIS 5b) with AMHs as producers[45]; Larache, Morocco (~ 90 ka/MIS 5b) with AMHs as producers[16]; Goukamma Nature Reserve sites 1 and 2 (~ 89 and 76, respectively/MIS 5b and 5a) with AMHs as producers[43,46]; Praia do Telheiro, Portugal (~ 82 ka/MIS 5a) with Neanderthals as producers (present work); Le Rozel, France (~ 80 ka/MIS 5a) with Neanderthals as producers[26]; Monte Clérigo, Portugal (~ 78 ka/MIS 5a) with Neanderthals as producers (present work); Mt. Songak, South Korea (~ 25.7–19.6 ka cal BP/MIS 2) with AMHs as producers[47–49]; Calvert Island, Canada (~ 13 ka/MIS 1) with AMHs as producers[50]; Pehuen-Co, Argentina (~ 12 ka/MIS 1) with AMHs as producers[51]. Map produced with Corel Draw X8 (www.coreldraw.com).

open-air eolianite surface on the shores of the Langebaan Lagoon on South Africa's west coast[54]. A trackway comprising three footprints in epirelief was described, and dated to ~ 117 ka[44]. Two more footprints with suboptimal morphological detail were described from an in situ ceiling of a small recess in coastal cliffs[55]. Brenton-on-Sea was the first of the new tracksites found in South Africa following a systematic study[45] and was subsequently dated through optically stimulated luminescence (OSL) between 89 ± 6 ka and 76 ± 5 ka[43]. Forty hominin footprints were identified in hyporelief and in profile on two eolianite surfaces in a coastal sea cave. One trackway, registered while moving down a gentle dune slope, exhibited a jogging gait pattern, making it the oldest reported ichnological evidence of a running hominin[43]. In the Goukamma Nature Reserve two sites dated to ca. 75–71 ka were described[43]. One of those was registered by a group of hominins of various ages/sizes, moving across and up a dune surface, and contained 32 footprints. In the northwest coast of Morocco, Sedrati[16] described 85 hominin footprints in beach sediments. The footprints were interpreted as representing at least five individuals of different ages and footprint sizes.

A total of 29 barefoot footprints were found in Calvert Island, Canada, imprinted in a paleosol. Analysis of entrained plant debris confirmed an age for the track horizon of between 13.317 and 12.633 ka BP[50,56]. This date has been questioned by Lucas[57]citing evidence that the prints may only be 2000 years old, pointing out that the tested charcoal "may have been introduced into the sediment long before the footprint was impressed." Further testing may be needed to resolve this. The footprints were made by at least three individuals[56].

On the shores of temporary interdune ponds of the Pampean Late Pleistocene, an exceptional record of animal tracks and trackways crops out on platforms along 5 km of the modern coast of Buenos Aires, Argentina[58]. The paleoichnological record shows more than 100 trackways and hundreds of isolated tracks belonging to 24 species of mammals and birds[59,60]. A trackway of 13 consecutive footprints, with alternated traces of the right and left foot, shows the walking gait of a single human individual. The length of each footprint ranges between

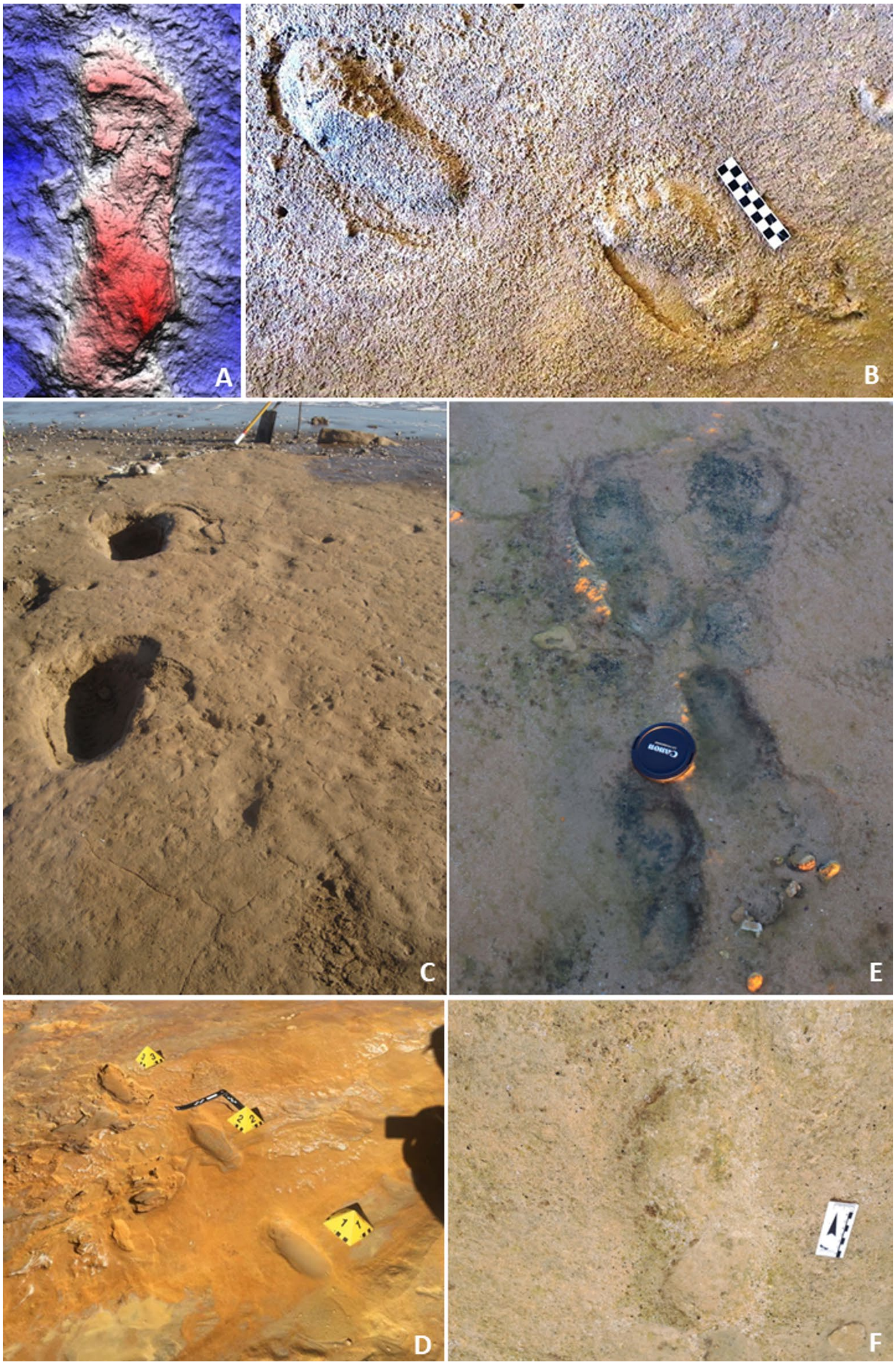

Fig. 2. Hominin footprints in Pleistocene coastal deposits. (**A**) 3D photogrammetry image of the oldest known AMHs footprint, dated to ~ 153 ka, from Gericke's Point in the Garden Route National Park, South Africa; the footprint is 24 cm long (image by Charles Helm). (**B**) Two of the Nahoon Point hominin footprints (avian tracks are also evident; photo by Charles Helm). (**C**) Pehuén-co ichnosite: human trackway following from close a giant ground sloth trackway in a drying muddy substrate; they were produced in very different substrate conditions, which enable questioning of the hunting interpretation (photo by Teresa Manera di Bianco; no metric scale was provided). (**D**) Matalascañas Trampled Surface with a Neanderthal trackway (photo by José María Galán; scale in cm). (**E**) Footprints of Neanderthals travelling in opposite directions and overlapping, on a beach substrate at Cape Trafalgar (photo by Florian Lipp; lens cap is 5.8 cm). (**F**) Detail of a male adult footprint from the same beach deposit at Cape Trafalgar surrounded by expulsion rims and showing the preservation of the toe prints (photo by the authors; scale in cm).

33 and 35 cm, and the maximum width between 13 and 15 cm. Only two footprints found have marks of toes, which is the result of walking in a highly desiccated substrate, as also indicated by the presence of mud cracks (Fig. 2C). In the same layer there is a *Megatherium* trackway parallel to the hominin trackway. In addition, it contains *Macrauchenia*, artiodactyl and flamingo trackways that cross the human one in different directions[60]. Nevertheless, the hunting scenario hypothesized by Bayón et al.[58] is difficult to support, with totally different preservational scenarios for the *Megatherium* and human trackways.

Regarding to tracksites attributed to Neanderthals, six sites were known prior to this study, all located in Europe, especially in Iberian Peninsula (Table 1). These include the exceptional site of Le Rozel in northern France[26]Matalacañas Trampled Surface (MTS) and two other coastal open-air sites in SW Iberia[33–35,61,62]besides the cave sites of Vârtop in Romania[63,64] and likely Theopetra in Greece[65]. Except for Le Rozel, all the other sites show single or few footprints, only in the MTS organized in short trackways.

The most remarkable Neanderthal ichnosite is Le Rozel on the coast of Normandy. This was a Neanderthal occupation site for processing prey, especially deer and horses[66]. 595 footprints and eight handprints[67] dated between ca. 86 and 75 ka[68]associated with archeological materials and abundant faunal remains, represent by far the largest known Neanderthal ichnological assemblage to date[26]. The footprints are distributed by six stratigraphic subunits, considered as a single brief occupation event[26]. According to Duveau et al.[26]this ichnoassemblage provides direct evidence for the size and composition of a Neanderthal social group. A minimum of 4 individuals, more likely 10 to 14 individuals, constituted a social group mainly composed of children (51.4% of the total footprints[67]). Despite Duveau et al.[26] concluded that Le Rozel, together with El Sidrón in Spain, are the only sites providing reliable information of the composition of Neanderthal social groups, Duveau[67] remarked that is impossible to know whether the D3b-4 track-making group is representative or not of the whole social group present at one time. Only a subset of 12 best-preserved footprints were used in geometric morphometric analysis, leading Duveau et al.[26] to conclude that the Le Rozel footprints were closer to the footprints of AMHs, although wider, especially at the midfoot, suggesting a less gracile morphology and a less pronounced plantar vault. The authors did not take into the account the morphological variability resulting from trampling in sand under different levels of moisture. Moreover, the small number of footprints used limits interpretations. The Le Rozel sample was likely derived from a mixed-age Neanderthal group. Ruff et al.[69] revised body mass estimates from Duveau et al.[26] by taking into account the body mass index, suggesting that this group included more adults than initially proposed and highlighting the difficulties in differentiating small adult from adolescent body sizes.

The Matalascañas (MTS) ichnosite in SW Spain was described for the first time in 2020[70], and since then regular studies have been detailing the ecology of a coastal interdune seasonal lacustrine system, that functioned as a congregation site where different mammals (including humans) and birds converged, presumably for water and food resources, and possibly also for reproduction (summarized in[33]). The association of Pleistocene hominin footprints and lithic industries is only known through a few occurrences worldwide and can be decisive, together with geochronology, in determining the hominin responsible for the footprints. This is the case of the MTS, where lithics were found in direct association with hominin footprints[33]. The classical association of Mousterian industry (Mode 3) to Neanderthals in Europe, together with new OSL dating of the MTS at 151 ± 11 ka[33]allowed for confident attribution of the hominin trackways to Neanderthals (Fig. 2D). Therefore, MTS represents the only case where Neanderthal footprints are temporally (no more than hours or a day) and spatially associated with other tracks and trackways of large herbivores (red deers, aurochs, straight-tusked elephants), as well as to in situ Mousterian lithics. The overstepping of animal tracks together with slow walking gait determined in the hominin trackways allowed for an inference of possible stalking behavior[35]and the presence of lithic tools

Site/country	Coordinates	Age/MIS	No. footprints/trackways	Measurements	Morphological features	Substrate
Vârtop Cave, Romania	46°32′26.64″N 22°46′50.53″E	~ 67.8–62 ka/ MIS 4	3 footprints	22 cm long and 10.6 cm wide	Broad morphology	Moonmilk
Praia de Monte Clérigo, Portugal (this paper)	37°20′41.67″N 8°51′02.10″W	78 ± 5 ka/MIS 5a	4 trackways and some footprints	11 to 28 cm long and up to 13 cm wide	Adult and child trackways negotiating a steep dune slope	Eolianite
Le Rozel, France	49°28′20.92″N 1°50′25.58″W	80 ± 10 ka/ MIS 5a	595 footprints/2–3 footprint trackways	11 to 28.4 cm long, 4.5 to 28.4 cm wide	Wider midfoot and less pronounced plantar vault than modern humans	Sandy muds in dune deposits
Praia do Telheiro, Portugal (this paper)	37°02′51.38″N 8°58′39.15″W	82 ± 5 ka/MIS 5a	1 isolated footprint	22.6 cm long and 7.6 cm wide	Footprint index of 0.34 under the range of AMHs	Eolianite
Cape Trafalgar, Spain	36°10′54.64″N 6°02′05.00″W	99 ± 12 ka, 107 ± 2 ka/ MIS 5d	Undetermined number, 1 footprint in vertical section	25–28 cm long and 10–12 cm wide	Adults	Eolianite and beach sandstones
Theopetra Cave, Greece*	39°40′53.54″N 21°40′52.27″E	~ 135 ka/MIS 6	4 footprints	13.8–15.1 cm long and 5.4–62.9 cm wide	Produced by children 2–4 years old	Clay
Catalan Bay, Gibraltar	36°08′06.58″N 5°20′28.75″W	140.4 ± 18.6 ka/ MIS 6	1 isolated footprint	17 cm long and 7 cm wide	Footprint index of 0.41 under the range of AMHs	Eolianite
Matalascañas, Spain	37°01′07″N 6°35′17″W	151.1 ± 22 ka/ MIS 6	87 footprints(??)/3 trackways composed of no more than 5 footprints	14–29 cm long and up to 13 cm wide	Footprint index average 0.37 under the range of AMHs	Interdune phreatic lake silty-sandstone

Table 1. Hominin tracksites geochronologically attributed to neanderthals.

showing expeditious knapping in a short-range distance from the footprints provided compelling evidence for animal processing in the surroundings[33].

At Gibraltar, a single hominin footprint showing typical five-toe morphology (with the D1 parallel to the longitudinal axis of the track) was described[34]. The deeper impression of the heel, poorly preserved D2-D5 prints together with the development of an expulsion rim in the toe region and an abnormally extended D1 are evidence for dragging through the sediment during the forward swing of the foot while descending the dune. It was considered to be produced by a Neanderthal infant, despite the very recent age of 28 ± 3 ka obtained[34]. New OSL dates obtained by the team of the National Museum of Gibraltar above and below the footprint level, bracketed between 135.2 ± 16.3 ka and 140.4 ± 19 ka, places this footprint clearly in the transition between Middle and Late Pleistocene (MIS 6–5).

Neto de Carvalho et al.[71] described a new ichnosite in the Cape (Cabo) Trafalgar area of SW Spain, dated from the Last Interglacial (107 ± 2 to 78 ± 8 ka)[72] and composed of a trampled surface in beach sandstone with aurochs trackways, together with several track-bearing beds in the overlying eolianite with roe deer/caprine, proboscidean and a possible single human footprint in section. More recently, in the lowest beach sandstone bed, sparse clusters of aurochs tracks, together with hominin footprints were identified for the first time (Fig. 2E, F).

Theopetra Cave at Meteora (Greece) preserves four footprints organized in a "trackway" but imprinted by two different, small producers, estimated from footprint length to be between three-four years old and 98.5 and 106 cm in height[65,73]. These footprints are associated with Levallois industry, in the same layer, and were re-dated to ca. 130 ka[74]. In fact, thermoluminescence dating of burnt Mousterian flint specimens provided an age range for the stratigraphic sequence of the cave of between 150 ± 15 ka and 57 ± 6 ka, although there was evidence of post-depositional mixing. Despite the age and the Mousterian industry, Kyparissi-Apostolika and Manolis[65] do not dismiss the possibility of the footprints having been produced by *H. sapiens*. Distinguishing between the footprints of AMHs and the track record of Neanderthals based on footprint morphology solely is still not reliable[75] despite claims to the contrary[26,63].

The very first footprints proved to be Neanderthal were described in Vârtop Glacier Cave, Romania. Onac et al.[63] reported three footprints dated between ca. 67.8 to 62 ka[64]that were attributed to a single Neanderthal, reflecting the robust anatomy expected for these humans. Two footprints were partials, consisting of either heel or forefoot impressions. A third footprint is longitudinally complete and well preserved, 22 cm long and 10.6 cm wide.

*Possibly made by either Neanderthals or AMHs[65].

Methods

Hominin footprint morphometrics and photogrammetry

Stratigraphic data where the tracksites are found were obtained by classic field mapping and comparison of the sections. A single track-bearing surface in dune foreset laminae is likely to record animals who lived at the same time and in immediate proximity to each other. These tracks showing similar preservational conditions may have been produced at the same instant or within minutes to no more than a day. Co-association is usually argued for, on the basis of cross-cutting relationships between different trackways and on similar level of footprint preservation[76]. Typical hominin footprint morphology in well-preserved footprints includes the presence of a forefoot ball, a medial longitudinal arch, a non-divergent and robust hallux and digits II to V becoming progressively shorter[23,77,78]. Relationship of foot pressure and print depth and quality varies with substrate conditions such as type of sediment and grain size, substrate moisture, as well as presence and depth of subsurface compaction levels[76].

The study of hominin footprints followed standard procedures of gathering descriptive morphological data and measurements in the field[76]. In the paleoichnological analysis carried out for the present work, the approach considered, in general terms, the following steps for each outcrop studied:

- Stratinomic orientation;
- Morphological description process;
- Intra- and interichnospecific cross-cutting relationships (overprinting);
- Analysis of preservation quality sensu[79];
- Taking general and detailed photographs in the field of ichnotaxa (using a Canon EOS100D + EF-S 18–55 mm f/3.5–5.6 IS STM + EF 40 mm f/2.8 STM);
- GPS tracking and compass measurements;
- Analysis of sections of ichnofossils and selected physical sedimentary structures and recording of dip directions.

Measurements were made in the field using measuring tape and compared with measurements made on the 2D orthophoto and 3D photogrammetric models. The lengths of the footprints were used to estimate the minimum number of individuals present and to estimate stature and age (see below). The limitations of estimating stature, velocity, and other measurements from track data have been described[23]therefore measurements provided here must be considered approximations. Samples were collected from track-bearing levels for making thin sections at the lab of the Geological Department of the Faculty of Sciences of the University of Lisbon for transmitted petrographic light microscopy (Olympus BX40 + Olympus DP21 digital camera).

For the study of footprints, we applied current standards of data acquisition and 3D image analysis using photogrammetry[80]. The main advantages of digital modelling applied are: (i) its great capacity for the 3D non-intrusive registration of surfaces and objects of interest, portraying the sites/objects of study with realism, high geometric and radiometric precision; (ii) the possibility to survey large areas and small objects[81]at different aerial and terrestrial scales[82–84]; (iii) the opportunity to analyse in a more appealing and interactive digital environment, enhancing and facilitating the tasks of visual interpretation and measurement and allowing the application of quantitative statistical methods[85,86] and automated data extraction[87]. For the modelling of trackways, a variable large number of photographs were taken in perpendicular and oblique views (resolution 6480 × 4320 pixels, in JPG format), using a Camera Samsung NX500 V2 with 16–50 mm lens. Three-dimensional scales were used to improve accuracy along the x, y and z axes. The photogrammetric processing of the tracks and trackways of was carried out with the free open-source software Meshroom 2020.1.1[88]. The post-processing was carried out using free open-source software MeshLab v2020.12[89] and CloudCompare v2.11.0[90]. The post-processing phase involved the analysis, treatment, fixation to the plane, orientation and scale assignment to the textured photogrammetric models obtained. The figures presented were compiled in the free open-source software Inkscape v0.92.3[91].

Network analysis
In this study, we employed network analysis to investigate the co-occurrence relationships between Neanderthals and other taxa within the Neanderthal-bearing coastal sites of the Iberian Peninsula. Our data set comprises presence-absence information for 20 taxa and two forms of Neanderthal evidence—body fossils and technocomplexes—across 12 sites in the region. Utilizing the methodology of paleontological network analysis[92–94]we translated the source data into a network by designating taxa as nodes and drawing links between taxa that co-occur in at least one paleontological site. For practical implementation, we utilized PAST software to organize the presence/absence data into a spreadsheet, from which an adjacency matrix was derived. Each entry in this matrix represents the Jaccard index[95] for a given pair of taxa, which facilitated the visualization of the network using Gephi software. We used the GeologyOracle platform for language revision[96] specifically for the network analysis part.

Geochronology
In order to obtain a geochronological control of the tracksites, OSL dating was employed. To avoid any sunlight exposure a thick black plastic cover was used and a sample (sample codes 243001 for Monte Clérigo, and 243015 for Praia do Telheiro track-bearing beds) of hard eolianite about 20 kg in weight was extracted from the selected units and covered by the black plastic. An extra sub-sample of the sediment was also collected, in order to be used to measure the field and saturation water contents, respectively. The preparation of the OSL mineral fractions from the core of the eolianite block was carried out in the sample preparation room of the Dept. of Earth Sciences-University of Coimbra, under subdued red light to prevent resetting of the luminescence signal. The 180–250 µm sand fraction was obtained via HCL (10%) dissolution of the eolianite. K-rich feldspars were floated off using a heavy liquid solution ($\rho = 2.58$ g/cm^3); measurement of a multigrain aliquot of the K-rich extract using the Risø XRF attachment gave a K concentration of 11.6% justifying the assumption of 12.5 ± 0.5% K for internal beta dose rate calculation[97]. The quartz-rich fraction ($\rho > 2.58$ g/cm^3) was etched using concentrated (40%) HF for 60 min, to remove the outer alpha-irradiated layer, followed by 10% HCl for 40 min[98]. Radionuclide concentrations (^{238}U, ^{226}Ra, ^{210}Pb, ^{232}Th and ^{4}K) in the bulk sediment were measured using high-resolution gamma spectrometry[99]. The radionuclide concentrations were converted to dose rate data using the conversion factors from Creswell et al.[100]. The contribution from cosmic radiation to the dose rate was calculated following[101] assuming an uncertainty of 5%. Large (8 mm) and small (2 mm) aliquots were prepared for quartz and K-rich feldspar, respectively. Quartz OSL and K-rich feldspar post-IR50 IRSL290 equivalent dose (D_e) values were measured using the SAR procedure[102] in the usual way[103,104] using a standard Risø TL/OSL reader. The beta source was calibrated using Risø calibration quartz batch 200. Table S3 summarises the radionuclide and dry dose rate information. Table S4 contains the De values, total dose rates and resulting quartz OSL and K-feldspar post-IR IRSL ages.

The radiocarbon ages previously obtained for the eolianite units in Castelejo and Praia do Telheiro sites[105,106] were calibrated using the OxCal 4.4. software provided by the University of Oxford and applying the Marine 20 radiocarbon age calibration curve[107].

Stratigraphic, geochronological and paleoclimate settings of the new tracksites in Portugal
Stratigraphy and geochronology
In the SW coast of Portugal, eolianites extend across the southern provinces of Alentejo and Algarve, between S. Torpes to Sagres, over a distance of 100 km. From S. Torpes, in the north, to Odeceixe further south, there is an almost continuous outcrop, facing cliff fronts or cropping out over the cliff, the so called Malhão Dune System[108]. From Odeceixe to Sagres, in the south-westernmost point of Europe, eolianites are found in small discontinuous outcrops, mainly in cliff fronts or filling deeply incised valleys. These are the cases of the Monte Clérigo and Telheiro tracksites, in the Vicentina coast of Algarve (Fig. 3). A culminant regional wave-cut abrasion platform and associated Pliocene sediments[109]built on Paleozoic and Mesozoic rocks, occur on a wide littoral area that extends from the Grândola and Cercal coastal mountain belts located east, to the present coastline, gradually lowering to the west[110,111]. The elevation of this planation varies from around 5 m a.m.s.l. (height *above mean sea level*) near Sines to up to 150 m a.m.s.l. along the southwestern coast of Algarve[110,112]where it is displaced by the São Teotónio-Aljezur-Sinceira Fault. Goy et al.[113] defined at least seven alluvial fan systems for the area of Sines-Vila Nova de Milfontes, situated north from the present study area. These alluvial fans are mainly made up of quartz-rich conglomerates with sandy or pelite matrices, thicker towards east, and reddish clayey sands with interspersed levels of gravel and paleosols, more developed in the coastal outcrops (Bugalheira formation).

The Pleistocene eolianite formations under study are strongly cemented by carbonate as result of a vadose early diagenesis, and may contain intercalated paleosols and colluvial levels. Incipient paleosols are marked by intensive rhizoturbation and the presence of land snails preserved in the eolianite. Tectonic activity in the region

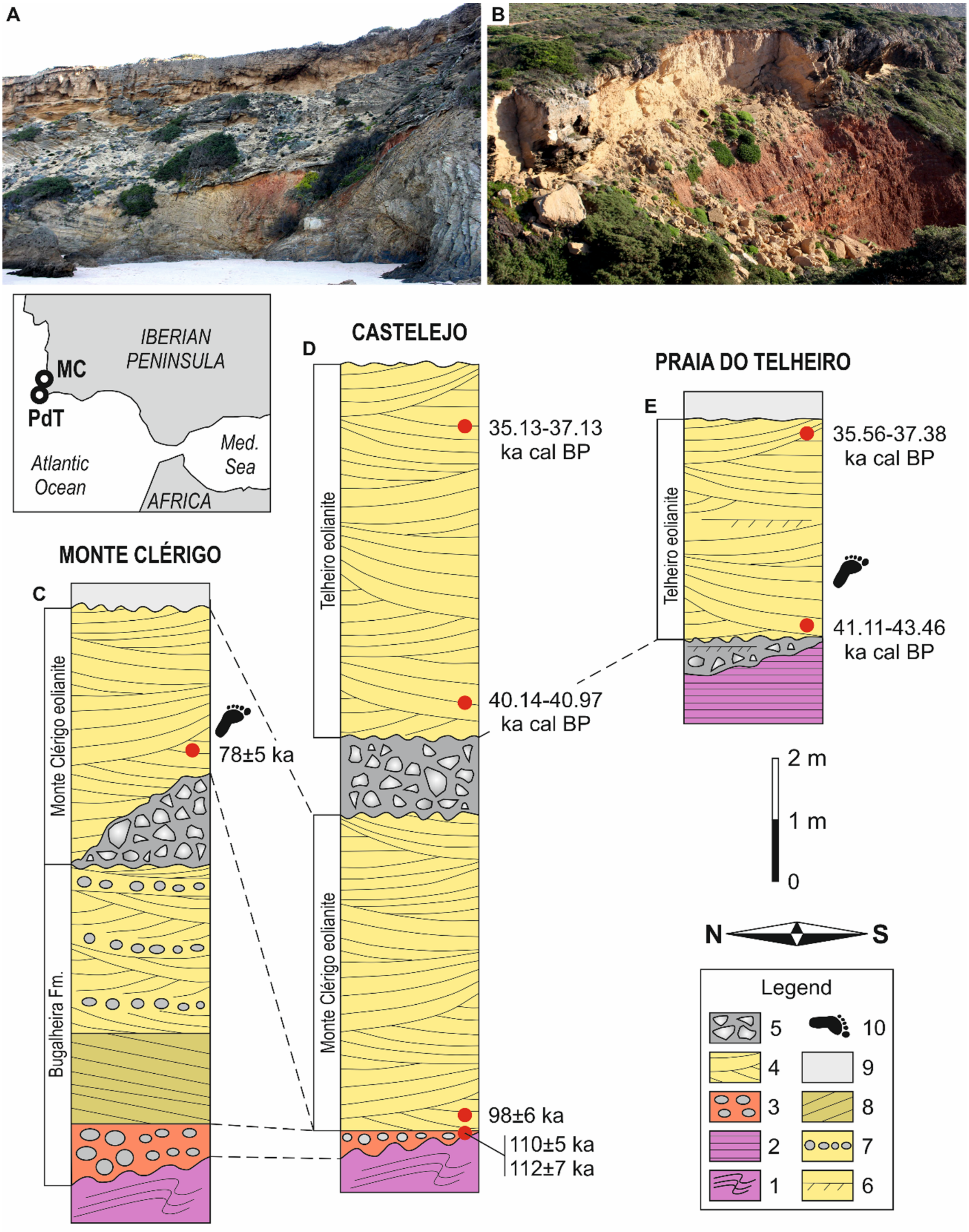

Fig. 3. Stratigraphic logs of the Neanderthal tracksites in SW Portugal: Monte Clérigo site (**A**), at the northern end of Monte Clérigo beach; Praia do Telheiro site, located in a small creek close to the beach. Correlation with the well dated Castelejo section geographically located between the two studied sections (**D**), Monte Clérigo (**C**) at north, and Praia do Telheiro (**E**) at south. 1—Paleozoic turbidites; 2—Lower Jurassic marls; 3—conglomerate; maximum clast size = 30–35 cm; 4—cross-bedded eolianite; 5—colluvial deposits; 6—paleosol; 7—gravel lens; 8—low-angle laminated sandstone; 9—Holocene unconsolidated dunes; 10—Hominin tracksite; OSL/^{14}C ages: Monte Clérigo and Praia do Telheiro in this paper; Castelejo OSL dates by Figueiredo[115]; Castelejo and Praia do Telheiro radiocarbon dates by Martins[106].

has been minimal in the past 125 ka[114–117] and did not change significantly the depositional location and dip of the eolianite lamina.

Monte Clérigo Sect. (37°20′N; Fig. 3A) is a cliff-front dune climbing from north the Espartal hill up to 60 m a.m.s.l. The section with hominin footprints was described and measured in the northern part of Monte Clérigo beach (Fig. 3C). Its starts by a beachrock conglomerate overlain by the alluvial fan deposits of the Bugalheira formation. A weakly-cemented sandstone of eolian origin shows dispersed pebbles of local (Paleozoic basement) origin. Colluvial deposits from the hill slope cover in part these sandstones and the remaining paleotopography was covered by the well cemented, coarse-grained eolianite. The eolianite shows variable thickness up to 20 m in the northwesternmost outcrop, but sharply reducing the thickness towards almost the top of the Espartal hill. The eolianite is formed by multiple bedsets between 1 and 3 m thick. The detrital composition of the sandstone is mostly composed of sub-rounded to rounded quartz (with rare lithoclasts), but bioclasts can still be identified in thin section (mostly coralline algae > 50% and rare bivalves). At 2.5 m below the top of the eolianite there is a wide track-bearing surface in a lamina dipping 35 – 20°, representing the dune ramp facing SW. Besides, two observational windows resulting from coastal erosion at an altitude of ca. 10 m a.m.s.l. are stratigraphically separated by 1 m in foresets dipping NE. In the section located in the northern end of Praia do Monte Clérigo we found a track-bearing surface with hominin trackways, an artiodactyl trackway and undetermined tracks. This bed was dated by quartz OSL to 78 ± 5 ka. The $pIRIR_{290}$ age of 75 ± 6 ka measured on K-rich feldspar confirms that the quartz OSL signal was fully reset at deposition and that there were no significant post-depositional changes in dose rate during burial. The track-bearing surface is intersected by mostly vertical (post-depositional) rhizoliths, up to 3 cm in (external) diameter, coming from an incipient paleosol developed in the top of the eolianite. The most distal part of the root systems develops sub-horizontally to the track-bearing level, and ramifies, with not less than 5 mm in (external) diameter. About 100 m further north, and in slightly lower stratigraphic levels, we found the two mentioned additional track-bearing surfaces with mostly shorebird and few artiodactyl trackways, also intersected by few sub-horizontal rhizoliths. The succession shows stacking dune cordons formed by opposite winds from NE and SW controlled by the widening of the Aljezur river estuary at north and the Espartal hill cliffs.

The Castelejo section (37°06′N; Fig. 3D) was described and dated by Figueiredo[115–117]and therefore is used here as reference because it is geographically situated between Monte Clérigo and Praia do Telheiro sections. The thin basal sandstone layer was dated using post- IR IRSL of K-rich feldspar to 112 ± 7 ka and 110 ± 5 ka; the basal eolianites were dated with quartz OSL to 84 ± 6 ka, while K-feldspar post-IR IRSL provided an age of 98 ± 6 ka[115]. This strongly suggests that this marine terrace might correspond to the highstand MIS 5c, and that the eolianites were started to be deposited during the lowstand of MIS 5a[115]. The upper eolianite unit was only dated by radiocarbon and may be correlated to MIS 3[106].

Finally, the Praia do Telheiro Sect. (37°02′N; Fig. 3E), located approximately 7 km southwest from the Castelejo section, is one of the south-westernmost eolianites in Europe and covers a small area between two creeks (Fig. 3B). The eolianite reaches 50 m a.m.s.l. Above an angular unconformity with Lower Jurassic red clays and marls, the Quaternary succession is composed of a lower colluvial layer covered by a rubefacted soil with the presence of land snails, overlain by the eolianite unit (~ 4 m thick). The eolianite is formed by bedsets 0.5–1.5 m thick. Four eolianite levels covering the whole eolianite were previously radiocarbon dated here between ~ 35.56 and ~ 43.46 ka cal BP[106]. Our results using OSL show that the track-bearing level is 82 ± 5 ka in age and therefore correlated with the Monte Clérigo eolinite. It also shows that the radiocarbon dates obtained for both Praia do Telheiro and Castelejo eolianites must be considered *terminus ante-quem*. The eolianite unit shows in the lower part several track-bearing levels with bird and mammal tracks, including a single hominin footprint. Tracks of an eagle-owl identified as *Buboichnus vicentinus* isp. nov. and a shorebird *Charadriipeda* isp. type II were described in this lower part of the section[118]. Rhizoturbation is abundant in the upper part of the eolianite, while the lower part is marked by the angular variations of the laminae in the sets, between 14° and 31° towards SW. Incipient paleosols in the topsets show the presence of land snails and small diameter rhizoliths. The sandstone is very coarse-grained with abundant quartz (~ 80%) and rare bioclasts composed of bivalves (up to 19%), coralline algae and echinoids. The dune system was developed with Ponta do Telheiro as obstacle to predominant northwestern winds, and by the filling of the incised valley of a stream that was parallel to the cliff, i.e. NNE-SSW.

Paleoclimate in the SW Iberia during the eolian deposition periods

The Monte Clérigo and Praia do Telheiro dune systems were developed during a warm stadial of the Last Interglacial. MIS 5 pollen record from deep-sea cores off the Iberian Atlantic coast, associated to estuaries, shows a continuous presence of pine and Ericaceae and relatively high percentages of deciduous oak throughout the period[119–123]. Beech populations existed within maritime forests of the Iberian Atlantic margin[124]revealing cooler and more humid periods. The expansion of cold-adapted taxa and attendant faunal renewal may have occurred around the Last Interglacial/Last Glacial transition (MIS 5a/MIS 4), with the eventual disappearance of species adapted to warmer climatic conditions of the Eemian[125]. This was a colder period than the previous Interglacial, but still a relatively benign climate in the Iberian Peninsula, and especially in the coastal areas[126]. The top of Monte Clérigo eolianite develops an incipient paleosol but rhizoturbation is intense and deep. The paleosols formed in Praia do Telheiro are incipient and rhizoliths can occur in dense associations but with small diameters, representing herbaceous cover.

Neanderthal tracksites in Portugal

The Monte Clérigo main track-bearing surface has a total area of 22.34 m^2 (Fig. 4A). At least five hominin short trackways were identified, besides few isolated footprints. A total of 26 footprints are described here. The footprints show variable preservation, which is usual for footprints made in soft sandy ground[15,26,77,127–129].

Also, exceptional anatomical fidelity would not be expected in substrates with this grain size, compared to silt or mud. In the dune ramp reaching between 35° and 28° dip, the footprint details are quite indistinct and not very well preserved. In a few footprints (e.g., Fig. 4B, C) we can notice more details, such as the trace of the hallux, the toe II–V angle of declination and the transverse arch in the ball. The surface with the footprints has been exposed for a long period of time. Being in a steep surface, the fossilized footprints were long-used by fishermen as a path. Besides, rain gutters are starting to form and plant pioneer colonization is happening in the soil that was still filling few footprints and rock crevices. Human transit together with weathering due to long exposure smoothed the edges and produced a more rounded shape of the prints (as in Roccamonfina[130,131]). For analyzing the footprints, we looked for criteria that can define hominin's walking in sloped surfaces, besides diagnostic morphological features not always present, such as an adducted hallux or the medial longitudinal arch:

◂**Fig. 4**. Hominin tracksites in eolianites from the SW coast of Portugal. (**A**) General view of the main tracksite with hominin trackways located in the northern cliff of Monte Clérigo beach (authors for scale); (**B**) Footprint D1 from the trackway D evidencing the differential preservation of the deeper forefoot print as result of moving upslope (scale in cm); (**C**) PI2 Isolated footprint with impression of the adducted hallux and toe declination angle (scale in cm); (**D**) Deformation of sediment laminae in the cross section of a footprint: downfold in the lateral margin of the footprint and upfold in the bottom of the footprint (scale in cm); (**E**) Very small footprint (P2T), with evidence for the toes and absence of the medial longitudinal arch. The apparent large width by comparison with the length results from lateral slippage; scale bar is 50 mm; (**F**) The footprint P1T with only the ball and toes, especially the hallux, well imprinted (scale in cm); (**G**) One of the footprints of trackway C with the heel as the deepest part and evidence for longitudinal slippage; ruler segments are 20 cm; (**H**) Footprint preserved isolated over a broken laminae at Praia do Telheiro stream, with displacement rim around the posterior area of the footprint (scale in cm).

Footprint #	Left(L)/right(*R*)	Length (mm)	Width (mm)	Footprint index	Footprint angle (°)	Pace length (mm)	Stride length (mm)
A1	R	255	87	0.34	0	600	
A2	L	260	90	0.35	0	550	
A3	R	265	112	0.42	− 10	400	1110
A4	L?	–	121	–	0	625	
A5	R	262	87	0.33	− 1	− 100	
A6	L?	–	–	–	− 8	475	1000
A7	R	–	95	–	0		
B1	R	275	107	0.39	2	650	
B2	L	282	98	0.35	− 15	575	1250
B3	R	251	83	0.33	6	275	
B4	L	–	111	–	3	200	525
B5	R	–	124	–	− 15	375	
B6	L	252	100	0.40	20		
C1	R	282	137	0.49	− 10	300	
C2	L	–	124	–	− 13	1250	
C3	R	265	107	0.40	− 1	750	2000
C4	L	295	119	0.40	3		
E1	L	110	60	0.55	–	–	–
E2	R	–	65	–	–	–	–
PI2	L	173	72	0.42			

Table 2. Hominin footprint measurements of the main trackways at Monte clérigo.

- expulsion rims according to the dip direction;
- strong depth asymmetry of the footprints with the deepest areas in the forefoot or in the heel (depending if walking upslope or downslope), or the preservation of halfprints;
- trackways with the pace length similar to the footprint length and variable pace angle resulting from walking at slow speed on a steep slope;
- Narrow or wide instep width depending on the slope's angle of attack;
- Deformation of the sedimentary laminae under the print (when viewed in section).

Footprint measurements are presented in Table 2. There are four main trackways (A-B-C and D). Trackway D corresponds to six, mostly poorly-preserved halfprints oriented up according to the steepest surface, with a total length of 245 cm. The best-preserved footprint D1 is found on the bottom (Fig. 4B). The depth of the metatarsophalangeal area in comparison with the heel print, representing plantar flexion to generate power during push-off, is consistent with upslope progression. The hallucal impression corresponds to the peak pressure at toe-off. The slightly abnormally elongated hallux was probably caused by forward drag. Also, the transverse and longitudinal arches are evident especially in the deepest part of the footprint corresponding to the forefoot. No measurements were taken in this kind of preservation but the footprint breadth of the footprint from Fig. 4B is comparable with the ones taken from the next trackways to be described and must be related with an adult male. Short pace length and pace angulation of 110° results from a climbing gait upwards and following the dip angle of the slope. The apparent difference in pace length between left and right prints may represent limping gait that could result from injury or carrying heavy weight on the left side.

Trackways A, B and C show deep footprints with mainly indistinct characteristics, but with syn-sedimentary deformation of the laminae (Fig. 4D). Medial longitudinal arch is typical from human foot as a critical adaptation for bipedal locomotion[132]. Flexibility of the arch deforms the underlying sediment in a convex-up fold and develops displacement rims with convex-down laminae. When it is possible to see sections of the footprints, concave-up deformation laminae of the imprinted sediment, and concave-down marginal folding are identified (Fig. 4D). Anterior or posterior parts of the footprints are recognized for being the deepest area in ascending or descending-oriented trackways, as well as by displacement rims according to the direction of movement in the slope, when they are available. Therefore, we used this criterion to orientate the footprints in the slope, with the forefoot marked deeper in an ascending trackway and the heel print deeper in a descending trackway. The main trackway results from the overlapping of trackways B and C (Fig. 5A). Apparently, a single producer, or producers with similar average footprint sizes, followed the same trajectory, first making some angle with the dip and then walking parallel to the strike in the upper part (and vice versa in the descending trackway). The intersection of footprints C1 and B6, C2 and B5, the sliding of C3 over B2 and C4 and B1, show that the first trackway to be produced was B and that some of the footprints of this trackway were used when trackway C was

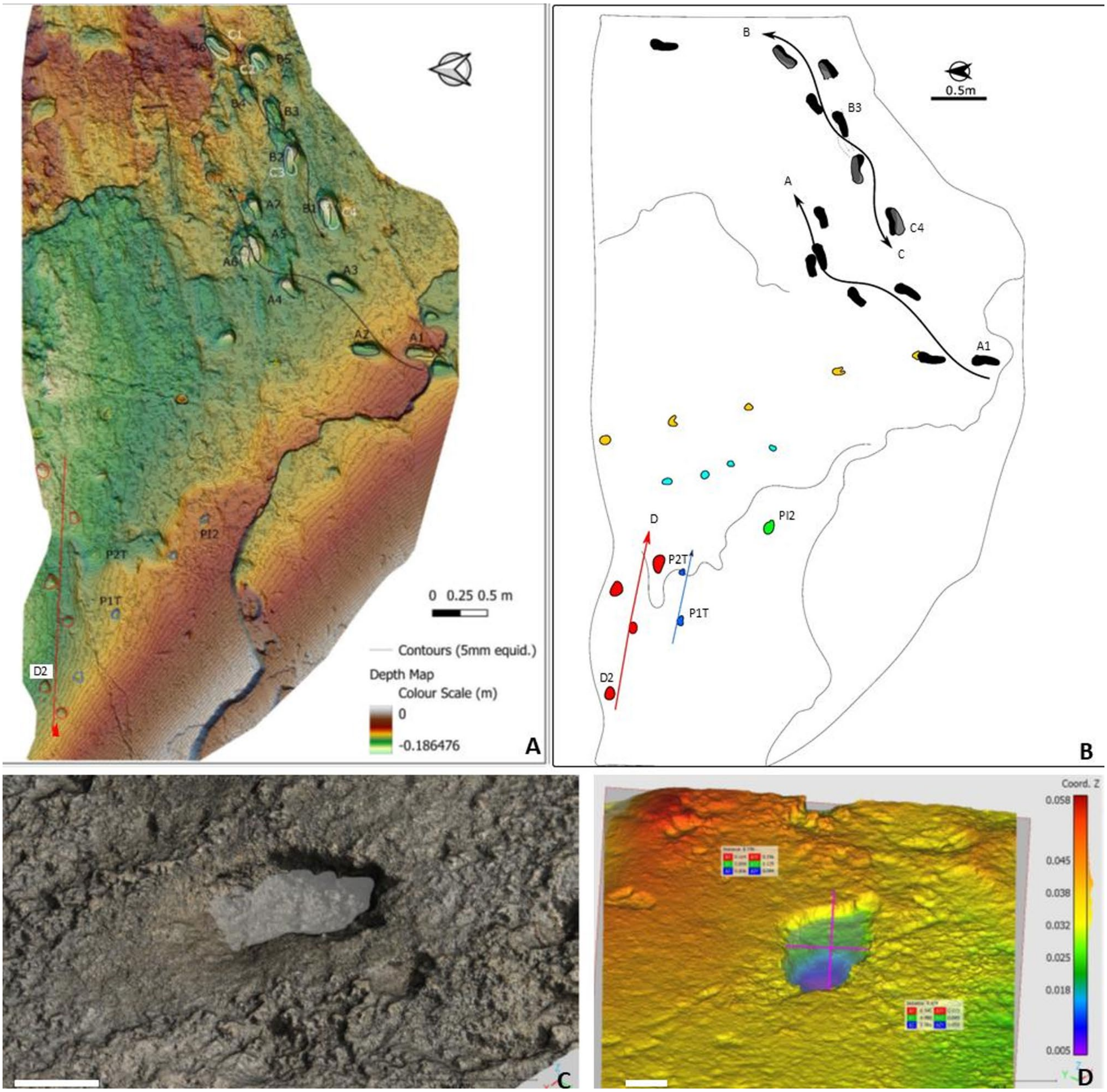

Fig. 5. Photogrammetric models from the main track-bearing surface from Monte Clérigo. (**A**) Depth map showing the distribution of the trackways and footprints described in the text. (**B**) Bidimensional interpretation of the trackways and locomotion trajectories described based on the 3D model; in yellow and light blue are represented the artiodactyl trackway and an undetermined trackway, respectively; (**C**) 3D image in real colors of the footprint P1T highlighting the main morphological features (scale is 5 cm); (**D**) Depth map of the PI2 footprint in an oblique angle to highlight the forefoot morphological features (scale is 5 cm). Depth maps and 3D image produced with MeshLab 2020.1288 (https://www.meshlab.net/) and CloudCompare 2.11.0.89 (https://cloudcompare.org/), and compiled using Inkscape 0.92.390 (https://inkscape.org).

formed (Fig. 5B). Only the pairs C1/B6, C2/B5 and B1/C3 show evidence for displacement rims. The steepness of the slipface of the dune was prone to avalanching as it can be seen by the development of the apron in the bottom of the slipface, and the general lack of displacement rims. Therefore, the missing of a few footprints may be related with the gravitational movement of the sand.

The composite trackway is about 600 cm long and composed of 10 footprints. Trackway A is 307 cm long and formed by seven footprints. The bottom two footprints are oriented parallel to the surface strike and then the trackway bends to 27°NE. Apparently, it was formed after the trackways B and C. Overall, footprints in trackways A, B and C are plantigrade, entaxonic, with an average length of 26 cm (A), 26.5 cm (B) and 28 cm (C) and an overall width of about 9.9 cm (A), 10.4 cm (B) and 12.2 cm (C). The measurements of these trackways are under the 10% error defined for footprints made in sand[23]especially in a slope surface, and therefore they were probably produced by a single individual ascending the dune in two different moments and descending in another moment (Fig. 5B).

Footprints indicate both inward and outward foot rotation with respect to the trackway midline, with values ranging between − 15° to 20°. In trackways A and B, the pace length is short relative to foot length and a pace angulation of 125°, a consequence of walking uphill on a yielding substrate[44]. In trackway C the stride length is two to four times larger than measured in trackways A and B, respectively, and pace angulation increases to 175°. In general, trackways show narrow instep or stride width but, as with the pace length, it can change abruptly. On a yielding dune slope, the resultant swiveling motion of the foot may produce a broad, smudged heel area and blurred digit impressions (Fig. 4G). Longitudinal slippage, internal and external rotation is consistent with individual's feet failing to gain the traction necessary to maintain forward motion before and during the midstance stage and during plantar-flexion in the later stages of stance[77]. Constant adjustments to travelling direction, abrupt changes in pace length and instep width, as well as gait asymmetries reflect walking perturbations while negotiating the dip angle variations in the very soft ground of the dune slipface. Overall, the choice of a diagonal curving trajectory on the dune slope would have eased progression by lessening the slope.

Very small footprints can also be observed at Monte Clérigo (P1T and P2T). It corresponds to a pair of left-right footprints located in the avalanched apron of the slipface, orientated uphill and separated by 42 cm. The left footprint (Fig. 4E) is 11 cm long and 6 cm wide. The medial longitudinal arch is not clearly defined as the footprint reveals lateral slippage, but also because it may likely be undeveloped in this very young producer (see below). This footprint is shallow and less mediolaterally narrow than the largest ones when better preserved, and the rounded heel is not evident, suggesting a flatter foot (width/length ratio or footprint index of 0.55). There are traces of toes preserved, although the hallux is tipping by forward dragging (Fig. 5C). A large displacement rim is developed around the heel in good accordance with the dip (Fig. 5C). The fainted right footprint (Fig. 4F) is preserved on the top of the avalanched sand accumulated at the bottom of the slipface. It shows only the toes I–IV well marked with the typical mediolateral decrease of the length of the toes. The proportions are similar to the previously described footprint, especially the footprint width. The hallux is the deepest toe which is in full agreement with the transference of peak pressure during foot-off. The pace length between the two small footprints is problematic and the preservation of, at least, two other shallow footprints in between should be missing.

A single left footprint (PI2) is displayed 1.6 m southeast from the last trackway, showing a rounded adducted hallux and toe angle declination, besides a broad rounded heel (Figs. 4C and 5D). Again, the deepest part of the footprint is in the hallux and agrees with the position of the footprint facing uphill. The footprint length and width are 17.3 cm and 7.2 cm, respectively, with a footprint index of 0.42.

The stature was estimated for the trackways A, B, C, footprint 1 in trackway E and isolated footprint PI2, following the classic Tuttle's approach[133]which is based on the ratio between foot length and stature in modern humans (foot lengths vary between 14 and 16% of stature). As for comparison, we used the equation of Duveau et al.[26] obtained from osteometric database encompassing different modern populations around the world to calculate stature (S) from footprint length (L):

$$\mathrm{S} = 6.51 \times \mathrm{L} \tag{1}$$

.

For age class estimates, we used the foot/stature ratio proposed for Neanderthals by Duveau et al.[26]. Their model was established from the osteological remains of 36 Neanderthal individuals including 11 children and 25 adults, based on allometric relationships between limb bone size and body height. Trackways A, B and C follow in the same range of statures (1.63–1.86, 1.66–1.89, and 1.75–2 m, respectively; note that trackway C shows evidence for longitudinal slippage), so it is fair to presume they were made by the same adult male individual, most likely measuring between 1.69 and 1.73 m according to Eq. (1). Footprint PI2 was produced by an individual 1.08–1.23 m tall (1.13 m estimated with Eq. 1), corresponding to a Neanderthal child between 7 and 9 years old (using the age-to-stature regression curve to Neanderthals[26]). Finally, trackway E was produced by an individual 0.69–0.79 m tall (0.72 m using Eq. 1), representing a Neanderthal toddler < 2 years in age (according to the same age-to-stature curve).

The stride length, as the distance between corresponding points of two successive right or left footprints, was measured for trackways A, B and C. Foot/stride ratio provides a measure of the relative walking speed[44]. Speed estimates were possible using step and stride length records[134]. The calculated speed based on the Alexander's equation,

$$\mathrm{v} = 0.25\mathrm{g}^{0.5}\mathrm{l}^{1.67}\mathrm{h}^{-1.17} \tag{2}$$

where v is speed (m/s), g is the constant for the acceleration of the gravity (9.8 m/s^2), λ is the stride length (m) and h is the estimated height (m), was for trackway A of 0.7 m/s (2.5 km/h), representing a slow walking speed which is expected for an adult climbing a 28–35° slope. Presumably, the individual even stopped on the way up in footprint pair A5 and A6. Furthermore, trackway B shows drastic slowing in travel speeds, from 1 m/s to 0.3 m/s (3.6 km/h to 1.1 km/h). As expected, the walking speed in trackway C is much faster descending the slope (2.3 m/s or 8 km/h), which is logically related with the increasing stride length.

Besides hominin trackways, there are some artiodactyl didactyl tracks, possibly produced by large red deer, taking into consideration the shape (longer than wide) together with the size (up to 13 cm in length) in the biogeographical context of SW Iberia[71]. One trackway is composed of five tracks and was produced by an animal walking SSE across the surface (Fig. 5B). One of these tracks was intersected by the footprint A2, providing the relative time order in which both artiodactyl and hominin prints were produced. One hundred meters distant from the main track-bearing level there are two more track levels trampled by different animals, including shorebirds, artiodactyls and other indeterminate forms. It thus appears that the unvegetated steep faces of the coastal dunes at Monte Clérigo have been often crossed by different small-to-large size animals, including Neanderthals, in different time periods.

A single possible hominin footprint was found in the eolianite from Praia do Telheiro (Fig. 4H). The footprint was exposed by the erosion of the eolianite cropping out in a deeply incised stream valley. Part of the slope collapsed revealing among the scree large boulders with several laminae surfaces exhibiting bird and undetermined tracks. Most of the tracks and the suggestive hominin footprint come from the lower part of the foreset dipping 14° SW. Unfortunately, the laminae where the footprint is preserved were partially chipped off obliterating the possibility of finding a trackway. The footprint is complete although it preserves the hallux exaggerated by dragging, the ball partially filled with sediment from the upper laminae, the medial longitudinal arch and the rounded hill. Displacement rims follow the margin of the footprint, but they are thicker around the heel. The other toes are not preserved, or they are covered by a thin displacement rim. The deepest parts of the footprint, i.e., the ball and the heel, are partially filled with sediment. The footprint is 22.6 cm long and 7.6 cm wide, representing a slim foot, with a footprint index of 0.34. The hallux is 4.6 cm long and tapers towards the tip. The stature estimate from footprint length is between 1.41 and 1.61 m, or 1.47 m using Eq. (1). Applying the age-to-stature regression curve to Neanderthals[26]the footprint can be attributed to an adolescent or an adult, most likely a female. The absence of a trackway prevents further descriptions and interpretations regarding this footprint.

In the Praia do Telheiro footprint, but especially in the Monte Clérigo trackways developed in sloped dune surfaces, there are no major displacement rims of sand, implying that the strain was accommodated via compression[77]. Moreover, wet sediment usually causes less displacement of sediment around the margins of the track. Softer substrates are associated with deep vertical-shafted prints and reduced medial longitudinal arches[77]. Traces impressed on damp sandy sediments are usually deeper than those printed in mud sediments. The contour of the prints are regular and the footprint walls are smooth. Therefore, our interpretation is that these trackways present at Monte Clérigo were produced in a rain-dampened sand surface, at the steep slipface of a dune. Tracks which show a similar preservation condition are assumed to be made simultaneously, or in a temporal proximity that can be measured by hours or a day or so[18,135,136]. Therefore, all the trackways preserved in the Monte Clérigo tracksite, including the different Neanderthal trackways and the artiodactyl trackway were produced in a very short time span between them. Due to the sedimentary dynamics in a mobile dune system and related foreset steepness it is very unlikely that the track-forming surface may have been reactivated. Foreset avalanching may have preserved some footprints, while destroyed some others, and removed and faded almost all displacement rims. The surface was covered by sand avalanches in the steep slipface which allowed the footprints to be protected from further surface erosion.

Results

Neanderthals in coastal habitats: contexts in the Iberian Peninsula

(a) Footprints and behavioral ecology.

Footprints provide direct evidence for the presence and persistence of hominins in oceanic coastal areas during the Pleistocene (Fig. 1 and Table S2). However, it is virtually impossible to identify any hominin taxon using morphological features of even the best-preserved footprints. For example, Neanderthal foot bone proportions and morphology are mostly indistinguishable from those of modern humans, with the exception of several distinct Neanderthal features in the talus[137]. Pleistocene hominins, including Neanderthals and modern humans, share foot proportions, morphology indicative of longitudinal and transverse arches and a fully adducted hallux[138,139]. However, Neanderthals differ from AMHs in having more robust tarsals, metatarsals, and proximal phalanges, which are suggestive of adaptations to increased locomotor loading[138,140,141]. These features can hardly be reflected in the Neanderthal footprints, especially when they are compared with modern communities that are used to walk unshod under intense locomotor regimes[142]. With extraordinary exceptions, taxonomic attributions of Pleistocene hominin footprints are not usually based on associated osteological remains, but indirectly assessed from chronostratigraphic criteria and, more rarely, lithic technologies[26,33]. Therefore, only with geochronological well constrained track-bearing beds, footprints become in vivo behavioral references and evidence for ecological interactions of a hominin species, of great archeological or paleoanthropological significance[23]. Monte Clérigo and Praia do Telheiro hominin tracksites, dated to ca. 78 ka and 82 ka, respectively, can be confidently attributed to Neanderthals, in a period where no other hominin was present in the most southwestern part of Europe[6,29,143–148]. This late demise in southern Iberia was probably related with the diversity and abundance of resources, as well as the relatively ecological stability of the Neanderthal territory[149] in Mesomediterranean and Thermomediterranean regions, especially in coastal areas under the climate amelioration of the ocean, until the Heinrich events[150–152].

Single track-bearing surfaces afford a degree of association seldom achieved in the skeletal fossil record[153]. This is the case of Monte Clérigo site in SW coast of Portugal, where hominin trackways are spatially and temporally associated with artiodactyl tracks by overprinting. When both human and animal tracks are analyzed having equal importance, they can provide unique information on past social behavior and ecology. The distribution of the footprints with respect to the proximity to the shoreline (coastal dune) provides a snapshot of the movements of multigenerational Neanderthal individuals (toddler, child and adult(s)) at the Monte Clérigo site (as for AMHs in the Atlantic coast of Morocco[16]). In this context, the bimodal orientation of the Monte Clérigo trackways in the dune slope towards the shore and returning could potentially indicate foraging food resources, whether marine edible food or search for game in the dune field departing from the campsite that should be in a close range. The presence of footprints of a toddler seem to reinforce the proximity of the campsite.

The Monte Clérigo's scenario is comparable chronological and ecologically to the well-studied Le Rozel tracksite found in a coastal dune setting from Normandy[26]. At Le Rozel, a rich lithic industry was found associated to the footprints, and about 8000 faunal remains which attest anthropic operations, such as butchery and lithic industry production[26]. Based on the stature estimate from the footprint length, a minimum of 4 individuals, more likely 10 to 14 individuals, constituted a social group mainly composed of children (51.4% of the total footprints[67]), including < 2 years old toddlers with a minimum height of 67 cm. Despite Duveau et al.[26] concluded that Le Rozel, together with El Sidrón in Spain, are the only sites providing reliable information of the composition of Neandertal social groups, Duveau[67] remarked that is impossible to know whether the main track-bearing surface is representative or not of the whole social group. The study of the slaughter periods of the fauna found associated with the footprints enabled to estimate that Neanderthal brief occupations in Le Rozel took place between autumn and spring[154,155].

The brief presence of Neanderthals in other coastal areas of SW Iberia directly associated to potential food resources in tracksites has been recognized. In the Matalascañas Trampled Surface, a congregation site with abundant presence of red deer, aurochs and mostly straight-tusked elephant calf and juvenile tracks shows hominin trackways with contemporary lithic artifacts in close spatial association, suggesting food procurement and processing during late spring[33]. At the Cape Trafalgar tracksite[71]a newly found track-bearing level corresponding to a beach deposit includes clusters of hominin footprints and aurochs tracks. The single hominin footprint attributed to a Neanderthal in the dune sandstone of Catalan Bay, in Gibraltar, is also associated to ungulate tracks[34].

Other tracksites recognize the visiting, and occasional recurrent presence of hominins in coastal areas, at least back to almost 1 Ma in Happisburgh, England[36]. This is certainly the case for the South Africa hominin tracksites found in dune settings and preservational conditions similar to Monte Clérigo and Praia do Telheiro and attributed to AMHs. Here they occur together with highly diverse track ichnoassemblages, some of them produced by large mammals that could potentially be food resources for humans during the Last Interglacial[43,45,46,55,156]. The mid-Holocene coastal environments of Formby Point, northwest England, show abundant animal tracks and human footprints in 31 track and footprint-bearing beds[157,158]. They represent the persistent return to the coastal mudflats by generations of people. The human trackways show a bimodal direction, with most of the trackmakers travelling in a southwest direction, towards the paleo-coastline, with fewer trackmakers travelling inland in a northeast direction[159]. The trackways suggest slower-paced activities by the women and children such as for shellfish gathering, and a longer stride length for the men with imprints, suggesting running after game, mostly deer and aurochs[160]. In fact, in one case a staggered wide-straddled gait suggests attempting to influence the animal's direction of movement[161].

One of the remarkable aspects of Monte Clérigo site is the finding in a dune slope setting of very small hominin footprints, with no clear medial longitudinal arch and heel. Flatter feet for the youngest Neanderthal individuals < 2 years old were also identified in the footprints of Le Rozel[26]. In modern humans, a child's foot elongates as it grows and the arch becomes fully established in the first 6 years of growth[162]. Typical features of footprints made by modern young children is tapering heel, the absence of a medial longitudinal arch and the relative proportions of the digits to the main body of the foot. Knowledge about the rate of growth and development of Neanderthal children is limited. Trinkaus[138] affirmed that during the first year of life, Neanderthal children are identical to the children of modern humans, but this morphometric comparison is mostly based on cranial remains. Rosas et al.[163] coincides with Trinkaus and go further in sustaining that Neanderthal's growth rate is very similar to that of AMHs, in general. In Theopetra cave, the four footprints attributed possibly to Neanderthals were made by young children whose ages and statures are estimated to 2–4 years and to 86 and 100 cm, respectively[73]. Altamura et al.[164] also recognized children potentially as young as 12 months old at Gombore II-2, Melka Kunture (Ethiopia), attributed to *H. erectus*[19,165]and associated to butchered hippo osteological remains. The fact that in the context of Monte Clérigo infant footprints were found together with those of older individuals suggests that children were present when adults performed day-to-day activities. This was also observed at Gombore II-A, Le Rozel, Formby coast and Monte Hermoso in the coast of Buenos Aires[58]which may indicate that children may have had to start learning these skills at a very young age[164].

(b) Neanderthal coastal sites and food resources.

Monte Clérigo and Praia do Telheiro tracksites mark the presence, although fortuitous, of Neanderthals in the SW coast of Portugal. Salazar-García et al.[166] indicate highly territorial mobility of Neanderthal groups with seasonal occupation of sites in southern Iberia. Studies in southwestern Iberia suggest that Neanderthals consumed predominantly medium and large-sized game[167], with some evidence for small prey[168]. In several areas, Neanderthals added marine resources. The non-specialized hunting strategy is associated with short, temporally separated occupation of the caves[166,168].

Neanderthal diets are usually reconstructed on the basis of stable isotope ratios, as well as dental calculus samples and fecal biomarkers. Osteological remains found in direct association with Neanderthals and Neanderthal-related lithic artifacts and hearths also contribute to reconstitute diet ecology, especially if they have evidence of cut-marks and cooking. Faunal evidence from Middle and Late Pleistocene sites in Spain, France, Italy, Germany, Russia, and Ukraine proved that Neanderthals had been proficient top-level hunters[169–178]. Stable isotope analysis of Neanderthal remains, e.g. from Spy Cave in Belgium and Vindija Cave in Croatia, corroborated the faunal evidence, suggesting that the Neanderthals in northern Europe, and especially during the cold stadials, obtained protein almost exclusively from animal-based food[179–183]. There is increasing evidence that Neanderthals also consumed small game, birds (birds provided not only meat, but also eggs and their feathers would be used for adornment) and plants, and that they frequented coastal areas since early times to consume fish, mollusks and marine mammals[3,8,184,185]. Collectively, archeozoological remains are considered by researchers as irrefutable evidence that these resources were gathered along the coast. Faunal skeletal remains, which are common on archaeological sites, provide the overwhelming abundance of evidence for Neanderthal subsistence. Although in many cases, such deposits result from carnivore activity or other factors. In fact, faunal assemblages may accumulate over long periods and in most cases, one can only make broad inferences and cannot rule out that some part of an assemblage had been naturally deposited[186]. Tracksites prove the capacity of coastal sedimentary environments to reliably preserve the track record of an ecological community in action, and therefore of Neanderthal ecology and their dietary behaviors[166]thus complementing the records obtained by the other study approaches.

The new tracksites in SW Iberia reinforces the ecological scenario in which Neanderthal groups made extensive use, at least seasonally, of coastal environments. An increasing number of Neanderthal coastal caves and open-air sites has been identified in the Atlantic and Mediterranean coasts of Iberian Peninsula (Fig. 6 and see Supplementary text S1).

All the coastal caves, open-air sites and tracksites have in common a brief but mostly recurrent (over 110 ka in Gibraltar and 60 ka in Portugal) presence of Neanderthals with a broad spectrum of food options seasonally available in the coastal flats, estuaries and lagoons. According to Mellars[187]Neanderthal groups practiced a relatively broad-spectrum foraging pattern, usually involving substantial exploitation of at least three or four different species, especially including reindeer, horse, large bovids, and red deer.

Many natural, social, and technological systems can be effectively described through web-like structures that capture the interconnections between their constituent units[188]. Examples include social networks, which connect individuals via friendship relationships; food webs, which map species through trophic interactions; and the World Wide Web, composed of webpages linked by hyperlinks. Adopting this network perspective, we modeled the Neanderthal-bearing sites in coastal Iberia of Fig. 6 as a single network that represents associated faunal taxa as nodes, co-occurrence relationships as links, and probability of co-occurrence as link weight (Fig. 7).

The resulting network, herein named the Neanderthal network, is made of 20 nodes (taxa) and 141 links (co-occurrence relationships). Since all the sites comprise evidence for Neanderthals, this network is an ego network, that is, a network consisting of a single actor (ego, that is, Neanderthals) together with the actors they are connected to (alters) and all the links among those alters[189]. Consequently, the topology of this network results from the ecological and taphonomical dynamics that influenced the formation of Neanderthal coastal sites in the Iberian Peninsula.

A fundamental aspect of network topology is the degree of a node, which quantifies the number of links incident to it, serving as a measure of prominence[190]. In the context of the Neanderthal network, which includes 20 taxa and does not include self-loops, the maximum possible degree a node can achieve is 19. This maximum degree indicates that a taxon is linked to every other taxon in the network, highlighting its extensive co-occurrences within the Neanderthal-associated ecosystem. This is the case of Equidae (degree = 19), signifying an association with every other taxon in the network (Table S5). This indicates the nearly ubiquitous presence of horses in Neanderthal-bearing assemblages, suggesting their significant ecological and nutritional role. In other words, the high degree of Equidae implies that horses were likely a crucial food resource for Neanderthals. Similarly, other high-degree taxa such as Leporidae, with a degree of 18, and Bovidae, with a degree of 17, are also highly connected within the network. These connections suggest that these animals were also central components of the Neanderthal diet, reflecting their ecological prominence in the coastal environments inhabited by Neanderthals. In stark contrast, Hippopomidae and Hystricidae exhibit the minimum degree of the Network (degree = 6), suggesting a low level of 'associatedness' within the ecosystem inhabited by Neanderthals. The low connectivity might be indicative of several underlying ecological and taphonomic factors. Ecologically, the rarity of species such as porcupines and hippopotamuses could contribute to their limited presence within the Neanderthal coastal ecosystem. These species may have been less abundant or geographically restricted, thereby reducing their interactions with other species and Neanderthals. The risks and efforts required to procure such prey may have outweighed the potential benefits, thereby influencing their low degree of network connectivity.

Node betweenness indicates 'how between' a node is by considering the shortest paths passing through a given node[190]. High betweenness nodes lie between many others, connecting distinct structural areas of the network. The high betweenness of Leporidae and Equidae suggests their ecological versatility and prominence within Neanderthal diets. These taxa likely occupied diverse environments, serving as consistent food sources irrespective of the specific habitats Neanderthals frequented. Specifically, the dietary preferences of Neanderthals are supported by the evidence of horse fossils co-occurring with taxa from marine taxa, such as mollusks, crabs and seals. This pattern suggests that the foraging strategies of Neanderthals were flexible, enabling them to exploit terrestrial prey like hares and horses even when their activities comprised marine foraging.

↓ Sites	NOR [c]	TAN [d]	NFT [e]	Shellfish	Fish	Crab	Shak	Seal	Dolphin	Tortoise	Birds	Porcupine	Leporidae	Capridae	Suidae	Felidae	Bovidae	Cervidae	Equidae	Hippo	Woolly rhinoceros	Elephantidae	Mammuthus
1		●																					
2		●																					
3	●	●			●				●		●		●		●		●	●	●		●	●	
4	●	●		●	●	●	●	●	●	●	●		●	●			●		●			●	
5			●															●					
6			●																				
7		●		●						●			●				●	●	●				
8		●																					
9		●	●								●				●	●	●	●				●	
10			●														●	●	●				
11	●	●	●	●				●	●		●		●	●								●	
12		●		●																			
13		●		●																			
14		●		●						●				●				●	●				
15	●	●								●		●	●	●				●		●			
16	●	●																					
17											●	●	●					●				●	
18		●		●						●				●			●	●	●		●		●
19	●	●																●	●				
20		●												●				●					

[a] **MTS :** Matalascañas Trampled Surface
[b] **Gibraltar :** Gorham's, Vanguard and Ibex Cave, Catalan Bay, Devil's Tower and Forbes Quarry
[c] **NOR :** Neanderthal osteological remains
[d] **TAN :** Technocomplexes associated to Neanderthals
[e] **NFT :** Neanderthal footprints and trails

Fig. 6. Distribution of Neanderthal coastal sites in Iberia. The selected sites include coastal caves, open-air sites and tracksites. The faunas stratigraphic and geochronological associated to the direct (bones) or indirect (footprints, artifacts) remains of Neanderthals provide diagnostic information to reconstitute their dietary ecology. Map produced with Corel Draw X8 (www.coreldraw.com).

In contrast, taxa typically associated with marine environments, such as Pinnipedia, Brachyura, and Selachii, display zero betweenness, underscoring the environmental specificity of these taxa and, plausibly, the fact that only some Neanderthal populations foraged on marine animals. These taxa are confined to particular niches, indicating a clear separation from terrestrial habitats associated with typical Neanderthal activity. Interestingly,

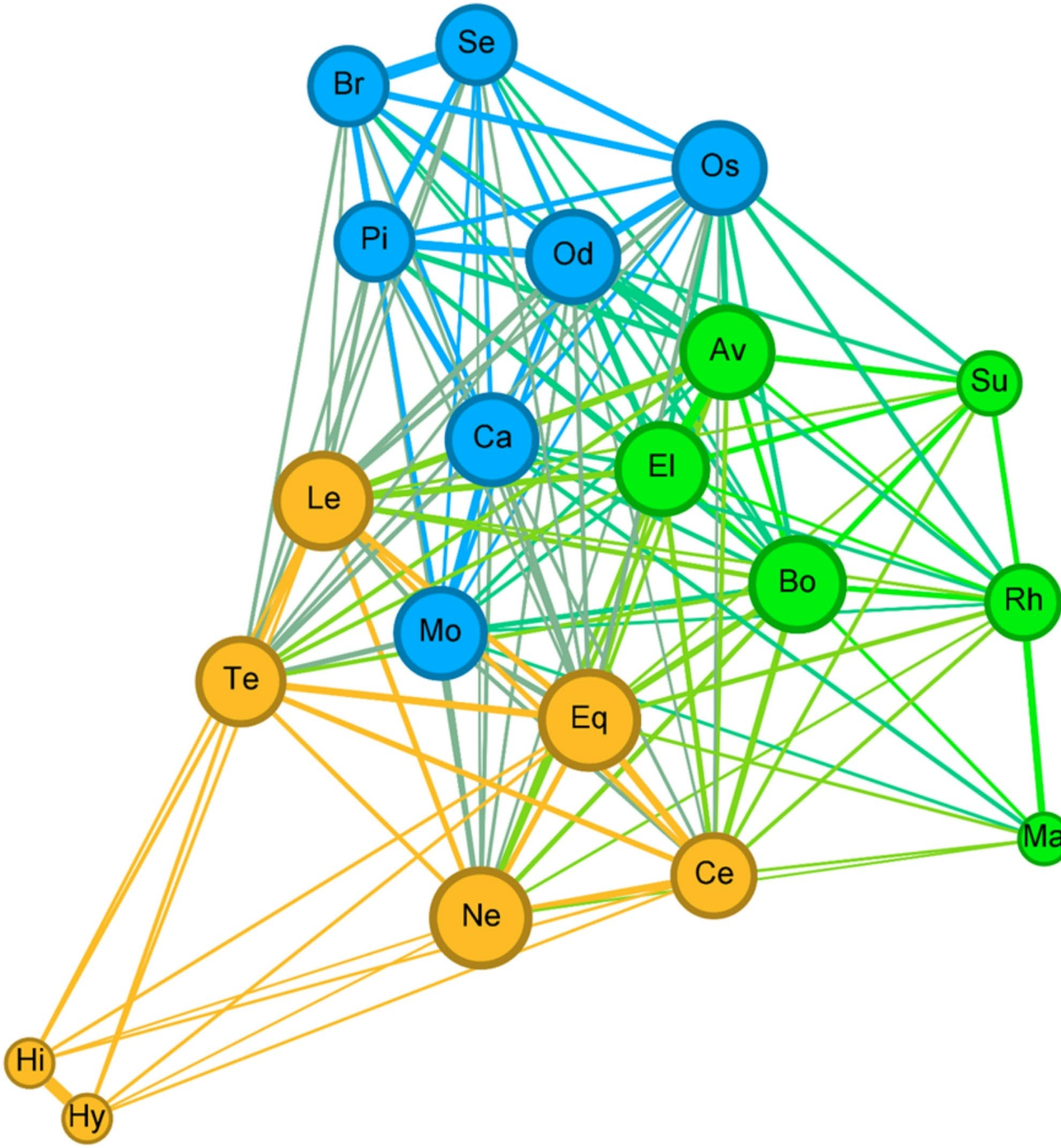

Fig. 7. Neanderthal network in coastal Iberian Peninsula. Taxa abbreviations: *Ne* Neanderthal, *Ce* Cervidae, *Te* Testudinidae, *Eq* Equidae, *Le* Leporidae, *Hi* Hippopotamidae, *Hy* Hystricidae, *Bo* Bovidae, *Su* Suidae, *Ee* Elephantidae, *Ma* Mammoths, *Av* Aves, *Rh* Rhinocerontidae, *Mo* Mollusca, *Ca* Capridae, *Od* Odontoceti, *Pi* Pinnipedia, *Br* Brachyura, *Se* Selachii, *Os* Osteichthyes. Node size is proportional to degree; link thickness is proportional to co-occurrence probability, quantified by the Jaccard index; node and link color reflect modularity-based clusters (see also Table S5).

some highly mobile terrestrial taxa—including Hippopomidae, Hystricidae, Suidae, and mammoths—also exhibit zero betweenness. The low betweenness centrality of these species may imply that they were habitat-restricted, which consequently affected their interactions with Neanderthal populations in coastal areas. Such restriction could mean that only specific groups of Neanderthals had access to these taxa as potential resources. For instance, Hippopomidae are typically associated with specific aquatic or semi-aquatic habitats, such as rivers and lakes. Such environmental constraints could limit their availability to Neanderthal groups occupying coastal ecological niches. In addition, low-betweenness taxa may suggest the influence of a taphonomic filter affecting their preservation within the fossil record. Taphonomic processes may have selectively altered the representation of these taxa, thus impacting their apparent connectivity within the network.

In many real-world networks, the distribution of connections is not uniform but rather organized into groups of tightly connected nodes, forming dense subnetworks within the larger network. These dense subnetworks, referred to as clusters, groups, or communities within network theory, are pivotal for understanding the large-scale structure of the network[122,191]. Identifying these clusters provides insights into the overall organization of the Neanderthal network, revealing how individual taxa are framed within the broader ego network. The challenge of detecting these clusters involves partitioning the Neanderthal network into sets of closely knit nodes, a process that can be quantitatively assessed using modularity optimization (see Blondel et al.[192]and Fortunato[191] for details on modularity optimization algorithms). The modularity of a partition measures the density of links inside it as compared to links between partitions[191,192]. By optimizing modularity, and considering link weights, it is possible to detect effectively three 'natural groups' (modularity-based clusters) within the Neanderthal network:

1. Group A: Neanderthal, Cervidae, Testudinidae, Leporidae, Equidae, Hippopotamidae, Hystricidae.
2. Group B: Bovidae, Suidae, Elephantidae, Aves, Mammoth, Rhinocerontidae.
3. Group C: Mollusca, Capridae, Odontoceti, Pinnipedia, Brachyura, Selachii, Osteichthyes.

These modularity-based clusters are best understood as sets of densely interconnected nodes, and low concentrations of links between these groups of nodes; hence, their constituting elements are likely to share common properties[191]. In the Neanderthal network, these clusters are taxa assemblages and the shared property is plausibly the habitat of the taxa. In fact, group C includes marine taxa, except for Capridae; group B includes terrestrial taxa, while group A includes taxa with terrestrial and semi-aquatic preferences.

The clustering of taxa into distinct habitat-related groups highlights the opportunistic foraging strategies employed by Neanderthals. The composition of each cluster likely stems from the specific ecological conditions encountered by Neanderthals during their activities. For instance, group C suggests a focus on marine resources during periods or in regions where these were abundant, whereas group B and group A indicate a reliance on terrestrial and semi-aquatic resources, respectively. Specifically, the formation of group C, which includes solely marine taxa, group B with predominantly terrestrial taxa, and group A comprising species with both terrestrial and semi-aquatic preferences, underscores the adaptability of Neanderthals to the resources available in their immediate environment. The composition of the modularity-based groups indicates that Neanderthals were adept at exploiting the diverse resources offered by the various habitats they inhabited.

In conclusion, from the correlation chart of Fig. 6 and the Neanderthal network provided in Fig. 7, the main food resources consumed by Neanderthals in Iberian coastal areas were large game (horse, aurochs) and leporids. Shellfish consumption has been documented in seven sites, although mostly in small proportions[3].

Monte Clérigo and Praia do Telheiro tracksites add to an increasing number of sites found in Western Europe, and especially in SW Iberian coastal deposits where hominin footprints were attributed to Neanderthals, under a time range of ca. 70 ka. These are Matalascañas Trampled Surface[33,35,61,62] and Catalan Bay[34] dated to late MIS 6-MIS 5 transition, Cape Trafalgar[71] dated to MIS 5d, Le Rozel[26], Praia do Telheiro and Monte Clérigo (this paper) dated to MIS 5a. Therefore, there is an increasing amount of information provided by the tracksites that can be added to our knowledge about the recurrent presence and persistence of Neanderthals in coastal habitats, during a period that goes from MIS 9–8 to virtually their late demise in southern Iberian refugia, ca. 32 ka[6,29,31,147,151,152,189–191]. The tracksites from SW Iberia, in most cases, could be associated to active procurement of mega-herbivores, such as hunting, stalking prey or opportunistic scavenging on weakened, or dead animals in a predictable, seasonal and spatial repetitive ecosystem[33]. Neanderthals were best sorted to ambush hunting large mammals[174] with the use of thrusting spears[177]. Dune systems offer a hilly terrain composed of a heterogenous plant cover dominated by grasses and bushes, and a loose sand substrate, that can greatly reduce the speed reactions of ungulates to predators. According to Braza and Álvarez[197], red deer is found in all different habitat types of Doñana National Park in the coast of Andalucia (southern Spain), although showing a slight seasonal preference for the shrub and dune areas. Indeed, red deer usually moves towards the more humid areas only during the summer and beginning of autumn. In the coast of Doñana and El Asperillo, female deer and juveniles are frequently found during summer refreshing in the shore. According to one of us (JMG pers. obs.), if they are stalked from the beach, e.g. by dogs, they don't hesitate to jump into the water and swim away. If they are stalked for a long time from ashore or cannot deal with the currents, deer may die by drowning, with their bodies washed up on the beach. Therefore, it is a likely scenario that sites such as Monte Clérigo (Fig. 8) and Matalascañas, where Neanderthal footprints overprint artiodactyl tracks in dune slopes and interdune seasonal lakes, constituted successful hunting grounds. These presumably seasonal sites were used by practitioners of ambush hunting or stalking prey on non-selective single prey.

Conclusions

An increasing number of hominin tracksites has been found in SW Iberia dated from the Neanderthal period. The first tracksites found in SW Portugal eolianites are attributed to Neanderthals by considering the chronostratigraphic context, dating to ca. 82–78 ka. The tracksites of Monte Clérigo and Praia do Telheiro are new additions to the increasing track record of hominins in Pleistocene coastal deposits. Southern Iberian Peninsula was arguably the home of the potentially latest surviving Neanderthals, the coastal areas providing a diverse mosaic of mild habitats and a menu of food resources during the cool interstadials and harsh climate of the Heinrich events. Hominin tracksites further support the ecological relationships between Neanderthal populations and coastal areas. When these tracksites are added to other open-air sites and coastal caves known in Iberian Peninsula, the functional ecological significance of coastal areas to Neanderthals is improved. They

Fig. 8. Reconstituted scenario of Monte Clérigo tracksite, generated by AI tools following the guidance, and final artworks of J.M. Galán (ChatGPT-4 was used to select the prompts, at https://openai.com/index/gpt-4/; Image Generator Pro to generate various versions, at https://imagegeneratorpro.com; DALL-E3 for the nuances and quality of the image, at https://openai.com/index/dall-e-3/; Photoshop 26.4.1 (www.adobe.com) and digital pencil of Procreate for iPad version 5.3.14, at https://apps.apple.com/us/app/procreate/id425073498, for drawing over the selected image version).

mark the presence of Neanderthals in beach and dune systems with abundance of marine resources and leporids, as well as interdune ephemeral lakes that served as congregation sites for potential large game prey. Network analysis offers a comprehensive view of the dietary preferences and ecological interactions of Neanderthals in coastal areas:

- Neanderthal diet was primarily centered on large game (Equidae, Cervidae) and hares (Leporidae). These taxa consistently appear within the Neanderthal menu, underscoring their importance as staple resources. The consistent presence of these taxa in coastal areas highlights their role as reliable food sources, irrespective of the varying environments Neanderthals inhabited.
- The Neanderthal diet also incorporated animals from neighboring habitats, indicating a broad foraging strategy that capitalized on local biodiversity. This approach allowed Neanderthals to exploit a range of available resources, adapting their dietary habits to the specific ecological conditions they encountered. Such dietary flexibility is indicative of their capacity to efficiently navigate and utilize the diverse resources offered by their environment.

Seasonal hunting campsites provide a good picture about the movement of family-sized groups in coastal dune systems. At the Monte Clérigo site, the presence of footprints attributed to, at least, one male adult, one child and one toddler, negotiating the steep slope of a dune, allow us to speculate about close proximity to the campsite. Overprinting with large mammal tracks shows that the presence of Neanderthals in these environments was intentional even if seasonal, possibly searching for food opportunities provided by the potential prey reproductive cycles and taking benefits from ambush hunting or stalking prey in a rugged dune landscape.

Data availability

Data refers to Neanderthal sites in coastal Iberian Peninsula; Review summarizing the main coastal caves and open-sites with Neanderthal remains in the Iberia Peninsula; Pleistocene hominin tracksites in coastal marine environments; OSL data.Data is provided within the manuscript or supplementary information files.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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