Longitudinal population dynamics of Mediterranean-Atlantic *Arbutus* during the last 30 ka

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ABSTRACT

The current distribution of the genus *Arbutus* in the Old World prompts questions about its long-term population dynamics, location and extent of refuge areas, and modern vulnerability in relation to climate change and human activity. Our work aims to address these questions by combining modern occurrence data with a comprehensive survey of pollen and macrofossil records. Range maps of past distribution have been produced for the last 32 ka to investigate geographical trends in population dynamics and the timing of the appearance of *Arbutus* across different biogeographical regions. In the Atlantic domain, *Arbutus* has been consistently present during the last 32 ka, even during the Last Glacial Maximum. In the central and eastern Mediterranean regions, it progressively increased since the beginning of the Holocene, appearing along the coasts of the Black Sea and in the Levant during the Middle Holocene. In addition, the dynamics of *Arbutus* in a number of peripherals stands (Ireland, Canary Islands, Cyrenaica, Crimea, and Black Sea coasts) is discussed. The palaeobotanical evidence suggests that the delayed emergence of eastern populations and peripheral stands in the fossil record may be ascribed to a very low population density, rather than to a sequential migration process from the western sectors of the range. The comparison of fossil records and modern occurrences highlights an overall temporal continuity between long-term persistence areas and current centers of gravity and calls for density-weighted ecological models that may contribute to an informed assessment of conservation actions and strategies.

1. Introduction

Arbutus is a genus belonging to the subfamily Arbutoideae within the family Ericaceae. Most of the diversity in the Arbutoideae is found in regions of Mediterranean-type climate in the Old World and Western North America. The cluster "*Arbutus* complex" is supposed to have colonised Western Eurasia across the North Atlantic Land Bridge as part of the so-called Madrean-Tethyan Geoflora, a broadleaved sclerophyllous vegetation that extended across North America and Eurasia during the Paleogene (Axelrod, 1975; Hileman et al., 2001). According to Palamarev (1989), the *Arbutus* complex was present throughout Central Europe starting from the Oligocene. It was still common during the Miocene and Pliocene, when it was also present around the Black Sea (Palamarev, 1989) and in the Canary Islands (Anderson et al., 2009), displaying a longitudinal range extension similar to the present one.

In the Mediterranean-Atlantic domain, four species of *Arbutus* occur (Fig. 1a), according to the present-day outputs of phylogeny and taxonomy (www.iucnredlist.org; www.ipni.org; www.powo.science.kew.org; De Santis et al., 2023). *A. unedo* naturally grows along the Atlantic coasts of Europe, where it consistently occurs from the French Aquitaine to the entire coast of Portugal, and the Strait of Gibraltar (Caudullo et al., 2017). Scattered coastal populations reach northward Brittany and western Ireland and extend southward to the Marrakesh-Safi region. In the western Mediterranean regions, *A. unedo* occupies part of the central-southern Iberian Peninsula, the Pyrenees, and inland Aquitaine (Castroviejo, 2020). It shows a continuous range from eastern Spain to French Occitania. It shows a gap in the Camargue, but it is abundantly represented in Provence and continuously occurs along the Tyrrhenian coast of Italy. It is quite abundant in Corsica, Sardinia, and the Balearic Islands. It is scattered in the Mediterranean regions of North Africa facing the Mediterranean Sea (Morocco, Algeria, and Tunisia), Sicily, and the Eastern regions of the Italian Peninsula along the Ionian and Adriatic coasts, with a single outpost in the Euganean Hills (Pignatti et al., 2018). It is common along the Balkan coast, from Slovenia to
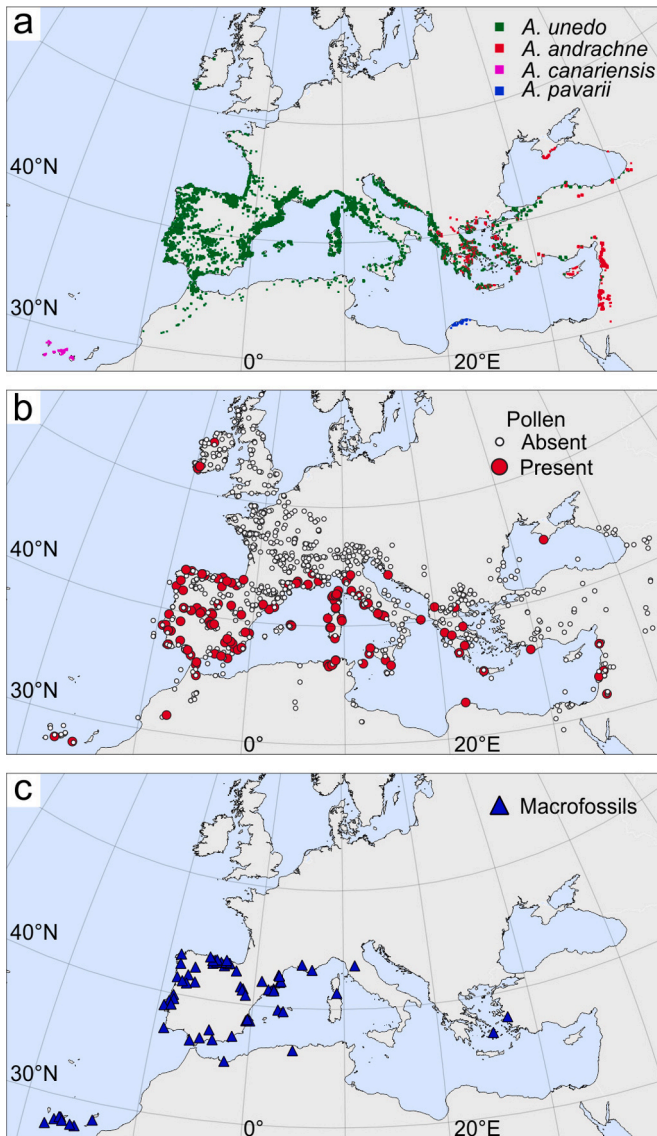

Fig. 1. Maps of (a) present-day distribution of the four *Arbutus* species in the Old World, b) fossil pollen records (*Arbutus* presence: red dots; absence: white dots), (c) macrofossil records (blue triangles).

southern Greece, including all the Ionian and Aegean islands, with a very restricted enclave in Cyprus and Lebanon, and scanty populations along the Mediterranean coast of Turkey and the southern coast of the Black Sea (Fig. 1a) (Davis, 1965; Strid, 2016). Most of the stands of *A. unedo* physiognomically conform to the so-called maquis, a thicket where *Erica* sp. pl., *Rhamnus alaternus, Pistacia lentiscus, Myrtus communis,* and *Phillyrea* sp. pl. dominate, sometimes with shrubby individuals of evergreen *Quercus* sp.pl. and other sclerophyllous taxa. It most often represents the result of a disruption of the broadleaved evergreen sclerophyllous forest rich in *Q. ilex* and *Q. suber*, or a permanent community on rocky outcrops and shallow soils (Pignatti, 1998). However, the stands along the Atlantic coast of France and Ireland stretch markedly outside the area of Mediterranean-type ecosystems, being hosted within coastal temperate deciduous forests, dominated by *Q. petraea, Carpinus betulus, Ilex aquifolium,* and *Betula pendula* as successional species, associated with *Taxus baccata, Buxus sempervirens, Corylus avellana, Sorbus aucuparia, Rubia peregrina, Calluna vulgaris, Ulex gallii,* and *Hedera helix.* Those stands belong to the so-called Lusitanian geo-element (sensu Dahl, 1998), a Mediterranean-like floristic stock extending along the Atlantic coast of Europe, shaping a

biogeographical disjunction between populations of the Northern Iberian Peninsula and Ireland, and often missing from Great Britain.

A. andrachne (Fig. 1a) is found in the Eastern Mediterranean Basin, from Istria (Croatia), through Dalmatia to western Greece and the Ionian Islands. It is abundant in eastern Greece, Crete, and the Aegean Islands, where it shares its geographic range with *A. unedo. A. andrachne* forms stands in Cyprus and the Levant, being one of the main components of the evergreen oak forests dominated by *Q. calliprinos*, of the semi-deciduous oak forests of *Q. aegilops*, as well as of the coniferous forests dominated by *Pinus brutia* and *P. halepensis* in south-western Anatolia, Syria, Lebanon, and Jordan. It displays scanty populations in Turkey with some isolated locations on the coasts of Georgia, stretching into the Euxino-Hyrcanian domain. Separate populations are located along the shores of southern Crimea, where they form pure stands.

A. canariensis (Fig. 1a) is confined to the Canary Islands, namely in the north-facing slopes of La Palma, El Hierro, La Gomera, Tenerife, and Gran Canaria. It is missing from Lanzarote and Fuerteventura, as well as from other Macaronesian islands (Madeira and the Azores).

A. pavarii (Fig. 1a) occurs in Cyrenaica (Libya), with abundant populations in the Al-Akhdar and Al-Jabal mountains, as a dominant element of the maquis, associated with other woody taxa such as *Ceratonia, Rhamnus, Pistacia, Olea, Cupressus, Smilax, Phillyrea*, and *Juniperus* (Hegazy et al., 2011; Kabiel et al., 2016).

A. x *andrachnoides* is a natural hybrid resulting from the cross between *A. unedo* and *A. andrachne*, native to the Balkan countries. It is hardly distinguishable from *A. andrachne* from leaf anatomy (Bačić et al., 1992), but molecular analyses provided a good tool to differentiate morphologically identical individuals (Bertsouklis and Papafotiou, 2016).

The modern geographical range of *Arbutus* prompts the question of how this complex distribution has developed since the last glacial period and more specifically it draws attention to locations and extent of refuge areas for *Arbutus,* postglacial dynamics in relation to dispersal capacity, spatiotemporal variations of the range, responses to climate fluctuations and increasing human pressure, and long-term persistence and potential vulnerability. Our work aims to answer these questions by analysing the fossil record available in the Old World and comparing it with modern ecology and distribution.

2. Biological traits of Mediterranean-Atlantic *Arbutus*

Arbutus species are evergreen small trees, often polycormic. Their habit suggests the persistence of a tropical atavism, as revealed by the yearly blooming simultaneous with the ripening of the fruits of the previous year. Larcher (2000) demonstrates their higher winter photosynthetic rate and resistance to frost compared to other sclerophylls. Adult trees tolerate frost without damage, but temperatures around −10 °C can eventually kill them (Sealy and Webb, 1950). Although low winter temperatures are a prominent limiting factor, summer drought is the ecological factor that most influences the reproduction system of blooming and seed germination (Martins et al., 2021). Both frost and drought concur with physiological stress. For example, the Irish populations often show dormancy and, even when looking healthy, they do not bear any fruit (Sealy and Webb, 1950). In Libya, *A. pavarii* propagates mostly in a vegetative way without producing flowers and seeds, because of the high rate of summer drought (Mosallam et al., 2017).

Arbutus has attitude for pioneering, displaying the ability to emit sprouts from a swollen stem base called lignotuber, shared with other species within the Ericaceae family (Freudenstein et al., 2016), and can escape fire when not sufficiently deep in the ground. This explains the steadfast persistence and longevity of some populations despite recurrent coppice and fire events, which eventually enable *Arbutus* to become a dominant constituent of the primary shrub/maquis vegetation type. However, *Arbutus* does not have a complete fire adaptation, since it does not propagate by seeds after fires and tends to disappear when repeated fires affect the soil at deeper layers (Bernetti, 1995). Sealy and Webb

(1950) noted its berries eaten by thrushes, blackbirds, and woodpigeons, although they observed that a large proportion of the fruits fall to the ground uneaten.

Palynologists are able to distinguish an *Arbutus*-type pollen grain from other Ericaceae. This pollen type, including all four species of the Old World, is characterised by a large diameter of the tetrad (D > 45 µm), with very thin exine, smooth sexine (usually psilate at the poles, and only faintly punctate in the mesoapertural zone), and the presence of isolated endocanalis (Mateus, 1989, www.paldat.org). According to several studies on current pollen deposition, *Arbutus* produces very small amounts of pollen; so it is seriously underrepresented even in communities where its abundance is high (Stevenson, 1985; Díaz Fernández, 1994). Pollination is entomogamus, provided by several species of insects, such as hive-bees, humble-bees of the genus *Bombus,* and moths (Rasmont et al., 2005; Ribas-Marquès et al., 2022). This type of pollination accounts for the low fidelity and dispersibility values of *Arbutus* pollen (Attolini et al., 2023), but it also makes this pollen type an excellent indicator for local stands in the fossil record (Servera-Vives et al., 2022).

Palaeobotanists hardly differentiate *Arbutus* at the species level from its wood anatomy (Schweingruber, 1990; Akkemik and Yaman, 2012; Crivellaro and Schweingruber, 2013; Cïhan and Akkemïk, 2013). The wood of *Arbutus* is characterised by diffuse-porosity, with solitary vessels, outlined angular, arranged in no specific patterns (element average length ≤ 350–800 µm), simple and scalariform perforation plate with 2–3 bars, small-sized polygonal alternate intervessel pits (4–7 µm), and conspicuous helical thickening. Most of the fossil wood findings consist of charcoal from archaeological contexts, especially hearths, accounting for the use of *Arbutus* mainly for fuel supply (Delhon et al., 2017). However, rare, waterlogged wood remains show woodworking marks, providing evidence for the use of *Arbutus* for the construction of wedges, beams, and sticks (Costa Vaz et al., 2016; Martínez-Sevilla et al., 2023).

Fruit remains of *Arbutus* are rare even in archaeological contexts due to their perishable nature, despite the medium-high productivity of the plant and low consumption by animals. The Late Neolithic findings of Lerna (Argolid, Greece) might have been coincidentally incoming into one of the pits from wild stands (Hopf, 1961). No evidence for domestication or semi-domestication is available. *Arbutus* was and still is collected from wild stands as an integration into the diet. Current ethnobotany and phytochemical studies report that wild *Arbutus* is used for its antiseptic, astringent, and diuretic properties, in addition to the production of alcoholic beverages and jams (Takrouni and Boussaid, 2010; Wahid et al., 2019; Beyhan et al., 2020). Some mid-Holocene remains from La Draga (Spain) have also been associated with medical use (Piqué et al., 2021). Experimental archaeology suggests the use of bark for dyeing (Martinez Garcia and Armero, 2013). The iconography of the Roman gardens of Villa of Livia near Rome, the House of the Fruit Orchard, and the House of the Golden Bracelet in Pompeii documents an ancient ornamental purpose of *Arbutus* (Ciarallo, 2004).

3. Materials and methods

To reconstruct the late Quaternary history of *Arbutus* in the Old World, we searched for pollen and macrofossil records of the last 32 ka in those countries where the genus is nowadays occurring and in the neighbouring countries (e.g., Great Britain; Egypt; Armenia) (Fig. 1b,c).

We compiled a fossil pollen database solely including chronologically controlled sites (radiometric dates and tephra layers). When needed, we calibrated the published radiocarbon dates, using the CALIB ^{14}C calibration program (CALIB rev.8; Stuiver and Reimer, 1993). Data was mainly retrieved from an extensive bibliographic survey, including synthesis works (e.g., Tonkov, 2021; Carrión et al., 2022a, 2022b), supplemented by data from the European Pollen Database (Fyfe et al., 2009), the Neotoma Palaeoecology Database (Williams et al., 2018; www.neotomadb.org), and PANGAEA (Felden et al., 2023). A total number of 1214 sites are included in our dataset (Fig. 1b;

Supplementary Data). Macrofossil data was collected from the literature. It includes radiocarbon-dated findings and archaeologically dated samples, mostly charred woods, from a total of 98 sites (Fig. 1c, Supplementary Data). In addition to the fossil datasets, modern pollen data was obtained from both the Eurasian Modern Pollen Database (Davis et al., 2020) and the literature (Fig. 2: Modern Pollen; Supplementary Data). The current distribution of *Arbutus* (Fig. 1a) is based on the modern occurrence record dataset published by De Santis et al. (2023).

We used the open-source software QGIS (ver. 3.28.15 'Firenze') to plot occurrence maps of the present and past distributions of *Arbutus* (Figs. 1–2).

To examine the past population dynamics of *Arbutus*, we presented pollen and macrofossils at thousand-year intervals (Fig. 3). Since the total number of available records affects the significance of the number of fossils finds, we divided the *Arbutus* pollen occurrences by the total number of pollen sites for each time interval (prevalence rate). The total number of pollen sites incorporates all sites within 30 km from the next closest modern stand of *Arbutus*. This distance is based on repeated measurements of the maximum distance between the modern pollen records (Fig. 2 and Supplementary Data) and the closest living stands of *Arbutus* (Fig. 1a). Considering that such distance falls in the interval 20–30 km in most of the cases, a 30 km distance is deemed conservative and adequate for reliably representing the local presence of *Arbutus*, while also minimising the regions where the species is unlikely to occur. The macrofossil occurrences were not displayed as prevalence rate since absence data cannot be assessed.

4. Results

A total of 420 occurrence records of fossil pollen (145), charcoal (71), and modern pollen (204) have been included in a series of maps representing different time windows, in order to summarise the range history of *Arbutus* (Fig. 3).

- *32–28 ka BP*: *Arbutus* pollen is present only in the Iberian Peninsula, with a macrofossil record near the coast of Portugal. It is not detected in the central and eastern Mediterranean Basin.
- *28–24 ka BP*: Two pollen sites mark the presence of *Arbutus* along the Atlantic coast of the Iberian Peninsula, complemented by a macrofossil in central Portugal.
- *24–20 ka BP*: Six sites confirm the presence of *Arbutus* in the northern and western regions of the Iberian Peninsula during the Last Glacial Maximum (LGM), with macrofossil and pollen records from the Cantabrian, Galician, and Portuguese coasts, down to the Guadalquivir Plain. *Arbutus* is still undetected in other regions of the Mediterranean Basin.
- *20–16 ka BP*. The range of *Arbutus* remains quite similar to the previous time interval but for an increase in macro remains in the Cantabrian Mountains and one new occurrence in south-eastern Spain.
- *16–12 ka BP*. No significant changes appear during the lateglacial interval with respect to the previous interval. *Arbutus* shows considerable regional persistence in the Iberian Peninsula.
- *12–10 ka BP*. At the onset of the Holocene, *Arbutus* appears in some central Mediterranean regions, including the French Riviera, Corsica, and Tuscany, as well as in the High Atlas in Morocco. It is also found in the French Bask Country.
- *10–8 ka BP*. A general increase in the number of occurrences is observed in the western and eastern sectors of the Iberian Peninsula, as well as in the central Mediterranean region. Besides, a new record appears on the northern coast of Tunisia.
- *8–6 ka BP*. *Arbutus* shows a considerable expansion, with increasing density in the Iberian and Italian Peninsulas, and appearance in new regions, including the area of Kerry in southern Ireland, the Algerian coast, Sardinia, Sicily, the Ionian coasts of Greece and the Aegean islands and coasts of Anatolia, as well as the Levant.
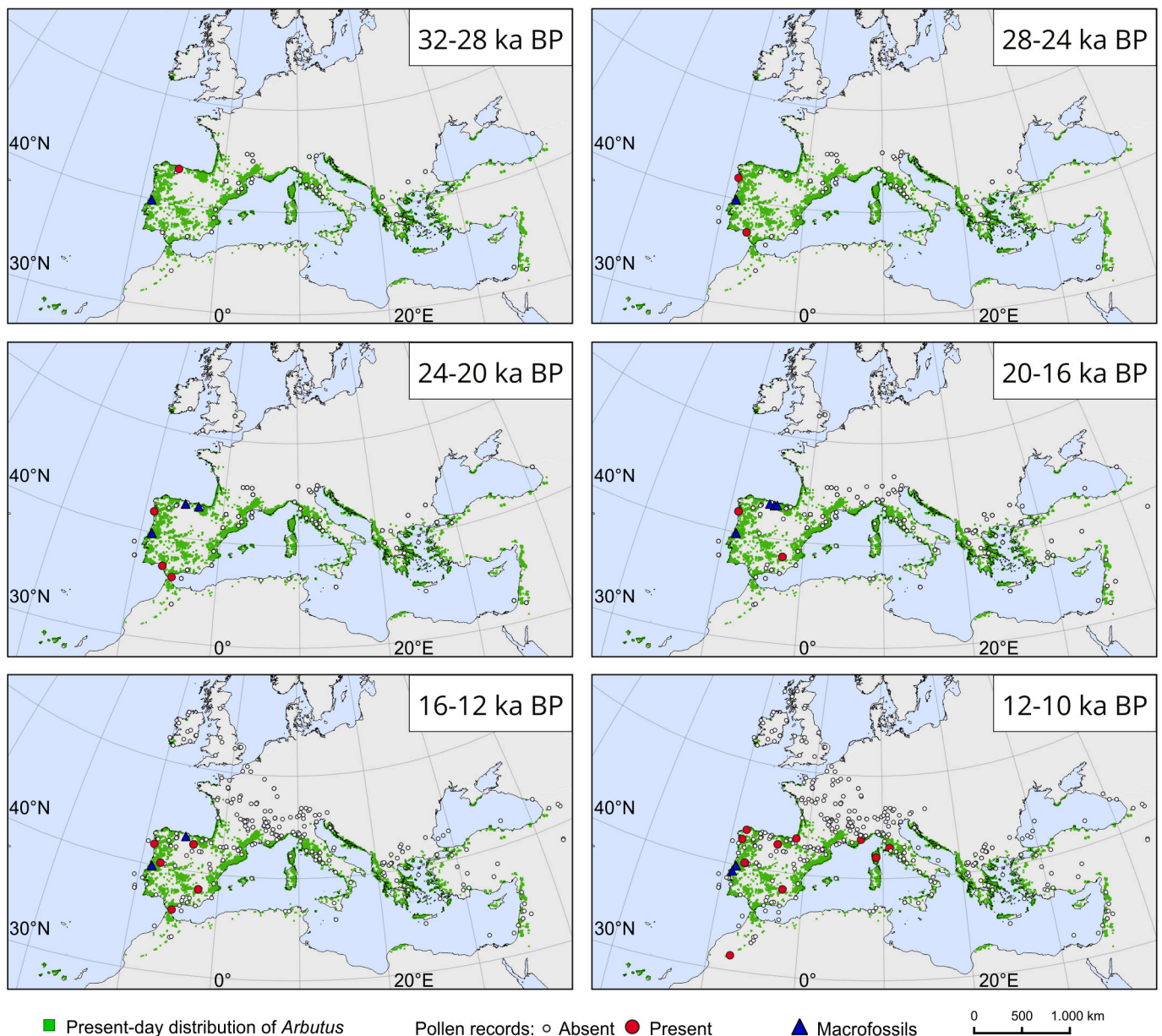
Fig. 2. Geographical distribution of *Arbutus* from 32 ka cal BP to the present. Red dots indicate *Arbutus* presence in pollen records, white dots represent its absence, and blue triangles represent macrofossils. Green areas represent the current distribution of *Arbutus*.

- *6–4 ka BP*. New appearances are recorded in the Balearic Islands (Menorca), Northern Greece, and Crimea. An overall increase in density is documented in the other regions.
- *4–2 ka BP*. *Arbutus* appears along the Adriatic coast of Apulia and Croatia and in southeastern Sicily, as well as in the Canary Islands (Gran Canaria). In the Iberian Peninsula, *Arbutus* spreads on the Montes de Toledo and Central System. In northern Ireland, it is recorded at the site of Sligo, which is the northernmost stand of its modern distribution.
- *2–0 ka BP*. *Arbutus* reaches its modern range. It appears in Albania, in Cyrenaica, and along the Syrian coast. Many anthracological remains are recorded in the Canary Islands, including Fuerteventura where the species is currently extinct. A decrease in the number of sites is apparent in the Iberian Peninsula.

5. Discussion

The dynamics of the Mediterranean-Atlantic distribution of *Arbutus* reveals two clear patterns (Fig. 2). In the northern and western Iberian Peninsula, *Arbutus* has consistently been present at multiple sites during the last 32 ka, with records of pollen and macrofossils even during the LGM. In the western and central Mediterranean regions, it progressively increased since the beginning of the Holocene, appearing along the coasts of the Black Sea and in the Levant during the Middle Holocene. The general feature emerging from these progressive appearances is a clear west-to-east oriented longitudinal pattern. In order to better describe and interpret this pattern, the continental range of *Arbutus* has been here subdivided into five regions, selected on the basis of known biogeographical divides described as follows (Fig. 3). The peripheral stands located in Ireland, Canary Islands, Cyrenaica, and Crimea are discussed separately.
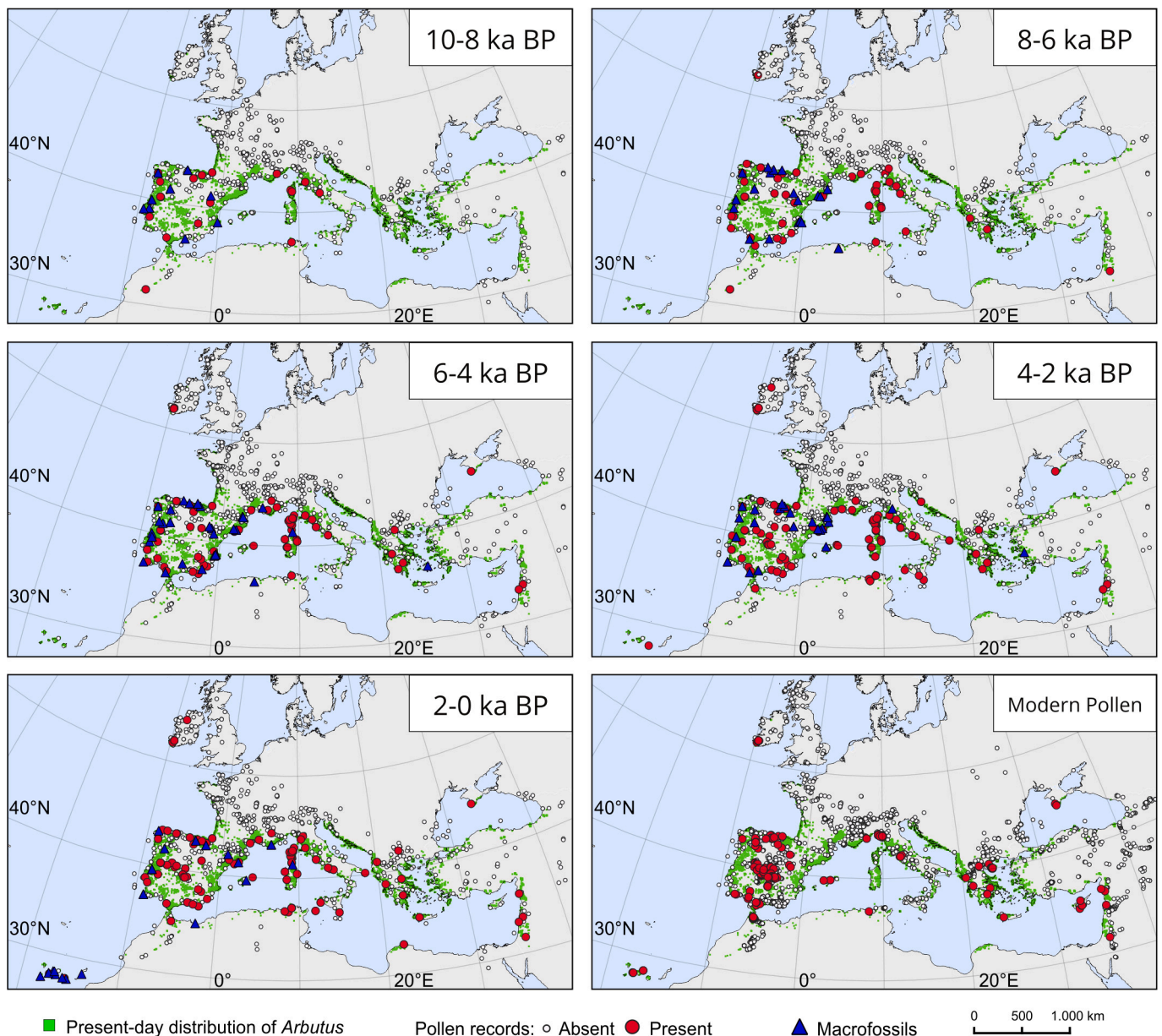
Fig. 2. (continued).

5.1. Biogeographical divides

Region 1. This includes Atlantic France, Atlantic Iberia, and Morocco. The western Iberian populations of *A. unedo* are separated from the eastern ones by a deep and often clear-cut genetic divide detected in several tree taxa, as thoroughly reviewed by Rodríguez-Sánchez et al. (2010), suggesting that both areas have independently sustained viable populations over prolonged time periods. This divide involves conifers (Bucci et al., 2007; Afzal-Rafii and Dodd, 2007), as well as deciduous (Olalde et al., 2002) and evergreen broadleaved trees (Petit et al., 2005; López de Heredia et al., 2007; Rodríguez-Sánchez et al., 2008; Alonso et al., 2022). Genetic data for *A. unedo* indicate that the Moroccan populations belong to the same cluster as the Atlantic-Iberian one (Santiso et al., 2016a), and for this reason they have been included in Region 1. The Strait of Gibraltar area, which is also included in Region 1, had a biogeographical role in species dispersal, as suggested by the genetic affinity of Ibero-Maghrebian relict species (Rodríguez-Sánchez et al., 2008; Migliore et al., 2012). The fossil evidence supports the role of Region 1 as a refuge area for *Arbutus* during the last glacial period,

with an unexpectedly consistent presence in the 32–29 ka BP and LGM intervals, both showing relative occurrence values even higher than the Holocene (Fig. 3). The potential of the Cantabrian and Atlantic coasts as well as of the Gibraltar area as climatic refugia is confirmed by temperature and precipitation models developed for the Iberian Peninsula. According to Salgueiro et al. (2014), the circulation pattern of the western Iberian margin during the LGM was characterised by an offshore southward flow of subpolar waters and an inshore poleward inflow of subtropical waters, resulting in mean annual temperatures only slightly colder than at present. The pollen record of core MD95–2039 from the Atlantic Iberian margin indicates for the LGM a rather warmer and moister climate than during many stadial events of MIS 3 (Roucoux et al., 2005). The same record suggests that the end of MIS 3 was colder and dryer than the LGM, which might explain the drop in *Arbutus* occurrences between 29 and 26 ka BP (Fig. 3). Relatively warm conditions during the LGM are also shown by Ludwig et al. (2018), who also highlights mean annual precipitations >700 mm over northwest Iberia and Gibraltar, which exactly is the district where *Arbutus* is represented in the 24–20 ka BP time window, indicating that
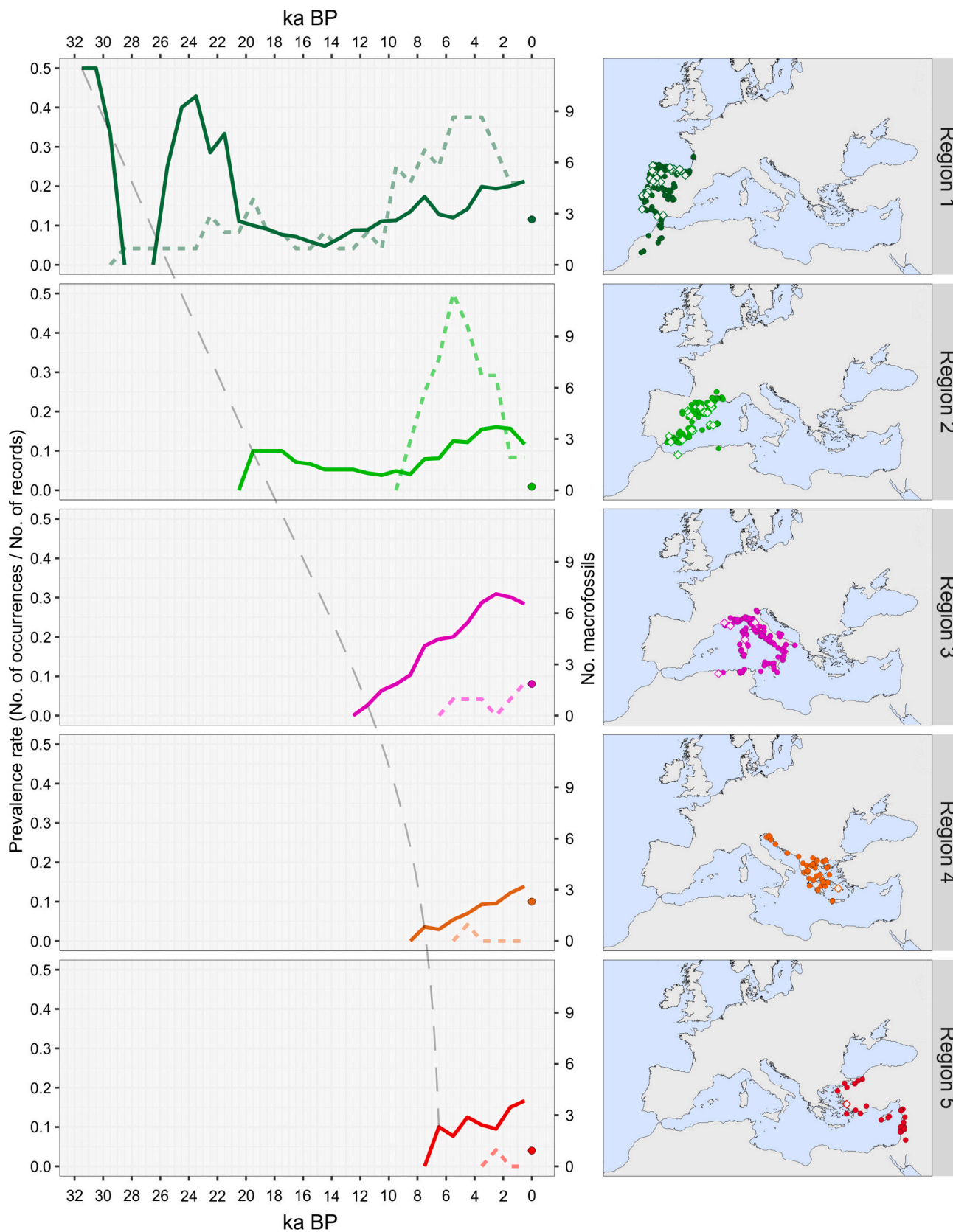
Fig. 3. Prevalence rate (solid lines) and macrofossil counts (dashed lines) of *Arbutus* for the five biogeographic regions examined in the discussion. Peripheral stands are not included. For the calculation of prevalence rate, see Materials and Methods. Modern pollen prevalence rates are represented by a single dot. The grey dashed line highlights the temporal shift of *Arbutus* appearance across regions. The maps show the fossil records of each region (dots = pollen; squares = macrofossil).

these areas were not so harsh and inhospitable. In contrast, the ecological modelling of bioclimatic variables by Almeida et al. (2022), highlighting very low to no suitability in northwest Iberia even along the coasts during the LGM, is inconsistent with the distribution of *Arbutus* based on fossil data (Fig. 2). The relative stability of the prevalence rate in Region 1 between 20 and 10 ka BP (Fig. 3) does not match the climate oscillations known for this time period, especially Heinrich 1 event (H1; ca. 18–14.7 ka BP; Naughton et al., 2023a) and Younger Dryas (12.9–11.7 ka BP; Naughton et al., 2023b). The general stability of Ericaceae in comparison to oaks and other temperate trees found in marine pollen records from the western Iberia margin (Naughton et al., 2007; Naughton et al., 2016; Jalut et al., 2010) implies that Ericaceae, including *Arbutus*, may have been influenced by other factors, such as annual precipitation, rather than temperature variations. At the beginning of the Holocene, the west–east biogeographical divide of the Iberian Peninsula is apparent from the distribution of *Arbutus*, which mostly occupied coastal areas. Later, during the postglacial, it progressively expanded inland with a massive colonisation of the Toledo mountains in the time window 4–2 ka BP. This pattern confirms the genetic-based hypothesis of prevalent survival of trees in glacial refugia along the coasts, followed by a subsequent increase in inland populations (Rodríguez-Sánchez et al., 2010). In the last two millennia, *Arbutus* has markedly decreased along the coasts of central Portugal and the Algarve, to the point of disappearing from some areas, since Mediterranean coastal vegetation has progressively been affected by human activities, being heavily occupied by urban, agricultural, and industrial settlements and related infrastructures (Di Rita and Magri, 2012). Some of the disappeared populations were located in coastal areas that hosted *Arbutus* even during the last glacial period, proving to be suitable long-term survival areas. The loss of these populations from potential climatic refugia may be irreparable damage in view of possible future range contractions and requires adequate consideration in conservation strategies.

Region 2. This consists of the Iberian Peninsula east of Region 1, the Balearic Islands, northwest Algeria (Babor Mountains), and the southern coasts of France west of the Rhône delta. This region is delimited to the west by the east–west divide of the Iberian Peninsula (see Region 1) and to the east by the distributional gap of *Arbutus* in the Camargue, where the Rhône River separates two biogeographical subregions of southern France (Lenormand et al., 2018). The latter divide is also clearly highlighted by the phylogeographic results of the Mediterranean evergreen species *Q. suber* (Magri et al., 2007) and *Q. ilex* (Lumaret et al., 2002). The molecular analysis of *Q. suber* includes the Balearic Islands and northeastern Morocco in the same cluster of eastern Iberia, for which reason we have added the records from northwestern Algeria to Region 2. The molecular analysis of *A. unedo* (Santiso et al., 2016b) confirms that genetically similar populations are found in the Balearics, northeastern Spain, and southern France west of the Rhône River delta. The oldest pollen record of *Arbutus* in Region 2 is found in the ODP site 976 at the MIS 12/11 transition (Sassoon et al., 2023). Then, *Arbutus* is recorded in the site of Padul around 40 ka BP (Pons and Reille, 1988). Starting from ca. 20 ka BP, it is always represented in the pollen records of the region, often supported by macrofossil findings. A continuous increase is detected both in pollen and macrofossils during the middle Holocene. In the last 2 millennia it has experienced a decline. These results indicate that *Arbutus* was present in Region 2 during the LGM, although it was less abundant than in Region 1. Similarly to Region 1, the *Arbutus* populations at the eastern Iberian margin were not affected by the climate oscillations of the lateglacial, not even by the minimum temperatures attained in the western Mediterranean Basin during H1 with the entrance of polar water through the Gibraltar Strait (Cacho et al., 2001). Instead, precipitation was likely the main limiting factor for *Arbutus*. This is supported by the consistency between the location of the first pollen record (ca. 20 ka BP) in the Sierra de Segura (Carrión, 2002), and the palaeoclimate maps modelled for the LGM and H1 (Ludwig et al., 2018), suggesting relatively abundant rainfall in the same region.

Region 3. In its northern margin, it extends from Provence, east of the distributional gap of the Rhône delta, to the Venetian Lagoon, where the Amphi-Adriatic divergence is located (Adamović, 1933; Falch et al., 2019). Southwards, Region 3 includes Corsica, Sardinia, the Italian Peninsula, Sicily, as well as the Tunisian and eastern Algerian stands of *A. unedo*, which are separated from *A. pavarii* by the extensive distribution gap of the Tripolitania province. The biogeographical affinity of Provence, Corsica, Sardinia, and Kabylies in North Africa is supported by geological (Rosenbaum et al., 2002) and molecular data (Burban and Petit, 2003; Magri et al., 2007). *Arbutus* appears in Provence, Corsica, and Tuscany at the onset of the Holocene (Fig. 2: 12–10 ka interval). Then it shows a progressive increase in Tyrrhenian Italy, Sicily, and northern Africa (10–6 ka BP), followed by eastern Sicily and Adriatic Italy (4–2 ka BP). In the last two millennia, it shows a decline, followed by an abrupt decrease in the modern pollen record (Fig. 3). Although *Arbutus* appears only during the Holocene, we can reasonably assume that it was present in Region 3 also during the last glacial period, as it was detected in central Italy already during MIS 13 (Di Rita and Sottili, 2019).

Region 4. It extends from the Amphi-Adriatic divergence zone, through the Balkan Peninsula to the Ionian and Aegean Islands. Based on molecular analyses (Bilgin, 2011), the Balkan-Anatolian Suture Zone separates the populations of the Balkan Peninsula from those of Anatolia. Region 4 is characterised by the coexistence of *A. unedo* and *A. andrachne*, as well as by the presence of the natural hybrid *Arbutus* x *andrachnoides*. The prevalence rate curve (Fig. 3) shows the first presence as late as 6.5 ka BP, with a moderate increase in the last millennia. However, the autochthony of *Arbutus* in the Balkan Peninsula should not be questioned, being supported by its presence at Lake Ohrid around 200 ka BP (Donders et al., 2021) and by the distribution of the hybrid *Arbutus* x *andrachnoides*, which suggests a long-term persistence of both *A. unedo* and *A. andrachne* in the region.

Region 5. This includes the populations of Anatolia (east of the Balkan-Anatolian Suture Zone) and the Levant. Cyprus is also encompassed in this region based on palaeogeographical patterns (Poulakakis et al., 2013). Except for Anatolia and scanty stands of *A. unedo* in Cyprus and Lebanon, this region is only occupied by *A. andrachne*. The appearance of *Arbutus* in the pollen record is documented starting from around 6.5 ka BP. Only one macrofossil site has been recorded. Despite the late appearance in the fossil record, *Arbutus* has been certainly present in the region for a long time, since the speciation of *A. andrachne* occurred long before the Quaternary (Hileman et al., 2001).

The different behaviour of *Arbutus* in the five biogeographical regions raises the question of whether the observed longitudinal pattern depends on a west-to-east postglacial population spread under suitable climate conditions, or on a progressive growth of the existing populations to a density sufficient for pollen to be detected in the fossil record.

The hypothesis of an eastward spread of *Arbutus* after the LGM contrasts with the palaeobotanical evidence, suggesting long-term persistence throughout the Mediterranean Basin (Di Rita and Sottili, 2019; Donders et al., 2021; Sassoon et al., 2023). Besides, the observed longitudinal pattern encompasses different species of *Arbutus* (Fig. 1), which excludes a sequential migration process. All the same, the most widespread species *A. unedo* shows a phylogeographic structure with a longitudinal diversification, probably deriving from an ancient divergence (Santiso et al., 2016b), excluding a migration process from the western sectors of the range in the Iberian Peninsula toward the central and eastern Mediterranean Basin.

Based on this taxonomical and molecular diversity, *Arbutus* is expected to have widely occurred in glacial refugia throughout its Mediterranean range even when it is not detected in the fossil record. Besides apparent survival areas, it is also reasonable to consider the existence of several cryptic refugia, too small or localised to be found using pollen analysis or other palaeoecological methods (Birks and Willis, 2008), as well as the areas currently below the sea level. The map of modern

occurrences, which provides information about the density of populations, displays sparse occurrences toward the edge of the range, for example in the eastern Mediterranean where *Arbutus* has a late appearance in the Holocene (Fig. 1). Dense stands are currently found in southern France, Corsica, and Central Italy, where *Arbutus* appeared already in the lateglacial. In northern and western Iberia, where *Arbutus* was always present in our 30-ka-long reconstruction, there are extensive and rich stands in the modern vegetation, suggesting a temporal continuity between long-term persistence areas and current centers of gravity (Fig. 4).

Overall, there is a general spatiotemporal correspondence between the present-day west-to-east decreasing pattern of occurrence and the west-to-east progressive timing of appearance (Fig. 4), which suggests that also in the past the western populations were larger and denser than the eastern ones, where refugia were probably reduced to extremely sparse stands. The oceanic influence on moisture availability has probably played a fundamental role in determining persistent higher population density in the Atlantic Iberian Peninsula during the last 30 ka.

Surprisingly, populations in the central and eastern Mediterranean Basin exhibit a significant rise in the prevalence rate during the Holocene, whereas the dense and persistent populations in the western portion of the range show only a slight increase (Fig. 3). This suggests that *Arbutus* might have found more favourable conditions for a postglacial increase in density in areas where its populations were exiguous during the glacial period than in the western regions where it was already widespread.

5.2. Peripheral stands

The nature of *A. unedo* as component of the Lusitanian geo-element in Ireland and along the Atlantic coast of France has been widely discussed (Reid, 1899; Corbet, 1962; Mitchell, 2006; Sheehy Skeffington and Scott, 2021). However, there still is no agreement whether the species: i) endured in its current location during the LGM; ii) spread to northern latitudes following the retreat of the ice sheets; iii) formed the modern stands by a long-distance dispersal through animals; iv) was propagated by humans.

Along the Atlantic coast of France, *Arbutus* was never found in the fossil record, although during the LGM it could have survived in the land now submerged along the Biscay Bay, which hosted several archaeological sites (Billard et al., 2020), or on cliffs and rocky slopes, as it does today within its entire Atlantic domain. In Ireland, many authors have dismissed the idea of its persistence in situ, addressing a more likely long-distance dispersal by zoochory (Sealy, 1949; Webb, 1983; Mitchell et al., 1993; Mitchell, 2006). However, this hypothesis contrasts with the biological traits of *A. unedo*, namely low seed and fruit propagation, as well as with its usual resprouting from the lignotuber, which altogether suggests a very low dispersal capacity. An anthropogenic introduction by copper miners of the Bronze Age was also proposed (Sheehy Skeffington and Scott, 2021), similar to other Lusitanian species, based on the trade between Spain and Ireland in antiquity and medieval times

Fig. 4. Barplot of the number of modern occurrences (10 × 10 km grid) for *A. unedo* (green) and *A. andrachne* (red) for each region. The light blue line shows the timing of the appearance of *Arbutus* in each region.

(Foss and Doyle, 1990). On the other hand, no direct historical or archaeological proof exists for the human introduction hypothesis, also considering that the oldest finding of *Arbutus* in Ireland dates as early as ca. 6.5 ka BP (https://data.neotomadb.org/14510; Mitchell, 1988). The population structure of *A. unedo* indicates a distinctive genetic nature for the Irish stands, which are more closely related to the populations of north-west Iberia than those of Atlantic France, for which reason a stepping-stone colonisation from south to north Iberia and then to Ireland, skipping France, has been proposed (Santiso et al., 2016b). Results of molecular analysis combined with ecological modelling of other Lusitanian species (*Daboecia cantabrica*, *Pinguicola grandiflora*, and *Saxifraga spathularis*; Beatty and Provan, 2013, 2014) suggest that they may have persisted during the LGM in several southern refugia and recolonized northwards after the retreat of the ice sheets. However, the pollen record does not support a progressive south-to-north spread, as *Arbutus* is completely missing from the French sites, despite the abundance of studied records (Fig. 2). Hence, similarly to other Tertiary relic plants, an in situ persistence in northern refugia cannot be completely ruled out (Webb, 1983; Coxon and Waldren, 1995; Valtueña et al., 2012).

The vegetation of the Canary Islands was shaped by a complex geological and biogeographic history determined by volcanic eruptions, submersion, and emergence (Rijsdijk et al., 2014), subsequent colonisation phases to and from the closest mainland (Médail and Quézel, 1999), as well as asynchronous evolution patterns with respect to other Macaronesian archipelagos (Gallego-Narbón et al., 2023). As evidence for this complexity, some Iberian populations of evergreen Tertiary species (e.g., *Laurus* and *Hedera*) show a closer genetic relation to populations in the Canary Islands and Madeira than to other circum-Mediterranean populations of the same species (Rodríguez-Sánchez et al., 2009; Alonso et al., 2022). *A. canariensis* may have also experienced an intricate history, as it is considered a Tertiary relict of the Macaronesian laurel forest (Kondraskov et al., 2015). During the Pliocene, it was already present in the archipelago as a component of the palaeoflora of this region (Anderson et al., 2009), where it would later adapt to a drier Mediterranean climate (Garzón et al., 2008). A chronological gap in the fossil record from the Pliocene to ca. 2 ka BP (Machado Yanes, 2007) may be explained by poor pollen production of the species and scarcity of records. Indeed, *A. canariensis* cannot have been introduced from any other site, being distinct from the other *Arbutus* species of the Old World. Despite human activity, the dominant vegetation of this region has remained unchanged in composition since the arrival of the first European colonisers in AD 1494 (De Nascimento et al., 2020).

The vegetation of the northern coasts of the Black Sea, more specifically of Crimea, is described as "Sub-Mediterranean" by classic phytogeographical works (Rikli, 1943; Walter and Straka, 1970; Zohary, 1973), as it includes thermophilous species like *A. andrachne, Pinus brutia, Pistacia mutica* and *Juniperus oxycedrus* which may have persisted in warm refuge areas during the Pleistocene (Yena et al., 2005; Cordova, 2016; Kukarskih et al., 2020). *A. andrachne* has its northernmost limit in Crimea, where it appeared at about 5.5 ka BP and retreated toward its present-day distribution along the southern coasts around 1.5 ka BP (Cordova and Lehman, 2005; Cordova, 2016). Contrasting hypotheses have been proposed concerning its history, including a post-glacial recolonization from the south and intentional/accidental seed introduction by humans (Cordova, 2007). The southern immigration of floral pioneers may have been influenced by the Black Sea currents regime and level changes in the Holocene, while human-induced disturbance (e.g., grazing and farming) may have favoured its establishment. On the other hand, we cannot exclude its local persistence in Crimea, as pollen assemblages from lateglacial deposits indicate the existence of a warm-temperate broad-leaved flora on the lower mountain slopes during the last glacial period (Gerasimenko et al., 2022).

On the Eastern shores of the Black Sea, *A. andrachne* is restricted to some rather isolated locations of Colchis, a region known to have been a
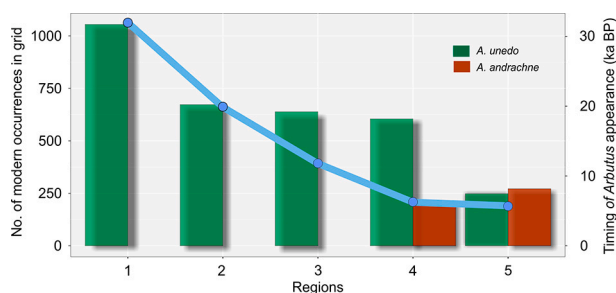
glacial refugium for thermophilic species, such as *Ilex colchica, Hedera colchica, Quercus pontica, Betula medwedewii, Corylus colchica*, and *Buxus colchica* (Denk et al., 2001; Connor et al., 2007; Melia et al., 2012). In this district, *Arbutus* occurs in coastal enclaves under a para-Mediterranean climate, relatively humid, nearly frost-free, and with low seasonal fluctuations, similar to the Atlantic climatic regime. This distribution endorses the opinion of Zohary (1973), who related *Arbutus* to the Arcto-Tertiary flora: the coastal broadleaved evergreen species of north-eastern Anatolia (e.g., *Laurus nobilis, Prunus laurocerasus,* and *Rhododendron ponticum*) should be considered as elements of a a laurophyllous biome of a the Euxino-Hyrcanian domain, preceding the Pleistocene Mediterranean xeromorphication (Mai, 1989), rather than the easternmost outposts of the Mediterranean biome.

In Cyrenaica, the scanty populations of *A. pavarii* found in the Al-Akhdar and Al-Jabal mountains are represented in the pollen record since 1.6 ka BP (Gimingham and Walton, 1954; Hunt et al., 2011). Despite this recent appearance, there is no doubt that *A. pavarii* locally persisted long enough to originate a distinct species. Probably its absence in the pollen record is due to low pollen production and dispersal capacity, as suggested by a demographic study highlighting that the species does not always produce flowers and fruits but displays self-replacing characteristics mostly relying upon clonal growth (Mosallam et al., 2017).

The history of peripheral stands suggests some general remarks. When interpreting northern and southern marginal populations, double standards are frequently applied according to prior conception. In Ireland and Crimea, *Arbutus* is primarily regarded as non-native or introduced, despite the fact that it appeared there earlier than in the Canary Islands and Cyrenaica, where an in situ persistence during the last glacial periods is not questioned. In both cases, the delayed emergence in the fossil record of isolated/disjunct stands of *Arbutus* might be ascribed to low population density and related to low pollen production.

A. unedo is included in the assessment of the IUCN Red List as Least Concern conservation status based on the Stable Trend of current populations (Khela and Malin Rivers, 2017). *A. andrachne* is listed as Critically Endangered in Bulgaria, Cyprus, and Jordan due to its restricted and declining populations (Tsintides et al., 2007; Peev et al., 2011; Taifour and El-Oqlah, 2014). However, its global status has been downgraded to Least Concern status because of the species' widespread distribution (Wilson, 2018). Fossil records have shown that the edges of the range may be vulnerable to extirpation due to natural or anthropogenic impact, as shown by the declining trend observed in part of the range in historical times (Figs. 2–3) and the local extinction in the island of Lanzarote about two thousand years ago (Machado Yanes, 2007). However, the fact that some populations endured over millennia through different climatic conditions at sizes not detectable by pollen analysis and then succeeded in expanding during the Holocene, demonstrates the outstanding resilience of *Arbutus*. This capacity suggests that *Arbutus* may successfully overcome long-standing unfavourable climatic constrains and future unpredictable global change. A proper identification of vulnerability status cannot therefore omit the analysis of long-term trends of marginal and exiguous populations, as well as their recovery capacity and rate, complemented by a detailed analysis of genetic diversity (Magri et al., 2020).

6. Conclusions

The compilation of fossil records of *Arbutus* spanning the last 32 ka points to a novel interpretive model for the dynamics of postglacial populations. The postglacial spread of tree populations in Europe is generally thought to have been south–north oriented from the Mediterranean Peninsulas (Hewitt, 1999; Feliner, 2011; Tzedakis et al., 2013), although many temperate species, including *Fagus, Buxus, Tilia,* and *Carpinus*, have been shown to have persisted at more northern latitudes (Magri et al., 2006, 2015; Di Domenico et al., 2012; De Benedetti et al., 2022; Mitka et al., 2023). We have shown a progressive west-to-

east increase in the density of refugial sparse populations of *Arbutus* that gradually became detectable in the pollen record. The identification of long-term persistence areas suggests the location of plausible distribution centers of gravity that may potentially ensure future preservation. On the other hand, even peripheral and sparse populations of *Arbutus* demonstrated remarkable resilience and capacity for population increase during the postglacial.

The late Quaternary history of *Arbutus* indicates that the issue of past population density is crucial with regard to its current and future distribution. For this reason, density-weighted ecological models are recommended, which should additionally consider population stability, timing and rate of change. A holistic understanding of the interconnection of modern occurrence records with past spatiotemporal patterns holds great scientific promise in producing a better comprehension of the ecological niche, ultimately leading to reliable assessments of potentially vulnerable populations and informed recommendations of conservation actions in response to the ongoing climate change and increasing human pressure.

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.

Acknowledgment

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2024.105099.

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