When and how did *Cannabis* reach Europe and the Iberian Peninsula?

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Abstract

Cannabis is among the oldest human domesticates and has been subjected to intensive artificial (human-mediated) selection throughout history to create a wide array of varieties and biotypes for diverse uses, including fiber, food, biofuel, medicine and drugs. This paper briefly reviews the available literature on the taxonomy, evolutionary origin and domestication of this plant, as well as its worldwide dispersal, in both its wild and cultivated forms. Emphasis is placed on Europe and especially on the Iberian Peninsula, which is the main target of this study. Today, it is accepted that *Cannabis* is a monospecific genus with two subspecies, *C. sativa* subsp. *sativa* and *C. sativa* subsp. *indica*, originating in Europe and Asia, respectively, by allopatric differentiation after geographic isolation fostered by Pleistocene glacial-interglacial cycles. Palynological and phylogeographic evidence situates the *Cannabis* ancestor on the NE Tibetan Plateau during the Oligocene (ca. 28 Ma). The timing and place of domestication is still a matter of debate between contrasting views that defend single or multiple domestication centers situated in different parts of the Eurasian supercontinent, notably central/southeastern China and the Caucasus region. Recent meta-analyses have suggested that wild *Cannabis* may have already been spread across Europe in the Pleistocene (ca. 1 Ma), and its domestication could have occurred during the European Copper/Bronze ages (7-5 kyr BP). According to the available reviews and meta-analyses, preanthropic dispersal of *Cannabis* into the Iberian Peninsula seems to have occurred only in postglacial times (18.5-15 kyr BP), and the earlier signs of cultivation date to the Early Medieval Ages (ca. 600 CE). However, the palynological and archaeological evidence used to date is insufficient for a sound assessment, and the development of thorough Iberian databases to address further meta-analysis is essential for more robust conclusions. Some clues are provided for these achievements to be fulfilled.

Keywords

Taxonomy, biogeography, evolution, domestication, dispersal, pollen, archaeology, hemp, drugs

Introduction

Since ancient times, *Cannabis* has been extensively utilized by humans for a variety of uses, such as textiles, paper, food, medicine, biofuel or recreational drugs. *Cannabis* has been an integral part of human life since the dawn of civilization and continues into the present (e.g., Clarke and Merlin 2013; Fike 2016; Gray et al. 2016a; Grotenhermen and Müller-Vahl 2016). However, research on this plant significantly decreased and almost ceased in the mid-20th century when the species and its varieties were declared illegal in most Western countries, regardless of the concentrations of psychoactive compounds (Duvall 2014; Warf 2014). Therefore, one of the most ancient crops, long-valued for its multiple uses, became largely ignored during the last 50 years. Thus, compared with other crop plants, *Cannabis* has not fully benefited from modern scientific technologies, which has created a major knowledge gap that remains to be filled (Gray et al. 2016b).

The last decade has witnessed a revival of interest in *Cannabis* research, especially in relation to the genetic and phytochemical features of the different varieties and to its evolutionary origin, domestication and further geographic diffusion (e.g., Clarke and Merlin 2013; Small 2015; Gray et al. 2016b; Vergara et al. 2016). For example, the use of modern methods of molecular analysis has helped clarify the taxonomy of the *Cannabis* complex and its genetic modifications over time as a result of artificial (human-mediated) selection during the domestication process (Clarke and Merlin 2016). Palynological and archaeological records have been used mostly to identify the center of origin of *Cannabis*, its center of domestication and further human-driven diffusion patterns throughout the world. Modern global and regional databases and associated handling facilities, notably geographic information system (GIS) tools, have been instrumental in this type of research (McPartland 2020).

This paper briefly reviews the available information on the center of origin and the center of domestication of *Cannabis* and its further worldwide dispersal, with a focus on Europe, where spatiotemporal diffusion patterns remain controversial, and the Iberian Peninsula, which represents a knowledge gap regarding the tempo and mode of *Cannabis* arrival and diffusion. This paper begins with a brief section regarding the current state of *Cannabis* taxonomy, ecology, phenology and uses. The next section discusses the evolutionary center of origin and the time of appearance of the original wild *Cannabis*, followed by similar geographic and chronological considerations on *Cannabis* domestication and diffusion of its cultivated forms. The next section focuses on Europe, where domestication and diffusion patterns are still under discussion. The last section highlights the scarcity of information in regard to the Iberian Peninsula, in comparison with other European regions, evaluates the potential causes for this paucity and suggests how further research could contribute to bridging this knowledge gap.

Present-day status

The genus *Cannabis* is in the family Cannabaceae, with 11 genera and approximately 170 species. Discussions on the existence of one (*C. sativa*) or two species (*C. sativa* and *C. indica*) started during the time of Linnaeus and Lamarck and have continued until very recently. Some morphological differences exist between the two taxa, as *C. sativa* is taller with a fibrous stalk, whereas *C. indica* is shorter with a woody stalk. There are also phytochemical divergences, as manifested in the tetrahydrocannabinol/cannabidiol (THC/CBD) ratio, which is higher in *C. sativa*. The discontinuous geographic ranges – the *sativa* lineage in Europe and the *indica* lineage in Asia – would also support the occurrence of two different taxa within *Cannabis*. The question is whether these differences qualify for defining two separate species or two subspecific taxa. Using quantitative criteria based on key molecular DNA sequences (DNA barcode), McPartland (2018) concluded that the genetic differences are in the rank of subspecies and that the proper nomenclature is *C. sativa* subsp. *sativa* and *C. sativa* subsp. *indica*. Therefore, *Cannabis* is now considered a monospecific genus (Barcaccia et al. 2020; Kovalchuck et al. 2020).

A number of new varieties have been obtained from these two original subspecies by artificial selection, which have different morphologies, phytochemical compositions, geographic distributions and uses (Clarke and Merlin 2016; Lynch et al. 2016; Rahn et al. 2016). According to Small (2015), the consequences of artificial selection make it impossible to determine if unaltered primeval or ancestral populations still exist. This author recommends that *C. sativa* be recognized as a single species with a narcotic subspecies (drug) and a non-narcotic subspecies (hemp), each with domesticated and ruderal varieties. A similar approach is the definition of four major biotypes of cultivated *Cannabis* with morphological and chemical differences submitted to different uses, either fiber/oil or drug production (Table 1). There is also a hybrid between NLD and BLD, known as “Sinsemilla”, which is highly psychoactive (high THC and low CBD) and, hence, is used mainly as a drug. The “Sinsemilla” cultivars were developed in the New World and diffused worldwide. In contrast to the former biotypes, this hybrid is only cultivated, with no feral escapes or ruderal populations. The current distribution of these biotypes is shown in Fig. 1.

Cannabis sativa is a sun-loving (heliotropic) species that requires well-drained and nitrogen-rich soils, warmth and moisture. Therefore, most natural populations are found seasonally across accommodating northern temperate latitudes. This plant grows well along exposed riverbanks, lakesides, margins of agricultural lands and other areas disturbed by humans. *Cannabis* plants are annual and usually dioecious, as determined by X and Y chromosomes, and anemophylous (wind-pollinated). The annual cycle extends from spring (germination) to summer (fast juvenile growing) and autumn (flowering). Male plants, which are slightly taller than female plants, die shortly before pollination. Female plants ripen viable seeds just before the arrival of winter killing frosts. Seed dissemination is carried out mostly by wind or feeding birds. During germination, seeds are surrounded by bracts with hairs that produce a resinous blend of cannabinoids and aromatic compounds as secondary metabolites, which are believed to protect seeds against pests and pathogens. Cannabinols may be psychoactive (THC) or not psychoactive (CBD) for humans (Small 2015; Clarke and Merlin 2016).

Almost all parts of the *Cannabis* plants are utilized for a variety of uses (Table 2). For example, stem bark and fiber are used for cordage, woven textiles, building materials, paper, animal bedding and fuel. Seeds and seed oils are used for human food, animal feed, industrial feedstock and fuel. Female flowers and seeds are used for medicine or recreational drugs. All parts of the plant, primarily bark, seeds and female flowers, are used in ritual and social activities (healing and life cycle rituals, inebriation). *Cannabis* populations may also be used for environmentally related activities, such as the control of soil erosion and to increase CO_2 sequestration. Aesthetic and educational applications include botanical gardens and the iconic character of the plant as a symbol of a very ancient crop deeply rooted in human culture (Gray et al. 2016b). An extensive database on the traditional uses of *Cannabis* (CANNUSE) is available at http://cannusedb.csic.es/. See Balant et al. (2021) for detailed explanations on this database.

Time and place of origin

Early attempts to identify the place of origin of wild *Cannabis* prior to human contact were based on the geographic distribution of its wild, cultivated and ruderal populations, combined with the known ecological requirements and reproductive strategies. However, the distribution of this plant and its biotypes/varieties is closely associated with human settlements and trade routes, and therefore, the original native range is obscured (Clarke and Merlin 2013). In spite of this, a broad area referred to as Central Asia (presently China) was proposed as the center of origin of *Cannabis* (Schultes 1969; Merlin 1972). Another, less generally accepted, possibility mentioned was South Asia (presently India). Regarding timing, accepting that the Central Asian steppes were colonized by humans by 35,000 years ago (Wells 2002; Finlayson 2005), it has been assumed that wild *Cannabis* could have originated earlier. These hypotheses, however, were based on circumstantial evidence, and robust empirical evidence was lacking. This empirical evidence was provided by the fossil record and the use of time-calibrated molecular DNA phylogenies.

The macrofossil record of *Cannabis* is relatively scarce and consists of only a few leaf and fruit/seed impressions with ages ranging between the Oligocene and the late Miocene (McPartland et al. 2019). However, microfossils, specifically pollen, are abundant and widespread and have commonly been utilized to reliably reconstruct the history of *Cannabis*. Nevertheless, the identification of *Cannabis* pollen deserves special attention because of its similarity with other members of the family Cannabaceae, especially *Humulus* (hop), a sister genus that bears contrasting ecological requirements and cultural connotations. Therefore, inaccurate identification might lead to erroneous conclusions (Rull and Vegas-Vilarrúbia 2014). This is why different authors have used broader taxonomic categories for this pollen type, such as *Cannabis*-type, *Cannabis*/*Humulus* or Cannabaceae. In addition, it is unclear whether pollen from wild and cultivated *Cannabis* may be distinguished morphologically.

Several morphological details have been suggested to be useful to differentiate *Cannabis* and *Humulus* pollen. Godwin (1967) emphasized several differential characteristics of the pore complex. Further statistical studies revealed that *Cannabis* pollen is generally larger than *Humulus,* but this character alone was not sufficient to allow reliable separation (Whittington and Edwards 1989; Whittington and Gordon 1987). Pollen size also seems to be an unreliable parameter to separate wild from cultivated *Cannabis* (review in McPartland et al. 2018). The combination of pore complexes and size seems to provide a more reliable, yet not universally accepted, identification criterion to differentiate between *Cannabis* and *Humulus* pollen (Fleming and Clarke 1998; Mercuri et al. 2002).

However, even in the case of conclusive *Cannabis* pollen identifications, comparisons with studies referring to this pollen type as *Cannabis*-type, *Cannabis*/*Humulus* or Cannabaceae remain problematic, which may be a handicap for the development of meta-analyses aimed at reconstructing past biogeographic and cultural patterns. Recently, some meta-analyses have been conducted using different criteria, such as considering the entire *Cannabis*/*Humulus* complex or taking into account only those studies that explicitly identified *Cannabis* pollen (Clarke and Merlin 2013; Long et al. 2017). These approaches tend to overestimate or underestimate the actual pollen record of *Cannabis*.

A different approach, called here the assemblage approach, has recently been proposed by McPartland et al. (2018). These authors noted that wild *C. sativa* is typical of open temperate steppe habitats dominated by grasses, chenopods and *Artemisia*, whereas *Humulus* is a vine plant that requires trees to climb and is common in temperate deciduous forests dominated by alder (*Alnus*), willow (*Salix*) and poplar (*Populus*). A third assemblage corresponds to cultivated *Cannabis*, which is usually found together with cultivated cereals such as *Avena* (oats), *Hordeum* (barley), *Secale* (rye) and *Triticum* (wheat), as well weeds such as *Centaurea* (cornflowers) or *Scleranthus* (knawels) species. Using these phytosociological affinities, McPartland et al. (2018) attributed the *Cannabis*-like pollen types recorded in the literature to wild *Cannabis* if this pollen occurred together with steppe assemblages; to cultivated *Cannabis* when it was part of crop assemblages; or to *Humulus* if the dominant pollen assemblage corresponded to temperate deciduous forests. Based on these premises, these authors developed a more complicated identification algorithm that also considers the relationship between arboreal (AP) and nonarboreal (NAP) pollen (Fig. 2).

Using these criteria, the oldest known pollen compatible with *Cannabis* was found in 19.6 Ma-old (early Miocene) rocks from the NE Tibetan Plateau (Ningxia, China), which was proposed as the center of origin of *Cannabis* (McPartland et al. 2019). Interestingly, this proposal generally coincides with the former hypothesis based on indirect biogeographic evidence. Regarding timing, the use of DNA molecular phylogenies calibrated with fossils of related genera such as *Humulus*, *Celtis*, *Morus* and *Ficus* (Fig. 3) allowed us to estimate the age of divergence of *Cannabis* and *Humulus* to 27.8 Ma (mid-Oligocene). Using the same DNA phylogeny and the associated molecular clock, the divergence between *C. indica* (or *C. sativa* subsp. *indica*) and *C. sativa* (*C. sativa* subsp. *sativa*) occurred in the Middle Pleistocene approximately 1 Ma (McPartland 2018). These authors noted that there is a gap of ca. 8 million years between the age of origin estimated by the molecular clock and the first fossil pollen encountered. In spite of this, they favored the mid-Oligocene age for the origin of *Cannabis* on the NE Tibetan Plateau (Fig. 4), assuming that, as demonstrated by the presence of *Artemisia* and other steppe elements, the region was covered by this type of vegetation, which would have been particularly well suited for the development of *Cannabis*, instead of favoring the Eocene-Oligocene boundary. A previous study using Bayesian calibration estimated the divergence between *Cannabis* and *Humulus* to have occurred 21 Ma (Zerega et al. 2005), which is closer to the age of the first fossil pollen evidence.

According to pollen and seed fossil records, *Cannabis* would have experienced some expansion from its center of origin to Europe and East Asia before the onset of human evolution (Fig. 4). The suggested dispersal agents are water (hydrochory) and animals (zoochory) (McPartland 2018; McPartland et al. 2019). The first expansions occurred to the west (eastern Europe) and the east (NE China) during the Miocene-Pliocene. Most parts of the Asian continent were colonized by *Cannabis* during the Pleistocene, before the onset of the Neolithic, when humans domesticated the plant. The case of Europe is discussed later in more detail. During the Pleistocene (the last 2.6 million years), glacial-interglacial recurrence could have contributed to *Cannabis* diversification without human intervention. It has been suggested that *Cannabis* underwent recurrent range contractions (glacials) and expansions (interglacials) that facilitated allopatric processes, possibly leading to the differentiation between the European (*C. sativa* subsp. *sativa*) and Asian (*C. sativa* subsp. *indica*) subspecies, which diverged nearly 1 Ma (Clarke and Merlin 2013; McPartland 2020). The first is considered the putative hemp ancestor (PHA), and the second is the putative drug ancestor (PDA) (Clarke and Merlin 2013).

Domestication and diffusion

In addition to fossils and DNA phylogenies, archaeological evidence is of paramount importance to reconstruct domestication and anthropogenic diffusion trends within *Cannabis*. The main types of evidence of *Cannabis* from archaeological sites are seeds, fibers, fiber/seed impressions, carbonized remains, phytoliths and chemical remains. During the historical period, written and graphic documents are also of fundamental help (Clarke and Merlin 2013). In this case, pollen identification has some additional clues related to its abundance in sediments, as *Cannabis* produces much more pollen than *Humulus*, which is usually underrepresented (Lewis et al. 1983). This is especially useful in cases of very high percentages of this pollen type, which are difficult to explain unless the sediments come from a former hemp-retting site. Indeed, when flowering male hemp plants are soaked in a retting pond to separate the fibers from the stalk, large quantities of pollen settle into pond sediments. In these situations, the percentages of *Cannabis* pollen in sediments may reach 80-90% of the total, but percentages over 15% or 25% have been considered sufficient to infer hemp retting (Peglar 1993; Mercuri et al. 2002; Demske et al. 2016; McPartland et al. 2019). The anemophylous pollen of *Cannabis* may be transported long distances; therefore, the finding of a few grains or their scattered occurrence throughout a stratigraphic section is not necessarily evidence for the local presence of the parent plant.

After a thorough review of the available historical evidence, Clarke and Merlin (2013) subdivided human-mediated *Cannabis* dispersal within and beyond Eurasia into six phases: 1) primary dispersal across Eurasia (10,000-2000 yr BP), 2) spread into Africa and SE Asia (2000-500 yr BP), 3) diffusion into the Americas from Europe (1545-1800 CE), 4) diffusion to the Americas from Europe and Asia (1800-1945), 5) expansion after World War II (1945-1990), and 6) proliferation of industrial hemp (1990 CE to present). In the first phase, paleolithic nomadic peoples – who were expanding their range during the postglacial ice retreat – could have contributed, either consciously or accidentally, to the dispersal of the wild hemp (PHA) and drug (PDA) precursors from their corresponding distribution areas located in the Caucasus region and SE China, respectively (Fig. 5). This was the onset of differentiation of the four major *Cannabis* biotypes. NLH evolved from the PHA via an intermediate form known as the NLH ancestor (NLHA), whereas NLD and BLD originated from the PDA through the intermediate ancestral form called the NLDA. BLH could also have evolved from isolated PDA populations in NE China. The second phase coincided with the expansion of the Arab Empire into Africa and the Indian Empire into SE Asia. These cultures used *Cannabis* mainly as a drug and introduced the NLD biotype in their dominions, primarily through adventurers and traders. After the initial introductions, migrants and traders spread the NLD biotype across much of Africa and Asia, whereas the hemp biotype (NLH) remained restricted to Europe until the colonization of the Americas (Fig. 5).

Diffusion into the New World (phase 3) occurred during European colonization and consisted mainly of the production of hemp (NLH) for cordage, cloth and seed (Fig. 6). It is speculated whether Vikings could have carried hemp to North America in pre-Columbian times, but there is no evidence for a sound assessment. In addition to domestic uses, hemp cultivation was stimulated by European governments of the colonizing countries to provide their sailing ships with ropes and sails. During this phase (1545-1800 CE), drug biotypes remained in the Old World, where the African expansion of NLD continued. It was not until the middle 1800s CE (phase 4) that Asian hemp (BLH) was introduced in North America through the Pacific Ocean (Fig. 6) to replace the inferior European hemp (NLH) in terms of fiber quality. The first psychoactive biotypes (NLD) were introduced from India into the Americas (mainly Latin America) by indentured laborers following the abolition of slavery in 1834.

After World War II (1945-1949), *Cannabis* cultivation and use were prohibited at the international level, which signified the end of legal diffusion of this plant and initiated the fifth spreading phase (Fig. 6). The illegal traffic of marijuana (NLD) for recreational use did not stop but has experienced a significant increase since the 1960s. Most producers of clandestine *Cannabis* were from Africa, Asia and Latin America, which inadvertently exported seeds to the main consuming centers from Europe and North America, where local cultivation attempts began. In the 1970s, Asian varieties of BLD were introduced into North America and western Europe, where the cultivation of NLD x BLD hybrids flourished.

During the last three decades (phase 6), *Cannabis* prosecution has generated new cultivation and dispersal modes to avoid legal detection. At the same time, renewed economic interest in hemp fiber has been sparked, which has promoted the legal industrial cultivation of hemp. Medical applications have also increased by artificial selection toward varieties with increased THC and other cannabinoids. New varieties have been created by hybridization of NLH and BLH biotypes aimed at expanding hemp cultivation to equatorial areas where European NLH does not grow well. Regarding drugs, the production of NLD/BLD hybrids has also increased and disseminated worldwide, and vegetative indoor cultivation of these hybrids has proliferated. As a result, the global genetic diversity of both hemp and drug forms experienced a significant reduction in comparison with the 1970s and 1980s, when the different biotypes were cultivated by traditional farmers in isolated geographic habitats.

The dispersion model of Clarke and Merlin (2013) assumes two centers of domestication, one in the Caucasus, where the ancestor of hemp fiber domesticated biotypes evolved, and another in SE China, the place where the precursor of narcotic domesticates originated (Fig. 5). The idea of at least two domestication centers situated in Europe and Asia is supported by archaeobotanical studies using pollen, seeds and fibers (Long et al. 2007; McPartland et al. 2018). This contrasts with the view that domestication occurred in a single region. For example, Small (2015) suggested that *Cannabis* was domesticated in the northern Caspian Sea (not far from the Caucasus region) and that the four different domesticated groups were transported to other parts of the world during the last millennium. These four groups coincide with the abovementioned biotypes NLH (Europe), BLH (E Asia), NLD (South-Central Asia) and BLD (Afghanistan). Others have proposed that *Cannabis* was domesticated in Central Asia (Mongolia-N China) by 12,000 BCE (ca. 10,000 yr BP), which would place *Cannabis* among the oldest human domesticates (Warf 2014). A recent genome-wide phylogeographic study supports a unique center of domestication in East Asia (China), from which all biotypes would have emerged and dispersed throughout the world (Ren et al. 2021). According to this analysis, early domesticated ancestors of hemp and drug types diverged from wild *Cannabis* ca. 12,000 yr BP, which indicates that the species had already been domesticated by early Neolithic times.

The debate regarding the *Cannabis* center of domestication has paralleled the taxonomic controversy on *Cannabis* species that, as seen before, was already active by the time of Linnaeus and Lamarck. See, for example, Clarke and Merlin (2013 2016) and Small (2015) for more details on this long-standing discussion. Whether single or multiple centers of *Cannabis* domestication occurred has profound implications for the tempo and mode of *Cannabis* diffusion in Eurasia, where the plant evolved and was domesticated. As mentioned above, diffusion to other continents occurred relatively recently and is well documented historically. This paper focuses on Europe and, especially, the Iberian Peninsula, which are analyzed in more detail.

***Cannabis* in Europe**

According to the single center of domestication hypothesis, European *Cannabis* would have been carried by humans from Asia already in a cultivated form. However, the finding of Pleistocene *Cannabis* pollen across Europe suggests that this plant had arrived to this continent before its domestication, and therefore, the plant had also been domesticated in Europe. Using the assemblage approach for the identification of *C. sativa* pollen explained above (Fig. 2), McPartland et al. (2018) performed a meta-analysis on nearly 480 sites and demonstrated that this pollen was widespread across Europe during the Pleistocene prior to human agency (Fig. 7). According to the same authors, no evident signs of *Cannabis* cultivation have been found either in the pollen or in the archaeological record for most of the European Neolithic. The first palynological evidence for potential *Cannabis* cultivation appeared in present-day Bulgaria during the late Neolithic-Copper age and expanded during the Bronze and Iron ages (Fig. 7). *Cannabis* cultivation expanded across the entire continent between 2000 and 800 yr BP during the Roman Empire and the Early Middle Ages. These results were supported by a further meta-analysis of archaeological evidence (textiles, cordage, fiber, seeds, pottery impressions and phytoliths) from almost 140 sites (McPartland and Hegman

2018). These authors concluded that *Cannabis* dispersed from Asia to Europe in its wild form during the Pleistocene and was domesticated in situ during the Copper and Bronze ages. This challenges the single-site domestication hypothesis, according to which *Cannabis* would have been domesticated in Asia and expanded worldwide as a cultivated plant.

The European domestication of *Cannabis* is consistent with the former view of Clarke and Merlin (2013), who proposed that the precursor of the European NLH biotype – the wild PHA, related to *C. sativa* subsp. *sativa* – would have been centered in the Caucasus region and expanded to western Eurasia and eastern Europe during the Pleistocene (compare Fig. 7 with Fig. 5, phase 1). Chronologically, this possibility also seems plausible, as *C. sativa* subsp. *sativa* diverged from its Asian sister *C. sativa* subsp. *indica* in the Middle Pleistocene, approximately 1 Ma (McPartland 2018), and the European records of wild *Cannabis* are younger than this divergence. In addition, the ages of these wild European records show consistent westward and southward dispersal patterns during the Middle and Late Pleistocene, with younger postglacial records situated in the west and south (Fig. 7). Notably, the European domestication of *Cannabis* (7-5 kyr BP) estimated from pollen and archaeological records (McPartland et al. 2018; McParland and Hegman 2018) occurred after the European Neolithic and much later than Asian domestication (12 kyr BP), as estimated by calibrated phylogenetic trees (Ren et al. 2021).

The Iberian Peninsula

The Iberian Peninsula (hereafter IP) is a key biogeographic region due to its intermediate position between the Eurosiberian and Mediterranean bioclimatic regions (Loidi 2017). The Mediterranean biome and its climatic features, which are the most widespread across the IP (Fig. 8), are well suited for the growth of *Cannabis*. In cultural terms, the IP is also a strategic spot due to its geographic location, which has promoted the interaction of a diversity of cultures over prehistoric and historic times, favored by numerous and varied land and sea connections. Therefore, it might be expected that the IP would also be a relevant place for the study of a plant such as *Cannabis*, which has been subjected to intensive and extensive natural and human-mediated dissemination. It should be noted, however, that the IP is far from any proposed center of origin for *Cannabis,* and the wild form of this plant seems to have reached the peninsula only in postglacial times (after 18.5 kyr BP), after a long journey from the Caucasus region (Figs. 4 to 6). Similarly, the former continental-scale meta-analysis of fossil pollen and archaeological evidence (McPartland et al. 2018; McParland and Hegman 2018) indicates that the IP was among the last European areas – along with the British Isles and the Scandinavian region – where *Cannabis* was cultivated, and this occurred during the Roman Empire and the Early Middle Ages (2000-800 yr BP).

However, these continental-wide analyses include only a few IP sites in their compilations. For example, Clarke and Merlin (2013) mentioned a single, yet representative, site (Lake Estanya; Fig. 8) where *Cannabis* was submitted to intensive cultivation and retting and used it to propose the arrival of *Cannabis* to the IP by 600 CE. McPartland et al. (2018) retrieved their Iberian sites from the European Pollen Database (http://www.europeanpollendatabase.net/index.php) and other internet facilities and considered 10 IP sites, including two from the Balearic Islands (Fig. 8). In this way, although the incoming of *Cannabis* to the IP may be placed within a rather general European context, the precise timing and pathways of arrival, as well as the internal and external dispersal trends, remain largely unknown. Due to the peculiar climatic, biogeographic and cultural features of the IP mentioned above, a thorough survey focused on this specific region to reconstruct *Cannabis* history is worth attempting.

The potential of the IP for providing useful information in this sense is high, as demonstrated by some studies that have recorded relevant historical developments in the hemp industry based on pollen analyses of lake sediments. Among them, the most significant examples were found in lakes Estanya and Montcortès (Fig. 8), where hemp was exploited since the Early Middle Ages. The advantage of these sites is that the amount of *Cannabis* pollen deposited in the sediments is consistent with local cultivation and/or retting rather than with dispersal from regional and long-distance sources. Indeed, some aerobiological studies have demonstrated that relevant amounts of north-African *Cannabis* pollen can be transported to the southern IP in a few days (Cabezudo et al. 1997). Similarly, a recent study of modern sedimentation in Lake Montcortès (Fig. 8) recorded significant percentages of *Cannabis* pollen, but the parent plant was absent from the region (Rull et al. 2017). This long-distance dispersal ability implies that only the presence of this pollen is not sufficient to infer the local occurrence of *Cannabis* populations. However, this is not the case for Estanya and Montocortès, as we discuss in the following section.

In the sediments of Lake Estanya, the first appearance of Cannabaceae pollen was recorded ca. 600 CE (Riera et al. 2004) during the Early Middle Ages (Fig. 9). From then, the record was continuous until the 1990s. Hemp pollen was accompanied by other cultivated plants, such as *Olea* (olive tree), *Secale* (rye) and other undifferentiated cereal pollen. Hemp percentages remained relatively stable (<10%) until the 14th century, when they underwent a significant increase of up to 25% around the middle of the 18th century (Modern Age). This increase was interpreted in terms of hemp retting in the lake, coinciding with a local increase in the cultivation of this plant (Riera et al. 2004). This phase coincided with the maximum hemp production in Spain due to the high demand from the Spanish navy (Riera et al. 2006). After these dates, hemp pollen decreased abruptly to values below 10% during the 20th century. The authors attributed this hemp crisis to a general decrease in cultivation due to the depopulation of the area during the first half of the 20th century.

The first pollen records of *Cannabis* pollen in Lake Montcortès sediments also occurred at approximately 600 CE and coincided with the disappearance of cereals (Fig. 10), which indicates a shift in local cultivation practices from cereals to hemp (Rull et al. 2021). Further increases in wild grasses and weeds such as *Artemisia* (mugworts) and *Plantago* (plantains) are consistent with the expansion of pastures. Hemp pollen experienced three main phases of abundance, separated by two phases of scarcity. The first two phases (ca. 600-750 CE and ca. 850-250 CE) were interpreted in terms of low-intensity cultivation/retting to cover local needs for fiber. The third phase, however, was characterized by significantly high abundances (50-60%) and was difficult to explain in terms of only local consumption (Rull et al. 2021). As in Lake Estanya, this phase (ca 1550-1850 CE) was coeval with the maximum development of the Spanish navy and, as a consequence, of hemp cultivation across the entire country. The same abrupt decrease in hemp pollen was recorded at the end of the 19th century, which has been related to the dismantling of the royal navy, the onset of hemp importation from other countries, the substitution of hemp fiber by other materials such as cotton and synthetic fibers, and the decrease in human pressure (Rull and Vegas-Vilarrúbia 2004; Trapote et al. 2018). The further increase in hemp pollen in the late 20th century may have been due to the renewed interest in hemp, likely favored by EU subsides (Trapote et al. 2018).

The combination of the meta-analysis discussed above (Fig. 7) and the case studies of Estanya and Montcortès may suggest that wild *Cannabis* reached the IP during the postglacial period (18.5-15 kyr BP) and that cultivated *Cannabis* entered much later, by 600 CE. Notably, both entries would have proceeded from the northeastern sector. However, in the present state of knowledge, it is still premature to confirm these assessments. The lag of sufficient localities also hinders knowing what happened on the IP with *Cannabis* during the large gap between postgacial times and the Middle Ages. The development of a thorough database for the IP, as a basis for further meta-analyses, is essential to understand when and how wild and cultivated *Cannabis* reached the IP, as well as what happened since those times.

In addition to the information available from the above reviews and meta-analyses, other sources of information should be accessed. For example, many other sites are available in the compilation by Carrión et al. (2012) that have not been included in the former studies. This compilation gathered almost all pollen records available for the IP by the time of publication and is now being updated with new studies developed during the last decade. There are also other individual sites with *Cannabis/Humulus* pollen that need more bibliographic research. A number of these studies are not easy to locate, as they are available only in dissertations and local journals. Finally, some studies do not include *Cannabis/Humulus* pollen in the diagrams due to its scarcity, but the authors have data in their counting sheets and they can be recovered. Therefore, personal contact with palynologists working on the IP is also needed. All these information sources, along with others that may be located further, should be included in an IP-wide study.

Table 1. The four biotypes of cultivated *Cannabis* as defined by Clarke and Merlin (2016), following the criteria of Small (2015). See Fig. 1 for the present geographical distribution of these biotypes.

Biotype	Name	Psychoactive	THC	CBD	Use	Origin	Diffusion
NLH	Narrow-leaf hemp	Rarely	Low	High	Fiber/oil	Europe	New World
BLH	Broad-leaf hemp	Mildly	Low/Moderate	High	Fiber/oil	East Asia	Europe, New World
NLD	Narrow-leaf drug	Very	High	Low/absent	Drug	South Asia	Africa, Europe, Middle East, New World
BLD	Broad-leaf drug	Moderately	Moderate/high	Moderate/high	Drug	Afghanistan	Europe, New World

Table 2. Examples of the variety of uses of the different parts of the *C. sativa* plants. Modified from Clarke and Merlin (2016).

Plant parts	Use category	Material type or benefits
Stem bark	Cordage	Long cellulose fibers
Stem fiber	Cordage, woven textiles, building materials	Long cellulose fibers, concrete reinforcement
Wood/bark	Paper, building materials, animal bedding, fuel	Long/short cellulose fibers, chip board, concrete matrix, heat, light
Female flowers/seeds	Medicinal	Herbal remedies, pharmaceuticals, nutraceuticals
Female flowers and associated resin glands	Recreational drugs	Marijuana, hashish
Seeds (oil)	Human food, industrial feedstock, fuel	Proteins/essential fatty acids, paint/plastic manufacture
Seeds (cake), foliage	Animal feed	Proteins and essential fatty acids
All parts	Ritual and social	Healing, life cycle rituals, inebriation
Plant-people interplay	Aesthetic	Intrinsic beauty of the plant
Genus	Educational	Iconic example of an economic plant and its ancient human relationships

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Figure captions

Figure 1. Worldwide distribution of the different *Cannabis* biotypes developed by humans (Table 1). Hemp biotypes are in red and drug biotypes in red. NLH, narrow-leaf hemp; BLH, broad-leaf hemp; NLD, narrow-leaf drug; BLD, broad-leaf drug; NLD/BLD, hybrid between NLD and BLD; PA?, putative *Cannabis* ancestor. Redrawn from Clarke and Merlin (2016).

Figure 2. Algorithm developed to differentiate between *Cannabis* and *Humulus* pollen in sedimentary records, using the assemblage approach. As explained in the text, crop pollen usually includes cereal and weed pollen. AP, arboreal pollen; NAP, non-arboreal pollen; *PAC*, steppe assemblage (Poaceae-*Artemisia*-Chenopodiaceae); *ASP*, forest assemblage (*Alnus-Salix-Populus*). Redrawn from McPartland et al. (2018).

Figure 3. Time-calibrated molecular DNA phylogenetic tree used for the estimation of the divergence rates within the Cannabaceae and some related families (molecular clock). Red dots are the nodes used for calibrating the phylogenetic tree using *Humulus*, *Celtis*, *Morus* and *Ficus* fossils of known age. Numbers are ages in million years before present (Ma). Redrawn and modified from McPartland (2018).

Figure 4. Center of origin (red dot) and preanthropic dispersal of *Cannabis*, based on fossil pollen data and the use of the assemblage algorithm explained above (Fig. 2). Dot colors indicate the age of first occurrences of *Cannabis* pollen (see legend), in million years before present (bold numbers) and in thousand years before present (normal numbers). Redrawn and modified from McPartland et al. (2019).

Figure 5. The first two phases of human-mediated *Cannabis* diffusion. As in Fig. 1, hemp biotypes are indicated by green letters and drug biotypes are in red letters. Redrawn and modified from Clarke and Merlin (2013).

Figure 6. Phases three to six of anthropogenic *Cannabis* expansion. As in Fig. 1, hemp biotypes are indicated by green letters and drug biotypes are in red letters. Redrawn and modified from Clarke and Merlin (2013).

Figure 7. Pleistocene (upper panel) and Holocene (lower panel) European pollen records consistent with *Cannabis*, according to the assemblage identification approach (Fig. 2). Note that, in the Pleistocene panel, post-glacial ages have been differentiated from the rest of Late Pleistocene ages. PHA is the precursor of the European *Cannabis* according to Clarke and Merlin (2013); compare with Fig. 5, phase 1. Ages in million years before present (bold numbers) and in thousand years before present (normal numbers). Raw data from McPartland et al. (2018).

Figure 8. Map of the Iberian Peninsula indicating the location of the sites included in the available reviews and meta-analyses (Clarke and Merlin 2013; McPartland and Hegman 2018; McPartland et al. 2018). The Eurosiberian bioclimatic region is in green and the Mediterranean region in yellow. The numbers in brackets above the site names are the age of the first appearance of the *Cannabis/Humulus* pollen, in kyr BP. Original references: Alcúdia (Burjachs et al. 1994); Andorra (Ejarque et al. 2010); Antas (Pantaleón-Cano et al. 2003); Algendar (Yll et al. 1997); Banyoles (Pérez-Obiol and Julià 1994); Coll del Moro (Alonso and Juan 1994); Estanya (Riera et al. 2004); La Roya (Allen et al. 1995); Montcortès (Rull et al. 2011); Rascafría (Franco-Mújica et al. 1998); Somolinos (Currás 2021); Totana (López 1988).

Figure 9. Pollen diagram of selected cultivated plants from Lake Estanya record, which was dated using radiocarbon and known historical events. Dashed lines are the percentage boundaries (15% and 25%) proposed by different authors for inferring retting practices (see text). The red arrow indicates the first appearance of Cannabaceae pollen. The boundaries of the cultural phases are approximate. Redrawn and modified from Riera et al. (2004).

Figure 10. Pollen diagram of selected cultivated plants and weeds from Lake Montcortès sediments, which were dated up to ca. 3000 yr BP using varves. Dashed lines are the percentage boundaries (15% and 25%) proposed by different authors for inferring retting practices (see text). The red arrow indicates the first appearance of *Cannabis* pollen. Modified from Rull et al. (2021).

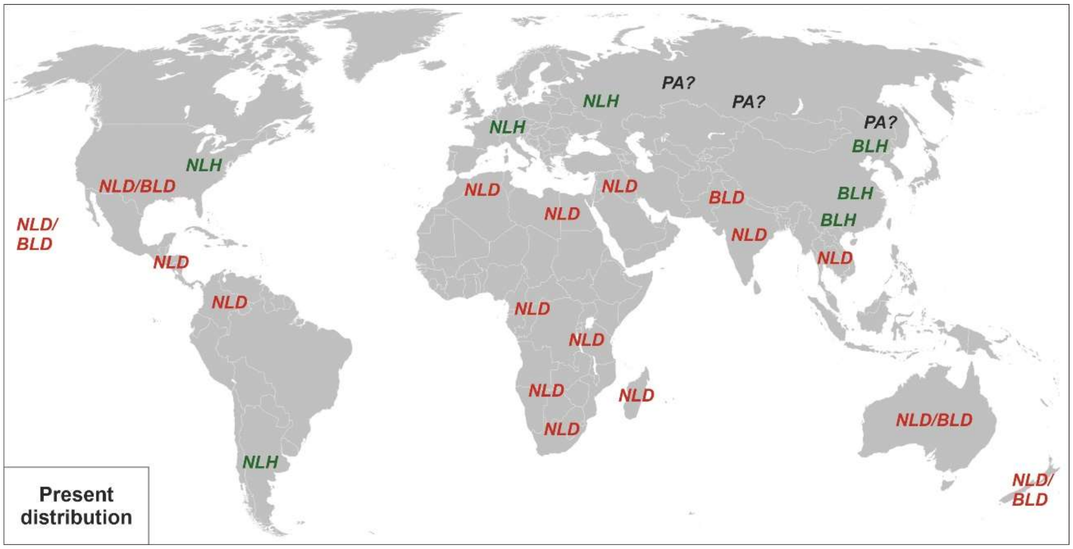

Figure 1

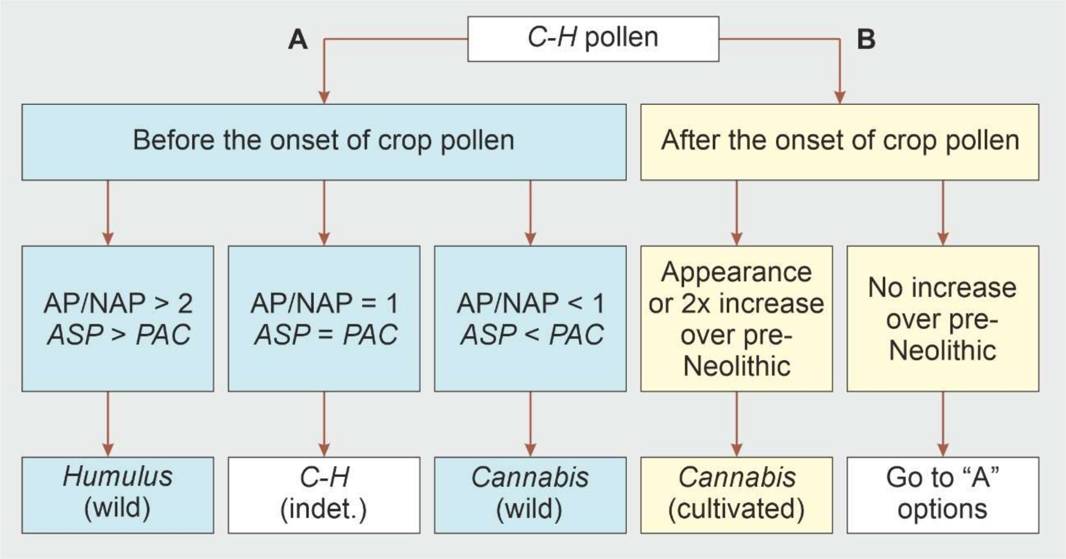

Figure 2

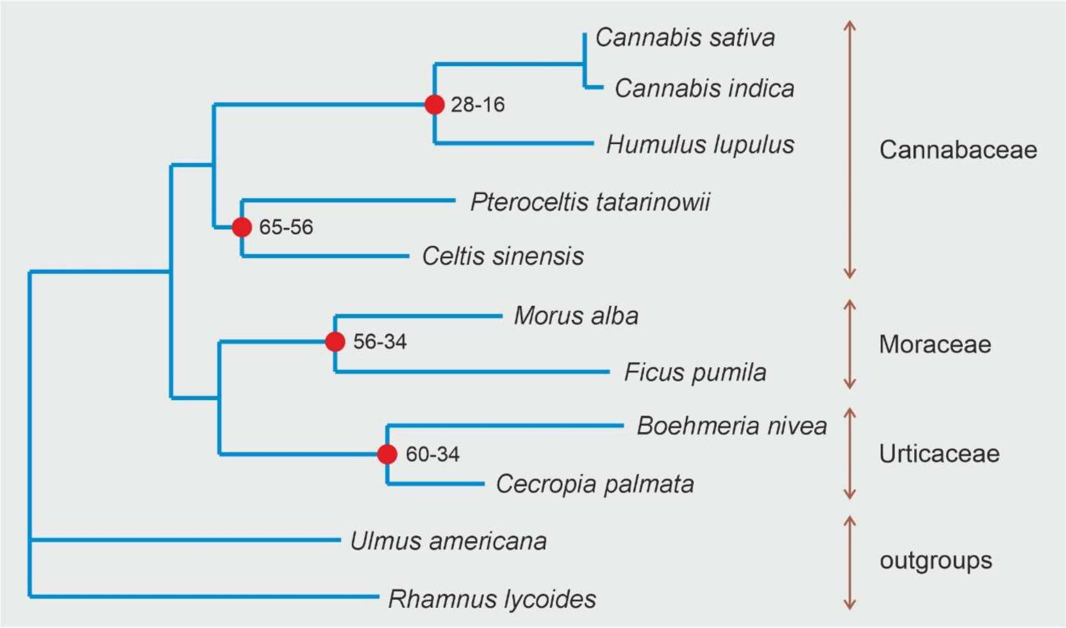

Figure 3

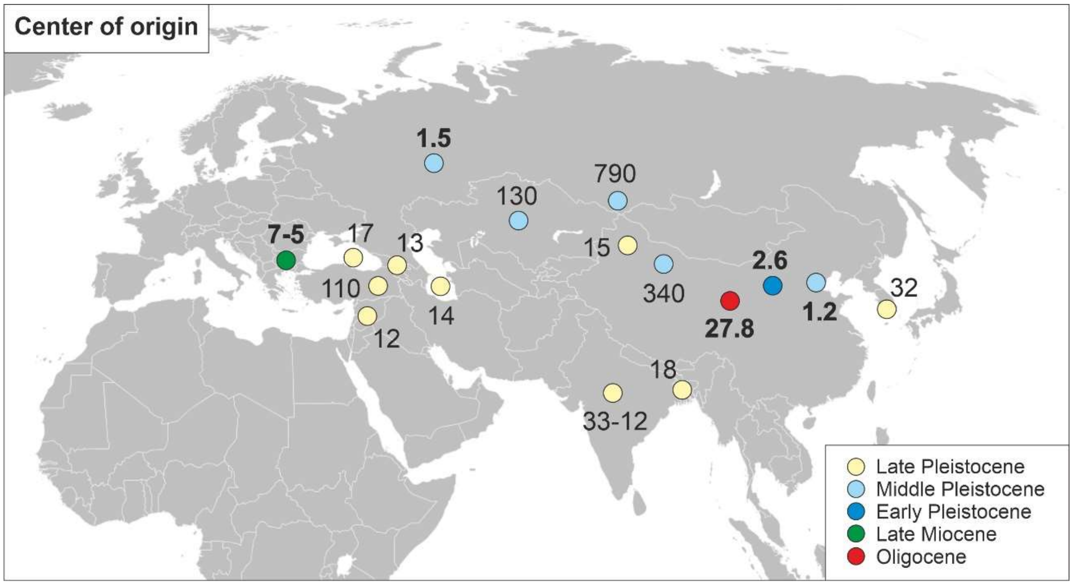

Figure 4

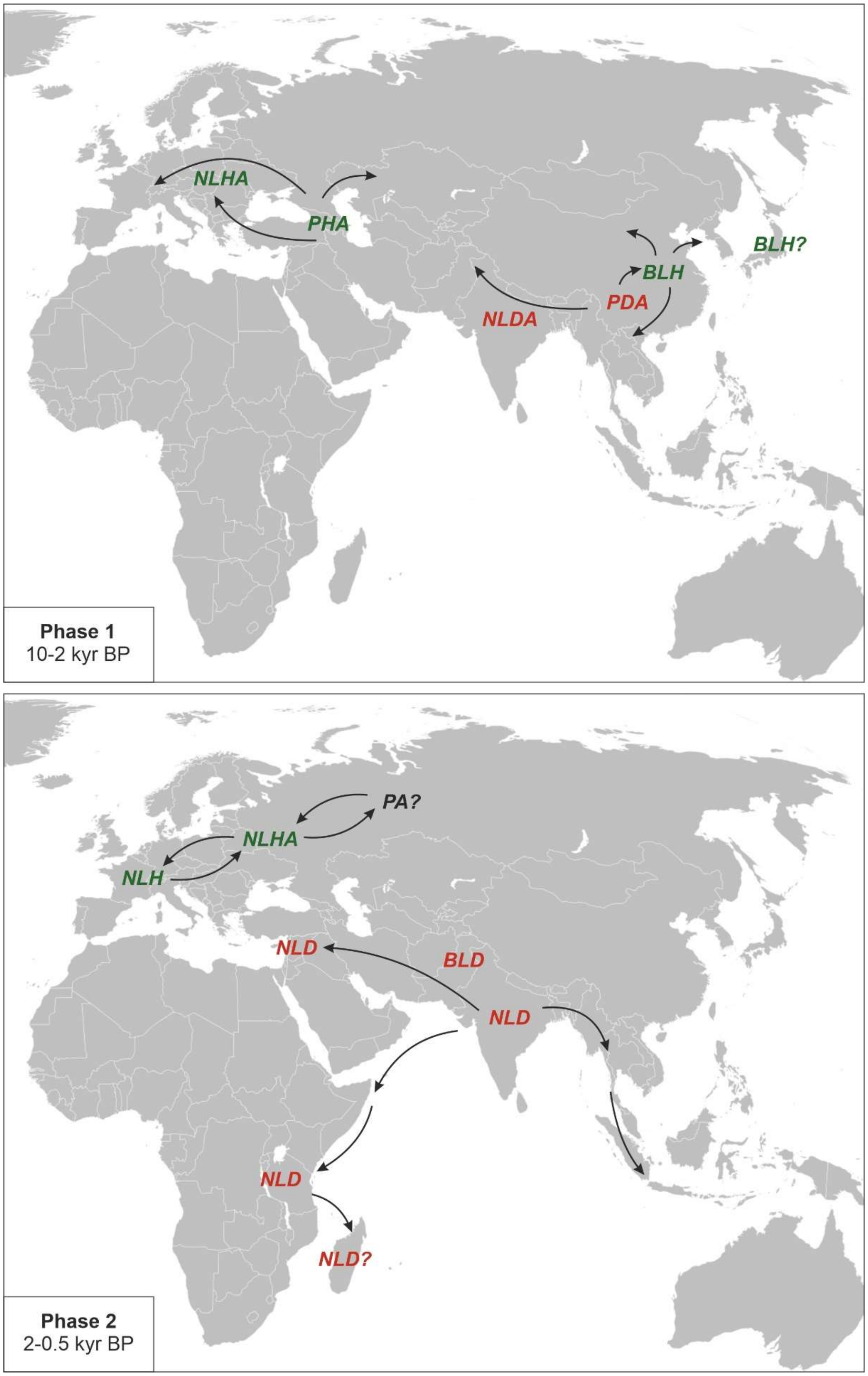
NLHA
PHA
BLH?
BLH
PDA
NLDA
Phase 1
10-2 kyr BP
PA?
NLHA
NLH
NLD
BLD
NLD
NLD
NLD?
Phase 2
2-0.5 kyr BP

Figure 5

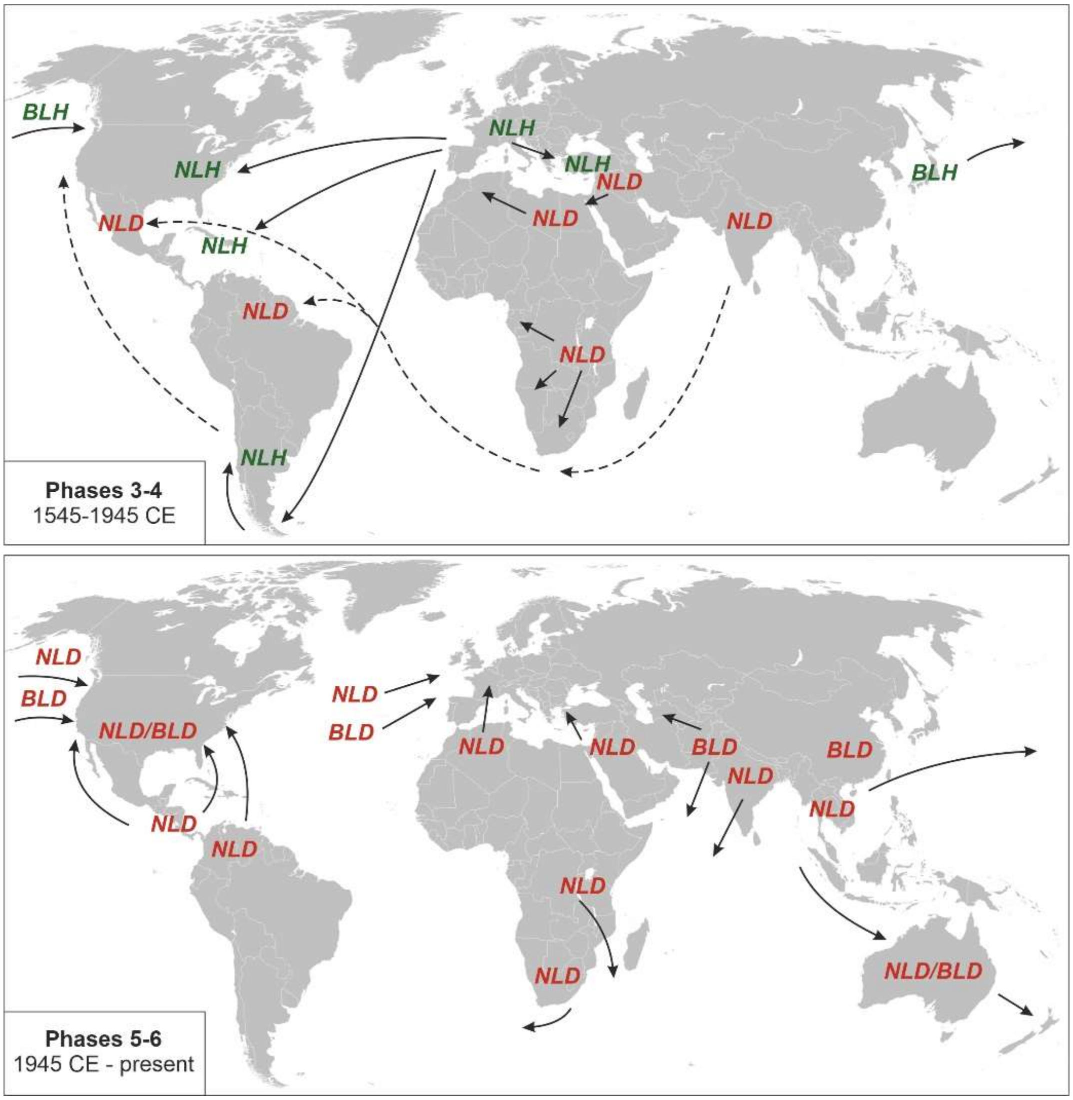
BLH
NLH
NLH
NLH
NLD
NLD
NLH
NLD
NLD
BLH
NLD
NLD
NLH
Phases 3-4
1545-1945 CE
NLD
BLD
NLD/BLD
NLD
BLD
NLD
NLD
BLD
NLD
BLD
NLD
NLD
NLD
NLD
NLD
NLD/BLD
Phases 5-6
1945 CE - present

Figure 6

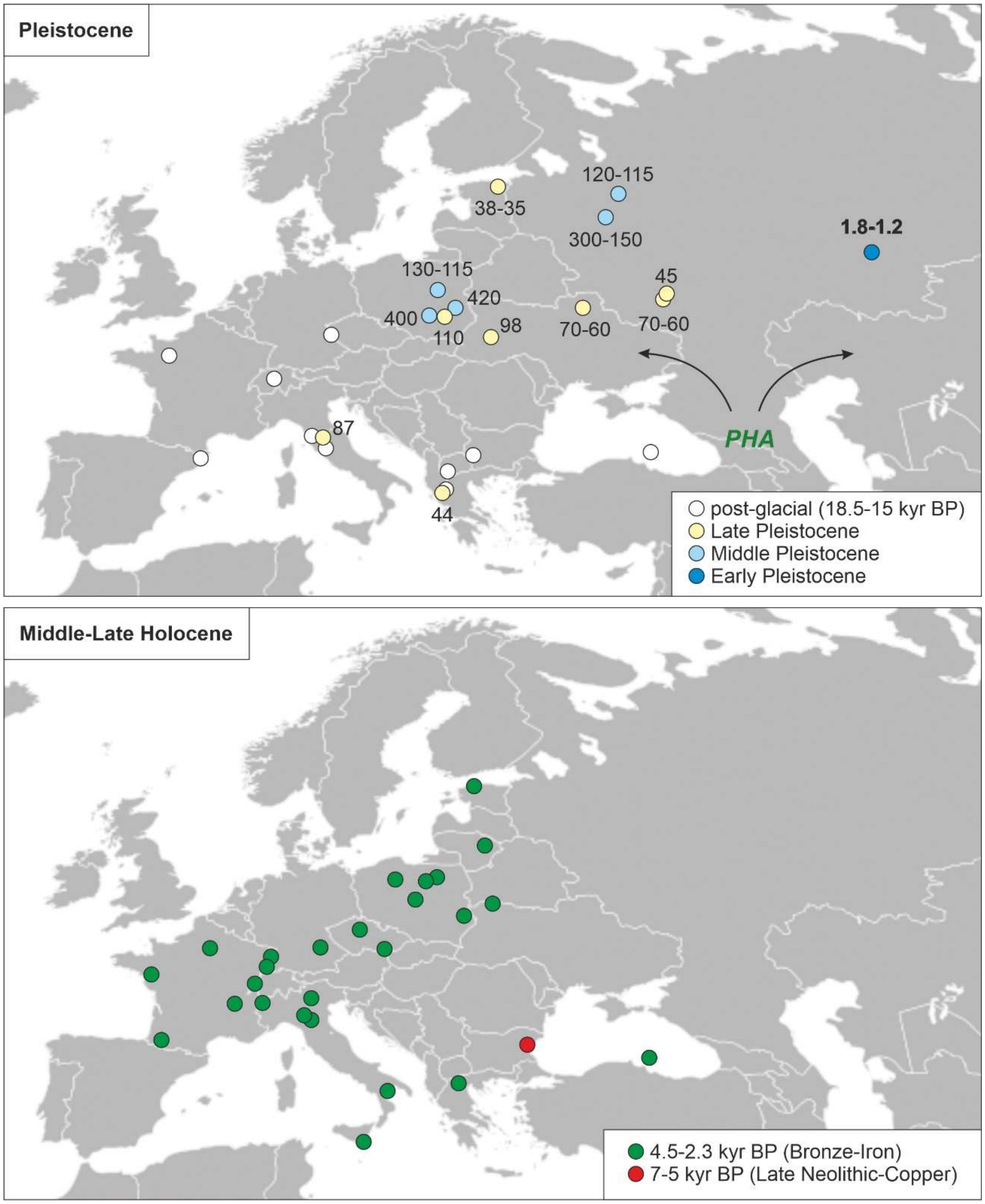
Pleistocene
120-115
38-35
300-150
1.8-1.2
130-115
45
420
400
110
98
70-60
70-60
87
PHA
44
○ post-glacial (18.5-15 kyr BP)
● Late Pleistocene
● Middle Pleistocene
● Early Pleistocene
Middle-Late Holocene
● 4.5-2.3 kyr BP (Bronze-Iron)
● 7-5 kyr BP (Late Neolithic-Copper)

Figure 7

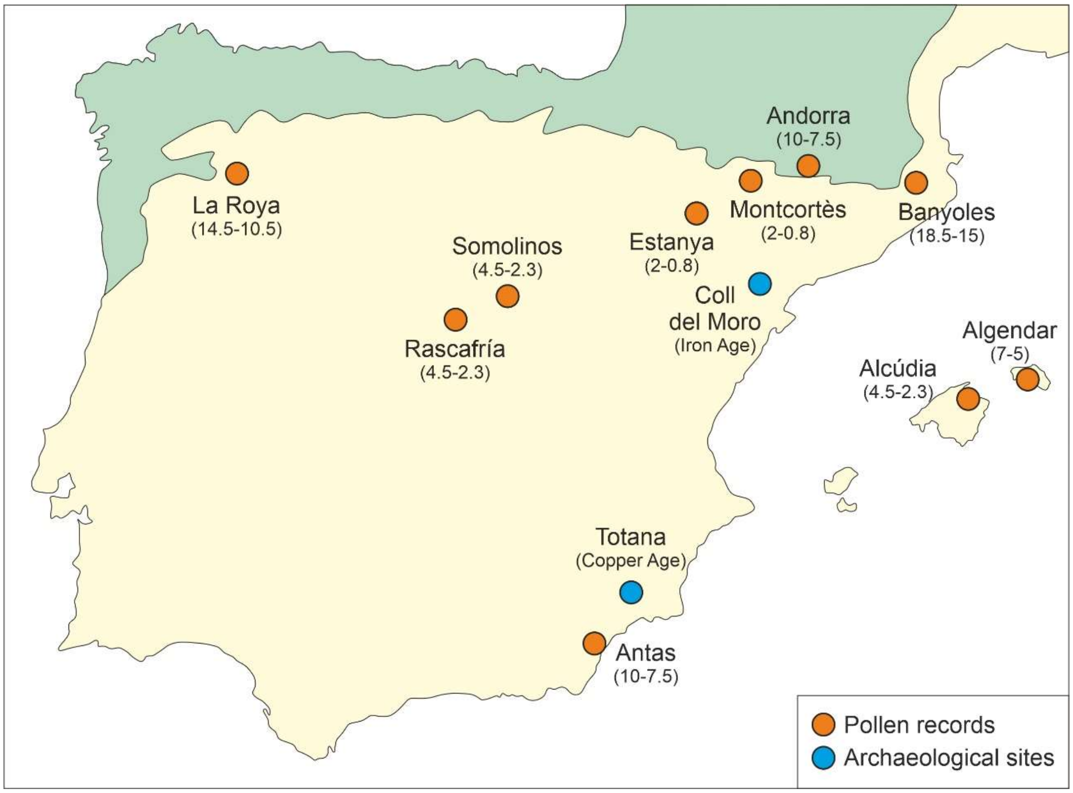
Andorra
(10-7.5)
La Roya
(14.5-10.5)
Montcortès
(2-0.8)
Banyoles
(18.5-15)
Estanya
(2-0.8)
Somolinos
(4.5-2.3)
Coll
del Moro
(Iron Age)
Rascafría
(4.5-2.3)
Algendar
(7-5)
Alcúdia
(4.5-2.3)
Totana
(Copper Age)
Antas
(10-7.5)
Pollen records
Archaeological sites

Figure 8

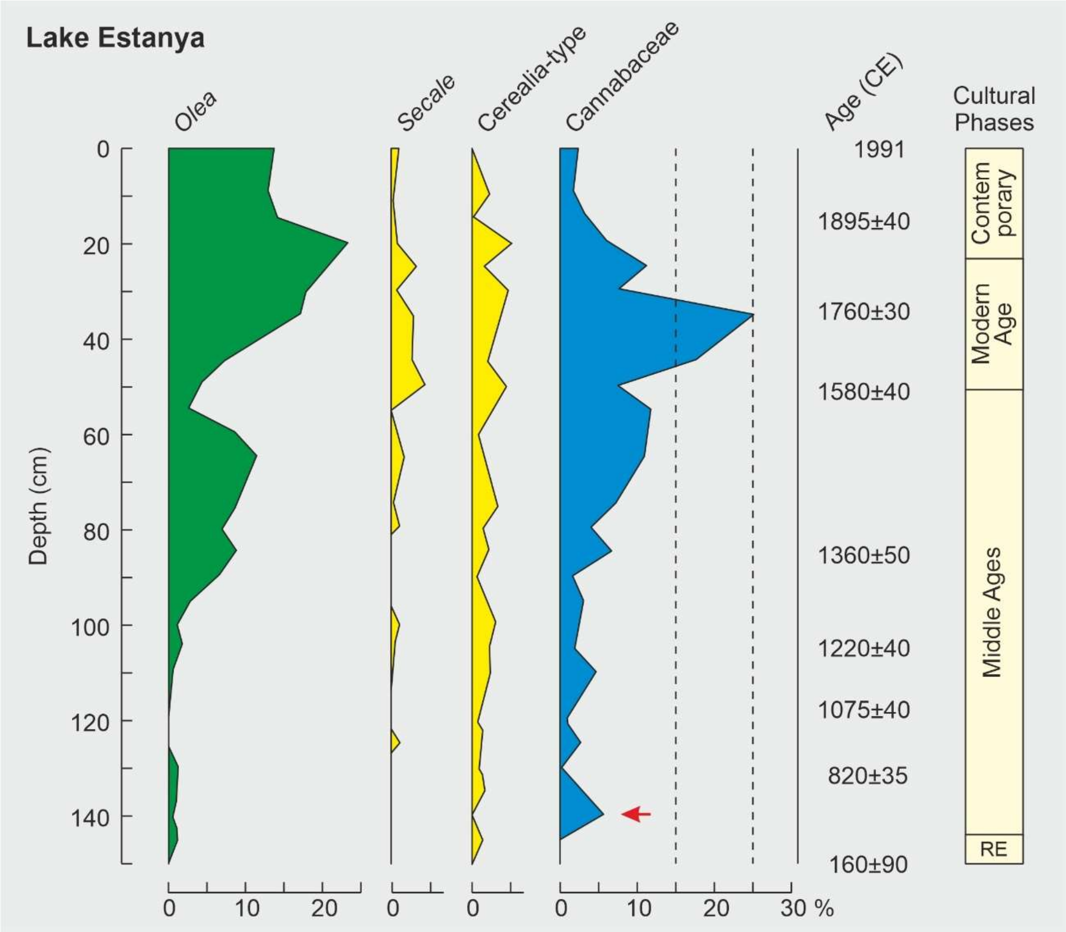
Lake Estanya
Olea
Secale
Cerealia-type
Cannabaceae
Age (CE)
Cultural Phases
Depth (cm)
0
20
40
60
80
100
120
140
1991
1895±40
1760±30
1580±40
1360±50
1220±40
1075±40
820±35
160±90
Contemporary
Modern Age
Middle Ages
RE
0
10
20
0
0
0
10
20
30 %

Figure 9

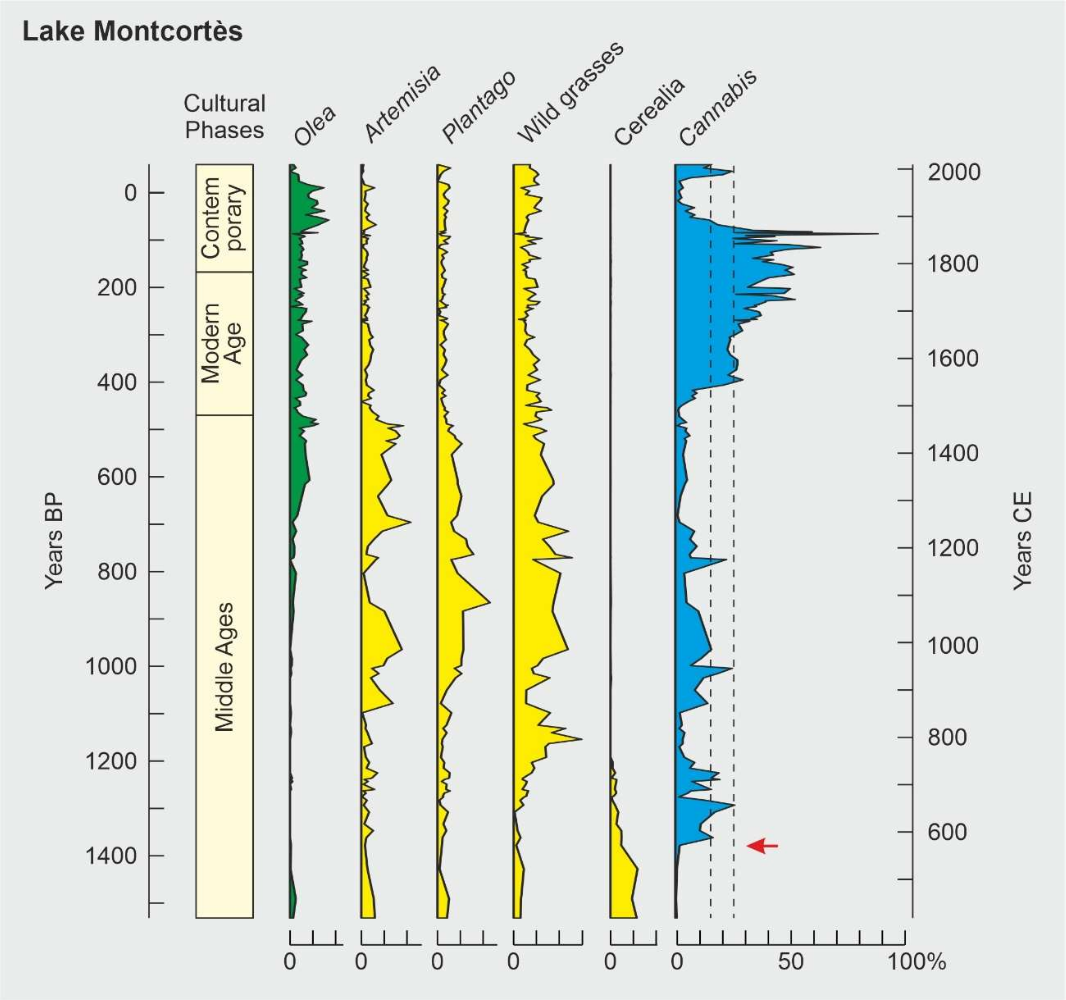
Lake Montcortès
Cultural Phases
Contemporary
Modern Age
Middle Ages
Olea
Artemisia
Plantago
Wild grasses
Cerealia
Cannabis
Years BP
0
200
400
600
800
1000
1200
1400
Years CE
2000
1800
1600
1400
1200
1000
800
600
0
0
0
0
0
0
50
100%

Figure 10