

Quantifying human impacts to tease apart cultural and climatic drivers of Holocene vegetation change

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Introduction

The current need for understanding climate change impacts on vegetation in light of the ongoing anthropogenic climate change prioritizes studying the drivers of vegetation change. Humans have emerged as a force of nature rivalling climatic and geologic forces in shaping the terrestrial biosphere and its processes, altering >75% of today's Earth's ice-free land surface (Ellis and Ramankutty, 2008). Disentangling anthropogenic and natural drivers of vegetation change is in turn of paramount importance in palaeoecology, especially where it is unclear whether climate or human activities have been the main force driving environmental change. For example, in the western Mediterranean, the underlying drivers of striking, region-wide vegetational changes are matters of debate (Ramos-Román et al., 2018), as some palaeoecological studies show an aridification trend on the late Holocene (Carrión et al., 2010; Jalut et al., 2009), while others suggest human impact as the main driver of late Holocene vegetation change (Jouffroy-Bapicot et al., 2021; Pedrotta et al., 2021).

In palynological studies, Holocene human impacts have been widely considered by inferring anthropogenic-induced environmental changes, for instance land use, by using cultural indicator pollen types (Behre, 1981). The cultural pollen indicators indeed constitute the most broadly used methodology to infer anthropogenic activities. This method comprises pollen types that refer to cultivated plant species (crops) or indirectly favored species (adventives), introduced by humans during agricultural activities or, to a lesser extent, plants that benefited from human activities (apophytes). Their selection was based on ecological requirements of species and often relies on geobotanical or phytosociological references (Behre, 1981; Brun, 2011). The selected taxa are basically associated with diverse farming contexts: winter cereals, summer cereals, root crops, fallow land, wet meadows and pastures, dry pastures, pastures within non-regenerating woodland, footpath and ruderal communities, and species frequent in natural communities (especially those of peaty soils). However, complex autecological properties of species as well as specific variations in pollen production and dispersal require a deep expert knowledge and the consideration of multiple environmental and ecological factors to reconstruct vegetation history or to correctly infer land use or climate changes, generating controversies in palaeoecological and palaeoclimatic research (e.g. Behre, 2008; Tinner et al., 2008). Furthermore, quantitative reconstructions drawing on pollen indicators are not always straightforward and there is a need for methodologies that allow to establish these relationships.

A series of palaeoecological methods aim at the quantitative reconstruction of past vegetation. For instance, the REVEALS model estimates regional vegetation composition using pollen from 'large lakes' that have small site-to-site variations of pollen assemblages even if vegetation is highly heterogeneous (Sugita, 2007). Other intermediate complexity methods, such as the 'pseudobiomisation' approach (Fyfe et al., 2010), assign pollen taxa to different land-cover classes (LCC) and the sum of adjusted pollen proportions for each class is used to determine a LCC affinity score for individual pollen samples. However, indices focusing on cultural pollen indicators are the prevalent methodology, given their flexibility and convenience. More specifically, the cultural indicators were originally calibrated for Central Europe (Behre, 1981), and their wide use and adaptation in other realms can pose complications that are not always sufficiently addressed. In addition, some issues were not specified when the cultural pollen indicators were described, e.g., their indicative capacity did not consider the inherent variability in pollen production, dispersal, deposition and taphonomy.

The present thesis is framed in the Swiss National Science Foundation (SNF) project QuantHum- Quantifying human impacts to tease apart cultural and climatic drivers of Holocene vegetation change, which aims to develop a quantitative index of human-impact intensity for paleoecological records. In this thesis, we study different aspects around the methodology of cultural pollen indicators and on the basis of studies that have used cultural pollen indicators over more than two decades at the laboratory of Palaeoecology at University of Bern. We draw conclusions of how this approach responds to different environmental contexts and check its implementation with independent evidence, as e.g. resulting from archaeology. Moreover, we aim to improve the use of cultural pollen indicators to achieve a more precise quantitative reconstruction of anthropogenic vegetation impacts.

Approaches and rationales

In this dissertation we first review the state of the art on cultural pollen-index approaches. **Manuscript 1** (Deza-Araujo et al., 2020) presents the most used cultural indicator indices and applies them to pollen sequences along Europe, evaluating their performance to detect and quantify past human impact. As theoretical means of validation, we define Holocene human impact as a function of human population and technology (Kremer, 1993). With these variables, we infer an expected steadily growing human impact, since humans first began to alter

landscapes for food production (or agricultural land use, Mottl et al., 2021). We divide the Holocene human impact in five stages of intensity: Very low, low, moderate, high and very high. The very low / non detectable human impact stage is typical of Paleolithic and Mesolithic hunter-gatherer economies (possible impact on regional fire regime; possible low-intensity or shifting cultivation and livestock grazing, expansion of disturbance-adapted shrublands or maquis). The low human impact stage is related with establishment of agricultural land use; an increase in fire activity; forest opening and an impact on wild species composition; typical of Neolithic farming economies. The moderate human impact intensity is associated with major opening of forest or alteration of natural vegetation; establishment of permanent arable agriculture and or grazing; starting at the Bronze Age. The high human impact stage corresponds with more intensive land use, during the Iron Age, Roman Period and Early Middle Ages. Finally, the very high stage of human impact corresponds with replacement of natural vegetation with cultural vegetation (fields, meadows); typical for Late Medieval and modern economies. We used this division of the Holocene human impact to analyze the performance of the studied methodologies. Here in manuscript 1, we analyze the following indices: the Primary Indicators- PI and Secondary Indicators -SI (Behre, 1981; Lang, 1994), which constitute a sum of the direct (crops) and indirect (weeds) anthropogenic taxa (Behre, 1981; Lang, 1994; the Cultural Indicators- CI, which considers the combination of Cerealia-type (excluding *Secale*) and *Plantago lanceolata*-type to infer agriculture (Tinner et al., 2003); the Anthropogenic pollen indicators – API , which sum *Artemisia*, *Centaurea*, Cichorioideae, *Plantago*, Cerealia-type, *Urtica*, *Trifolium* (Mercuri, Bandini Mazzanti, Florenzano, Montecchi, Rattighieri, et al., 2013); OJC and OJCV, which sum the pollen types of cultural tree crops *Olea*, *Juglans*, *Castanea* (and liana *Vitis*; Mercuri, Bandini Mazzanti, Florenzano, Montecchi and Rattighieri, 2013); the Pollen Disturbance Index – PDI, that considers *Centaurea*, Cichorioideae, *Plantago*, *Ranunculus acris*-type, *Polygonum aviculare*-type, *Sanguisorba minor*-type, *Urtica dioica*-type and *Pteridium*. Finally, we also analyse the behaviour of the AP/NAP ratio, that means relative abundance of arboreal pollen with respect to non-arboreal pollen. Values are interpreted as: >10, very close forest; 4–10, close forest (at 4, first relevant vegetation openings); <1, open vegetation (Berglund et al., 1991; Favre et al., 2008). We hypothesize that the magnitude of human impact on the environment will monotonically increase towards the present across the stages of population and technological development of European societies during the Holocene, as inferred from archaeological and historical evidence.

A remarkable limitation of the cultural pollen method is embedded in palynology itself, as the identification of pollen types is determined by their morphological characters and their more or less complex identifications result in the achievement of different, often low to moderate, taxonomical resolutions. The application of traits (such human indicative value) to pollen-stratigraphical data is greatly hampered by the taxonomic imprecision (Birks, 2020). The cultural pollen indicators were thus originally defined by different degrees of taxonomic resolution (Behre, 1981). Additionally, the taxonomical precision in the pollen identification varies among palynologists, according to their schools, aim of the study, taphonomic characteristics of the study core, among others.

Manuscript 2 (Deza-Araujo et al., 2021) deals with the taxonomic resolution of cultural pollen indicators and how it influences their indicative value. We selected sixteen postglacial pollen sequences produced with high resolution and by using established tables of taxonomic harmonization (Giesecke et al., 2019), we simulate two additional levels of hierarchical taxonomic resolution for each dataset and compare the results in terms of capacity of the indicators to infer past human impact. We hypothesize that reducing the taxonomic resolution will cause a decrease in the specificity and sensitivity of the pollen indicators for detecting and quantifying anthropogenic land use, with different pollen types having more or less influence on this change according to the biogeographical region. Further, we also hypothesize that lowered taxonomic levels in pollen identification will result in misleading reconstructions of past human land use. These hypotheses are checked by a comparison of the available pollen evidence with historical and archaeological sources.

On the basis of the outcomes of Manuscripts 1 and 2, we were able to propose a new probabilistic method in **Manuscript 3**, the agricultural Land Use Probability index – LUP, for detecting and quantifying human impacts through cultural pollen indicators. We refine the established list of cultural pollen indicators by Behre (1981) and assess their anthropogenic indicative value based on criteria adapted from bioindication. We train the index using twenty palynological datasets along an environment gradient between Sicily and Swiss Plateau and perform two external validations, by (1) applying them to independent pollen sequences and (2) comparing the results with an archaeological proxy of human population density (number of radiocarbon dates from cultural layers). We use Anthropogenic Indicator Values (AIV) to weight the relative abundance of the cultural pollen indicators, according to their biogeographical context. We assume that pollen samples having more pollen-types of indicator taxa with a higher AIV are more likely to express human land use, which is then mirrored numerically in its LUP.

Aspects on Human Pollen indicators	Overall indicative capacity	Adventiveness	Taxonomic resolution	Pollen production/ deposition	Abundance and significance in pollen diagram	Over-representation in the pollen diagram
Manuscript in which the topic is considered	Manuscript 3	Manuscript 1	Manuscript2	Manuscript 3	Manuscript 3	Manuscript 1

Figure 1. Scheme explaining where the most defining aspects for cultural pollen indicators are dealt in my dissertation.

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A critical assessment of human-impact indices based on anthropogenic pollen indicators

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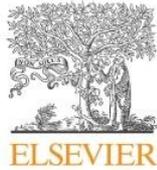
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ABSTRACT

Anthropogenic pollen indicators in pollen records are an established tool for reconstructing the history of human impacts on vegetation and landscapes. They are also used to disentangle the influence of human activities and climatic variability on ecosystems. The comprehensive anthropogenic pollen-indicator approach developed by Behre (1981) has been widely used, including beyond its original geographical scope of Central and Western Europe. Uncritical adoption of this approach for other areas is risky because adventives (plants introduced with agriculture) in Central Europe can be apophytes (native plants favoured by human disturbances) in other regions. This problem can be addressed by identifying region-specific, anthropogenic-indicator pollen types and/or developing region-specific, human-impact indices from pollen assemblages. However, understanding of regional variation in the timing and intensity of human impacts is limited by the lack of standardization, validation and intercomparison of such regional approaches. Here we review the most common European anthropogenic pollen-indicator approaches to assess their performance at six sites spanning a continental gradient over the boreal, temperate and Mediterranean biomes. Specifically, we evaluate the human-indicator approaches by using independent archaeological evidence and models. We present new insights into how these methodologies can assist in the interpretation of pollen records as well as into how a careful selection of pollen types and/or indices according to the specific geographical scope of each study is key to obtain meaningful reconstructions of anthropogenic activity through time. The evaluated approaches generally perform better in the regions for which they were developed. However, we find marked differences in their capacity to identify human impact, while some approaches do not perform well even in the regions for which they were developed, others might be used, with due caution, outside their original areas or biomes. We conclude that alongside the increasing wealth of pollen datasets a need to develop novel tools may assist numeric human impact reconstructions.

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1. Introduction

Palaeoecology provides valuable records of past ecological change and its drivers over centennial to millennial timescales at decadal to centennial resolution. Environmental drivers of ecosystem change (e.g. climate, human activities, natural disturbances) may operate simultaneously and thus it may be difficult to

disentangle their specific role (Nelson et al., 2006). In Europe, human activities became a major driver for landscape dynamics, land-cover change, species distributions and disturbance regimes as early as ca. 9000–7000 years ago with the onset of farming at the beginning of the Neolithic. As a result, the transformation of forests into heathlands (e.g. *Calluna vulgaris*), shrublands (e.g. *Corylus avellana*, *Alnus viridis*), maquis, garrigue, grasslands, or meadows may have resulted from human-induced deforestation including excessive fire disturbance and/or browsing (Gobet et al., 2000; Tinner et al., 2005; Carrión et al., 2010; Rey et al., 2019). These examples illustrate the role of discrete disturbance events and

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highlight the need for high-resolution reconstructions of past land use and environmental change to disentangle anthropogenic and natural forcing. The contribution of the various forcing factors may be assessed using multi-proxy palaeoecological studies providing independent lines of evidence (Birks and Birks, 2006; Colombaroli et al., 2007), where the results are ideally validated with local archaeological evidence (Hjelle et al., 2012).

Vegetation changes inferred from palynological sequences have traditionally been linked to climate change when occurring more or less synchronously over broad areas (Jalut et al., 2009), but this assumption might result in overlooking the role of broad-scale concurrent human activities (Tinner et al., 2013; Walsh et al., 2019). Previous research has also shown that climate change may exert a strong influence on land use, leading to synchronous patterns over wide areas (Gobet et al., 2003; Tinner et al., 2003; Oliver and Morecroft, 2014). For instance, widespread forest opening reconstructed from several Mediterranean pollen records for the past ca. 7000 years has been attributed to either a continental-scale decrease in moisture availability (“aridification” hypothesis; see Jalut et al., 2009; Sadori et al., 2011), increasing human activity, including burning (e.g. Tinner et al., 2009; Bisculm et al., 2012) or a combination of both factors (e.g. Carrión et al., 2010). This controversial Mediterranean example illustrates challenges in unambiguously inferring anthropogenic impacts.

Reconstructing human impacts on the environment using palynology has largely relied on the presence and abundance of anthropogenic pollen indicators. Pollen of adventives (i.e. plant species not native to a specific area) track intentional or unintentional (i.e. cultivated crops vs. weeds) introductions by humans and are therefore considered to be reliable indicators for past human activities (Behre, 1981, 1988; Huntley and Webb, 1988). Although with less diagnostic capacity than adventives, the pollen of apophytes (i.e. native plant species favoured by human activities) also provide information regarding anthropogenic impacts on the landscape (Behre, 1981; Lang, 1994). Offsite and onsite palaeorecords (e.g. pollen, macrofossils, megafossils, aDNA), in combination with archaeology, provide the only unambiguous evidence for determining the native ranges of cultivated plants and weeds. Such evidence has shown that depending on the region of interest, many plant species may be regarded either as adventives or apophytes (di Castri et al., 1990; Lang, 1994; Conedera et al., 2004; van Leeuwen et al., 2008; Krebs et al., 2019). In the case of palynology, data interpretation requires a strong background knowledge of the processes controlling pollen, spore and other microfossil production, dispersal and preservation (Webb and Goodenough, 2018). This condition adds further complexity to the inference of human impacts from palynological data (Behre, 1981), especially in a quantitative manner, and limits the use of pollen-inferred reconstructions of land-use history by a broader community.

Early applications of the pollen-indicator approach used pollen from plants particularly sensitive to winter frost for palaeoclimatic reconstructions (Iversen, 1944). This methodology has later been extensively applied to land-use reconstruction. Behre (1981, 1988) assembled lists of reliable anthropogenic pollen indicators for Central and Western Europe (north of the Alps). Behre’s pioneering work was later extended to other areas (e.g. the Middle East, Behre, 1990; China, Li et al., 2015; Mexico, Franco-Gaviria et al., 2018) and refined in Western Europe (Mazier et al., 2006; Brun, 2011). Moreover, Behre’s comprehensive account of anthropogenic pollen indicators has been widely used in European areas outside of its original calibration area (e.g. Novenko et al., 2017; Cartier et al., 2018; Fredh et al., 2018; López-Sáez et al., 2018), although the chosen indicator taxa may not be necessarily suitable in these regions (apophyte vs. adventive problem; Moore et al., 1991; Lang,

1994).

The presence and abundance of anthropogenic pollen indicators provide valuable evidence for the occurrence and intensity of past land use (Behre, 1981). The sum of the percentages of these pollen types is often plotted separately in pollen diagrams as curves of Principal and/or Secondary Indicators (‘PI’, ‘SI’; e.g. Lang, 1994). In contrast to other fields of palynology (e.g. treeline studies), absolute values such as influx are less often used for human-impact reconstructions (Koff and Punning, 2002). To characterize and quantify past land use, pollen indices based on anthropogenic indicators were first developed to estimate the ratio of arable to pastoral farming (Steckhan, 1961; Turner, 1964; Kramm, 1978; Riezebos and Slotboom, 1978). More recently, new semi-quantitative indices of human impact are being applied, especially (see summary in Table 1): the Cultural Indicators (‘CI’) approach (Tinner et al., 2003), the Anthropogenic Pollen Indicator ‘API’ index (Mercuri et al., 2013a), the *Olea-Juglans-Castanea* ‘OJC’ index (Mercuri et al., 2013b) including its modification incorporating *Vitis* (‘OJCV’; Berger et al., 2019), and the Pollen Disturbance Index ‘PDI’ (Kouli, 2015). Complementarily, the ‘AP/NAP’ ratio between the percentages of arboreal (sum of trees and shrubs) and non-arboreal (sum of upland herbs) pollen has long been used to reconstruct changes in forest cover quantitatively, including anthropogenic clearance of forests (Aario, 1944; Berglund et al., 1991). Conventionally, the interpretation of AP/NAP is straightforward; very high (>10, corresponding to ca. 91% AP), intermediate (>4, 80% AP) and low (<1, 50% AP) values, represent very closed

Table 1

Main qualitative approaches to reconstruct human impacts on European landscapes based on abundances (usually in %) of anthropogenic pollen indicators.

Approach	Original Scope Area	Pollen types included
PI	Central Europe, North of the Alps	Cereals: <i>Secale cereale</i> , <i>Hordeum</i> -type, <i>Triticum</i> -type, <i>Avena</i> -type, <i>Zea</i> . Dicotyledonous crops: <i>Fagopyrum</i> , <i>Linum usitatissimum</i> -type, <i>Vicia faba</i> , <i>Cannabis</i> -type
SI	Central Europe, North of the Alps	Adventives: <i>Centaurea cyanus</i> , <i>Lychnis/Agrostemma</i> -type, <i>Scleranthus annuus</i> , <i>Spergula arvensis</i> -type, <i>Polygonum convolvulus</i> -type, <i>Polygonum aviculare</i> -type, <i>Polygonum persicaria</i> -type (<i>Persicaria maculosa</i> -type), <i>Plantago lanceolata</i> -type, <i>Plantago major/media</i> . Apophytes: <i>Rumex acetosella</i> -type, <i>Rumex acetosa</i> -type, <i>Trifolium repens</i> -type, <i>Succisa</i> , <i>Jasione/Campanula</i> -type, <i>Urtica</i> , <i>Artemisia</i> , <i>Melampyrum</i> , <i>Pteridium</i> , <i>Polypodium</i> , <i>Calluna</i> , <i>Juniperus</i> -type
CI	North and South of the Alps	<i>Plantago lanceolata</i> -type, Cerealia-type (excluding <i>Secale</i>)
API	Mediterranean (Italy)	<i>Artemisia</i> , <i>Centaurea</i> , Cichorioideae, <i>Plantago</i> , Cerealia-type, <i>Urtica</i> , <i>Trifolium</i>
OJC	Mediterranean (Italy)	<i>Olea</i> , <i>Juglans</i> , <i>Castanea</i>
OJCV	Mediterranean (Italy)	<i>Olea</i> , <i>Juglans</i> , <i>Castanea</i> , <i>Vitis</i>
PDI	Mediterranean (northern Greece)	<i>Centaurea</i> , Cichorioideae, <i>Plantago</i> , <i>Ranunculus acris</i> -type, <i>Polygonum aviculare</i> type, <i>Sanguisorba minor</i> -type, <i>Urtica dioica</i> -type and <i>Pteridium</i>
AP/NAP	Northern Europe	Relative abundance of arboreal pollen with respect to non-arboreal. Values are interpreted as: >10, very close forest; 4–10, close forest (at 4, first relevant vegetation openings); <1, open vegetation.

PI: Primary anthropogenic indicators & SI: Secondary anthropogenic indicators (Behre, 1981; Lang, 1994); CI: Cultural indicators (Tinner et al., 2003); API: Anthropogenic pollen indicators (Mercuri et al., 2013a); OJC: *Olea*, *Juglans*, *Castanea* (Mercuri et al., 2013b); OJCV: *Olea*, *Juglans*, *Castanea*, *Vitis* (Bevan et al., 2019; Roberts et al., 2019); PDI: Pollen Disturbance Index (Kouli, 2015); AP/NAP: Arboreal pollen/non arboreal pollen ratio (Berglund et al., 1991; Favre et al., 2008).

forests, semi-closed forests and open vegetation, respectively (Mitchell, 2005; Favre et al., 2008; Zanon et al., 2018). However, detailed interpretation of intermediate values of this ratio remains unclear (Favre et al., 2008). When AP/NAP is combined with Behre's cultural indicators, inferring the start of farming-induced forest opening in Europe is possible (e.g. Lang, 1994;; Tinner et al., 2003; Rey et al., 2019).

In summary, although the potential of anthropogenic pollen indicators to reconstruct the impact of human activities on past vegetation dynamics has long been recognized and broadly used, no comparative evaluation of their performance is available yet. The emphasis of previous studies (e.g. Steckhan, 1961; Turner, 1964; Kramm, 1978; Riezebos and Slotboom, 1978; Behre, 1981; Lang, 1994; Koff and Punning, 2002; Tinner et al., 2003; Mercuri et al., 2013a,b; Kouli, 2015; Berger et al., 2019) on local to regional approaches is due to the different vegetation (e.g. biomes) and land-use (e.g. farming) conditions in space and through time. The aim of this study is to provide an overview of the existing methodologies and to understand their relative advantages and limitations. Here, we apply the most commonly used human-indicator species approaches to six study sites distributed over a wide latitudinal gradient across Europe, spanning from boreal to Mediterranean ecosystems. To evaluate their performance we compare the palynologically inferred human impacts with archaeological evidence. A specific aim of this study is to identify the performance of the chosen approaches inside and outside their region or biome of origin. Finally, we briefly address potential future avenues in the field, including validation using archaeological data, the value of taxonomically highly resolved records, and the difficulty to produce generalized and standardized approaches that may identify human impact at the continental scale.

2. Materials and methods

2.1. Study sites and anthropogenic pollen indicator indices

We applied eight previously developed anthropogenic pollen-indicator approaches (PI, SI, CI, API, OJC, OJCV, PDI, and AP/NAP ratio, see Table 1 for details), to six post-glacial lake pollen sequences with high time resolution and spanning a latitudinal and ecological gradient from Scandinavia to Sicily (Table 2, Fig. 1). The pollen datasets were obtained from the European Pollen Database (EPD; Fyfe et al., 2009; Giesecke et al., 2014) and the Alpine Pollen Database (ALPADABA) via Neotoma (Williams et al., 2018). We harmonized pollen nomenclature for consistency amongst the different sequences (Giesecke et al., 2019), and calculated pollen percentages with respect to the terrestrial pollen sum, i.e. excluding

pollen from aquatic and wetland plants and spores. We processed the data with the R packages 'Neotoma' version 1.7.4 (Goring et al., 2015) and 'Rioja' version 0.9–15.1 (Juggins, 2017) running in R environment (R Core Team, 2018). We then plotted the obtained values for the various pollen indices at each site as stratigraphic-pollen diagrams against age in calibrated years, using the age-depth models published by the authors in the original papers and stored in the databases (except for Lago di Origlio, where the calibration curve has been updated).

2.2. Archaeological validation framework and its limits

We validated the capacity of the indices to express quantitatively the human impact by comparing the results with the regional archaeological record at each study site. To convert the archaeological evidence into a quantitative scale, we grouped the main archaeological and historical periods according to five stages of human impacts on the European environment: (1) very low/non detectable (corresponding to the Palaeolithic and Mesolithic), (2) low (Neolithic), (3) moderate (Bronze Age), (4) high (Iron Age, Roman Imperial Period and Early Middle Ages), and (5) very high (Middle Ages and Modern Era; Figs. 2 and 3). This classification assumes that the archaeological and historical periods correspond with economic stages and temporal transformation of technology (Kremer, 1993; Lemmen et al., 2011). The economic and technological developments alongside the assumed resulting population growth are, in turn, major determinants of human impact during the Holocene (Kremer, 1993; US Census Bureau, 2018).

To delimit the timeframe of each human-impact stage at each site, we synchronized the reference chronologies of the main, well-established archaeological and historical periods in Europe in a regional scheme (Fig. 3). While the definition of historical periods is established by events that are documented in historical sources (i.e. precisely dated), archaeological epochs are based on regionally different typo-chronological changes in material culture (i.e. classification of objects and architecture; Besserman, 1996; Shackley, 2001; Carson, 2016). When absolute dates (e.g. radiocarbon, dendrochronology) were available in the literature, we used them for the proposed chronologies (e.g. Knutsson and Knutsson, 2003; Bietti Sestieri, 2013a, 2013b; Capuzzo et al., 2014; Lo Vetro and Martini, 2016; Pacciarelli et al., 2016; Stöckli, 2016; Natali and Forgia, 2018; Radi and Petrinelli Pannocchia, 2018; Alessandri, 2019). Conversely, we referred to relative dating where no absolute chronologies were available. Because the limits of the different archaeological periods are not always supported by radiocarbon or dendrochronological dating, the presented supra-regional synchronization of periods is tentative, and some period boundaries

Table 2
Main features of the palynological records considered in this study.

Site	Elevation (m asl)	Size (ha)	Age range (cal yr BP)	Vegetation type (Lang, 1994)	MAT (°C)	Reference
(a) Holtjämen, Sweden	232	1	-15 -10500	Boreal spruce and pine forests.	4.2	Giesecke (2005)
(b) Lake Gosciaz, Poland	64	70	-35 -12900	Central and Eastern European mixed oak forests.	7.9	Ralska-Jasiewiczowa and van Geel (1992), Arnold et al. (1998)
(c) Burgäschisee, Switzerland	465	21	-59 -18650	Western, Central and Southeastern European beech and beech fir forests.	9.1	Rey et al. (2017)
(d) Lago di Origlio, Switzerland	416	8	-45 -19400	Montane and subalpine mountain coniferous forests and <i>Krummholz</i> bushes.	12.0	Tinner et al. (1999)
(e) Lago dell'Accesa, Tuscany, Italy	157	14	95-11550	Meso-mediterranean evergreen and deciduous oak forests.	14.0	Colombaroli et al. (2008)
(f) Gorgo Basso, Sicily, Italy	6	2	-50 -10200	Thermo-mediterranean evergreen oak forests and olive carob tree woodlands.	17.6	Tinner et al. (2009)

MAT: Mean annual temperature (Fick and Hijmans, 2017).

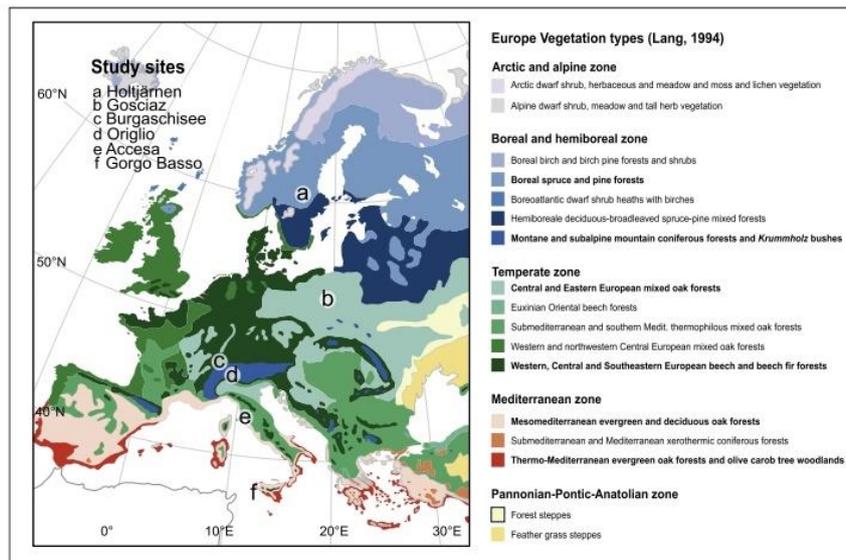


Fig. 1. Location of the study sites. Background colours in the map represent European vegetation types (Lang, 1994).

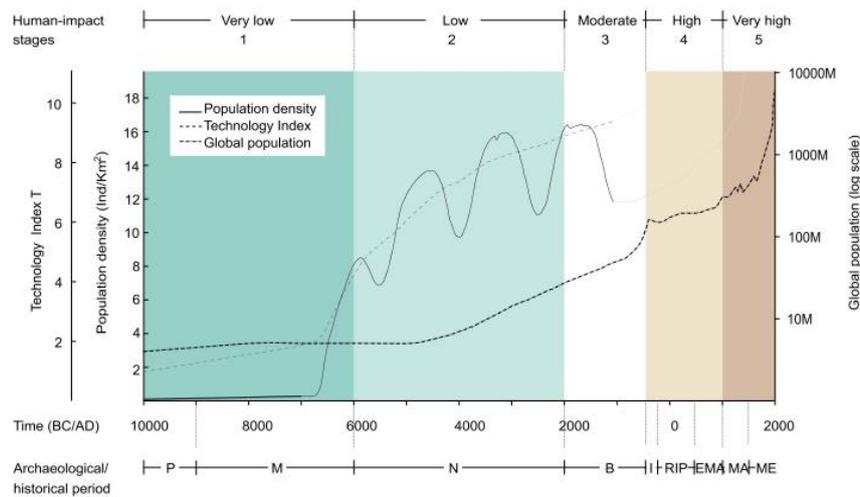


Fig. 2. Human impact stages on the environment in the Old World, defined by their population density and technology development (modified from Kremer, 1993; Lemmen et al., 2011; US Census Bureau, 2018). P= Palaeolithic, M = Mesolithic, N= Neolithic, B= Bronze Age, I= Iron Age, RIP = Roman Imperial Period, EMA = Early Middle Ages, MA = Middle Ages, ME = Modern Era. The exact boundaries for each study case are shown in Fig. 3.

are uncertain. Furthermore, as Neolithisation is not a one-time event but rather a long and complex process, assigning precise dates to the boundary between the Mesolithic and the Neolithic in each region is often difficult (Dolukhanov et al., 2005; Gronenborn, 2005; Lemmen et al., 2011). Moreover, Mesolithic and Neolithic lifestyles may have coexisted simultaneously for several centuries in some regions (as e.g. proposed for Poland; Nowak, 2013). Nevertheless, the temporal resolution of our approach refers to long prehistorical and historical periods, which partially offsets possible chronological errors.

2.3. Performance of the indices

To evaluate the performance of the indices, we compared the results at the different study sites according to the technological stages (Fig. 3). To make the results comparable, we first rescaled the values of the different indices between 0 and 1 using a minimax transformation:

$$Z_i = (V_i - V_{\min}) / (V_{\max} - V_{\min})$$

where Z_i is the minimax-transformed value of the index V for the i

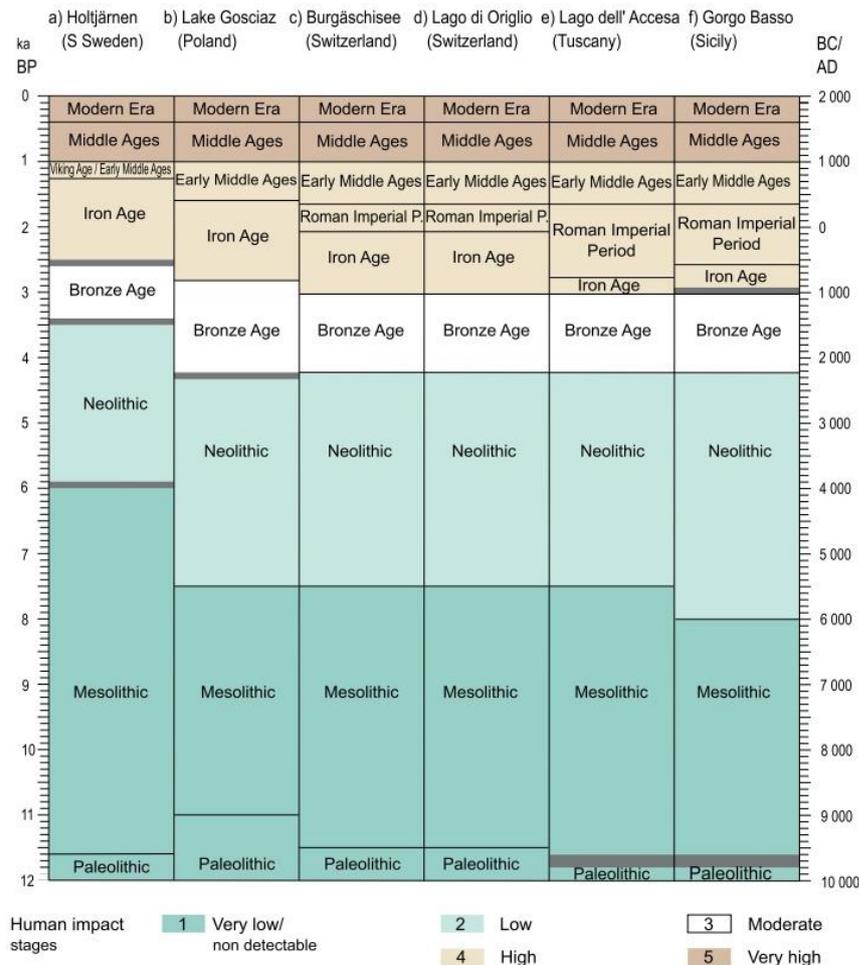


Fig. 3. Historical and regional archaeological periods corresponding to each study site, with uncertain boundaries marked in grey. Assumed human impact stages, expressed by the technological development and estimated population size are shown in different colours (see Fig. 2 for the conceptual framework). Sources for absolute and relative dating of the cultural periods in the study regions (Pulsiano and Wolf, 1993; Peroni, 1996; Zvelebil, 1998; Chwalba and Basista, 1999; Leighton, 1999; Derwich and Zurek, 2002; Flutsch et al., 2002; Knutsson and Knutsson, 2003; Windler et al., 2005; Olsen et al., 2011; Bietti Sestieri, 2013a, 2013b; Czebreszuk et al., 2013; Herschend, 2013; Nowak, 2013; Nowakowski et al., 2013; Thrane, 2013; Capuzzo et al., 2014; Larsson, 2014; Niffeler, 2014; Gron et al., 2015; Lo Vetro and Martini, 2016; Pacciarelli et al., 2016; Stockli, 2016; Larsson, 2017; Foxhall, 2018; Natali and Forgia, 2018; Radi and Petrinelli Pannocchia, 2018). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

-th sample of a given record (V_i), and V_{max} and V_{min} are the maximum and minimum values of V in the entire sequence. Secondly, we averaged the values of every index for each chronological human-impact stage and plotted boxplots to visually assess the trends in the values of the indices. We hypothesize that the magnitude of human impact on the environment will monotonically increase towards present across the stages of population and technological development of European societies during the Holocene as inferred from archaeological and historical evidence (Fig. 2). To test this hypothesis, we ran pairwise comparisons between the five considered human-impact stages on the environment (Figs. 2, 3) using the non-parametric Mann–Whitney U test (Wilcoxon rank–sum test), whose null hypothesis is that the two samples of the pairwise comparisons come from the same population.

3. Results

In northern and north-central Europe, the primary

anthropogenic indicators index (PI) only increases during the last 1000–500 years at Holtjärnen (southern Sweden) and Lake Gosciadz (central Poland) (Fig. 4a and b). This striking increase during the most recent human impact stage is coupled with minimum AP/NAP values at both sites, although Lake Gosciadz records earlier openings during the Bronze Age and Iron Age. Similarly, although OJC and OJCV show null values (i.e. 0% *Olea*, *Juglans*, *Castanea*, and *Vitis*) throughout much of the Lake Gosciadz record, most of the non-zero values occur in the last 2000 years, with the exception of a peak around 6000 BC. In contrast, OJC and OJCV are zero for the entire Holtjärnen record. The secondary indicators (SI) and anthropogenic pollen indicators (API) indices have high values at the beginning of both pollen sequences (Mesolithic at Holtjärnen and Palaeolithic at Lake Gosciadz) that later decrease, to start increasing progressively from the Neolithic (Lake Gosciadz) and Bronze Age (at both sites) onwards. At Holtjärnen, CI has a discontinuous and sparse record from the Neolithic onwards and only contains continuous and remarkable values during the last millennium. At this Scandinavian site, significant values of PDI occur during the Neolithic and Iron

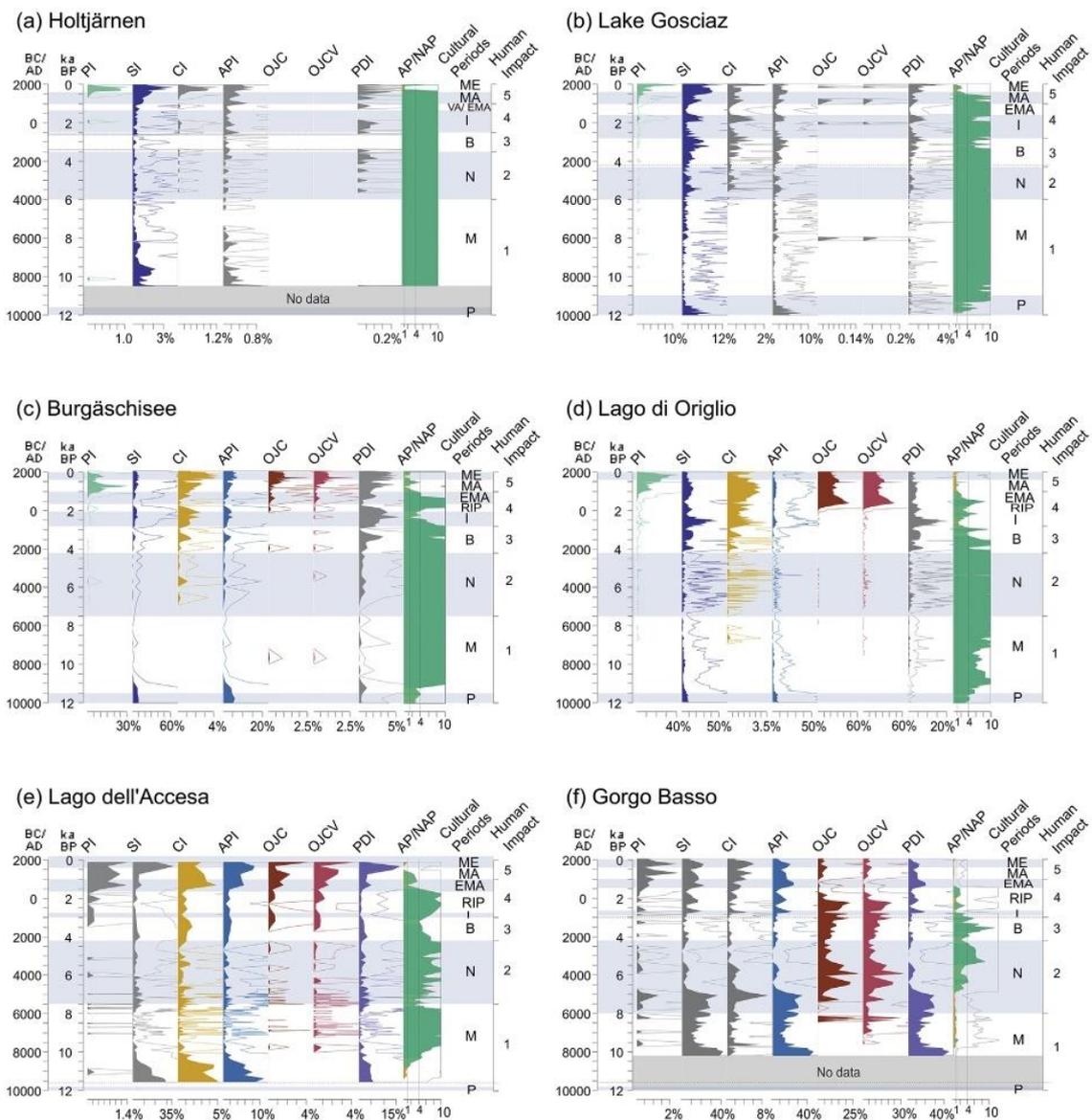


Fig. 4. Comparison of the anthropogenic pollen indices at different sites across Europe. Empty curves represent 10 × exaggeration. Indices used outside their geographical scope are shown in grey. Dashed lines delimit cultural periods with uncertain chronology. PI= Primary indicators, SI= Secondary indicators, CI= Cultural indicators, OJC= *Olea-Juglans-Castanea*, API = Anthropogenic pollen indicators, PDI= Pollen Disturbance Index, AP/NAP= Arboreal pollen/non-arboreal pollen ratio (graphics restricted to 10 as maximum values, values of 1 and 4 are highlighted). P= Palaeolithic, M = Mesolithic, N= Neolithic, B= Bronze Age, I= Iron Age, RI = Roman Imperial Period, VA= Viking Age, EMA = Early Middle Ages, MA = Middle Ages, ME = Modern Era. Note the different scales in the X-axes. Human Impact stages range from 1 = very low to 5 = very high.

Age but the most continuous and highest values of this index are only present during the last millennium. In contrast, the CI record at Lake Gosciadz starts during the Neolithic and is continuous until the present, with conspicuous increases at the end of the Bronze Age, and substantial increases during the Iron Age and the last millennium. PDI mirrors the main trends of CI despite its nearly continuous record throughout the Lake Gosciadz sequence (Fig. 4).

In Central Europe, the records of PI and CI from Burgäschisee (Swiss Plateau) suggest that the first noticeable human impact occurred during the Neolithic (ca. 4500 cal. BC), with remarkable stepwise increases from the Iron Age onwards and particularly during the past millennium (Fig. 4c). The Lago di Origlio sequence records the presence of PI and CI on the southern Alpine forelands

as far back as ca. 7000 cal. BC, although the records are discontinuous until the onset of the Bronze Age (ca. 2300 cal. BC). As at Burgäschisee, PI substantially increases at Lago di Origlio during the last millennium, largely because *Cannabis*-type pollen reaches very high shares within PI. This taxon represents $67.0 \pm 20.2\%$ at Burgäschisee and $84.1 \pm 11.3\%$ at Lago di Origlio. At these two sites, respectively located south and north of the Alps, API, SI and PDI bear high values during the Younger Dryas and the onset of the Holocene (until 9500-9000 BC, during the Palaeolithic). These three indices contain (nearly) continuous records with noticeable increases after the Neolithic and particularly from the Bronze Age onwards. At Burgäschisee and Lago di Origlio, OJC and OJCV only have continuous records since ca. 1900 cal BP, where their main

increases occur at ca. 1500 and 500 cal. BP, respectively. *Juglans* is largely dominant at Burgäschisee (48.8 ± 26.1% of OJC, 46.7 ± 25.0% of OJCV) while at Lago di Origlio, *Castanea* is the dominant taxon (89.3 ± 5.9% of OJC, 88.8 ± 5.9% of OJCV). The AP/NAP ratios show marked signs of forest opening during the Bronze Age (AP/NAP < 4) at both sites and a significant enhancement of this process during the Iron Age (ca. 500 BC).

In southern Europe, SI, CI, API, and PDI are high at Lago dell'Accesa (Tuscany, central Italy) during the early Holocene (Mesolithic; Fig. 4e). Later, their abundances decrease but their records remain continuous. PI, OJC and OJCV show discontinuous occurrences between ca. 8000 and 6000 BC, during the late Mesolithic and early Neolithic. At the Mesolithic-Neolithic transition (ca. 5800-5500 BC), an abrupt drop in the AP/NAP ratio occurs followed by increases in indices summing up weed abundances (CI, SI, PDI, API). Another remarkable decrease in the AP/NAP ratio at the beginning of the Bronze Age (ca. 2000 BC) is followed by the onset of continuous records for PI, OJC and OJCV as well as moderate increases in SI, CI, API, and PDI. The final drop in AP/NAP values dates to Early Medieval Times (ca. AD 500) and is accompanied by major increases in all the indices (i.e. PI, SI, CI, API, OJC, OJCV, and

PDI). At this site, *Olea* pollen dominates the composition of the OJC (62.5 ± 47.9%) and OJCV (43.8 ± 38.3%) indices during the last millennium.

PDI, API and SI show very high values (up to 40% pollen) during the early Holocene (ca. 8000 BC) at Gorgo Basso (Sicily), whereas PI, OJC and OJCV are absent (Fig. 4f). At this site, SI, API, PDI and, to a lesser extent, CI present consistently high values (ca. 30% pollen) throughout the Mesolithic and the early Neolithic (ca. 8000-5000 BC), when the AP/NAP ratio shows very low values (<1). At the beginning of the Neolithic (ca. 5500-5000 BC), PI shows a prominent increase that is almost synchronous with a major peak in CI. Immediately after, from ca. 5000 BC, OJC and OJCV notably increase alongside the AP/NAP ratio and oscillate but maintain moderate to high values (10–20% pollen) for approximately 5000 years, until Roman Times. At Gorgo Basso in the thermo-mediterranean belt, *Olea* pollen is dominant in the composition of the OJC (98.6 ± 5.4%) and OJCV (91.2 ± 23.8%) during the fourth human-impact stage (Fig. 5), while *Juglans* is completely absent.

The behaviour of the studied cultural indicator approaches through time shows that only a few of them, particularly CI, fit our hypothesis of monotonically increasing human impact throughout

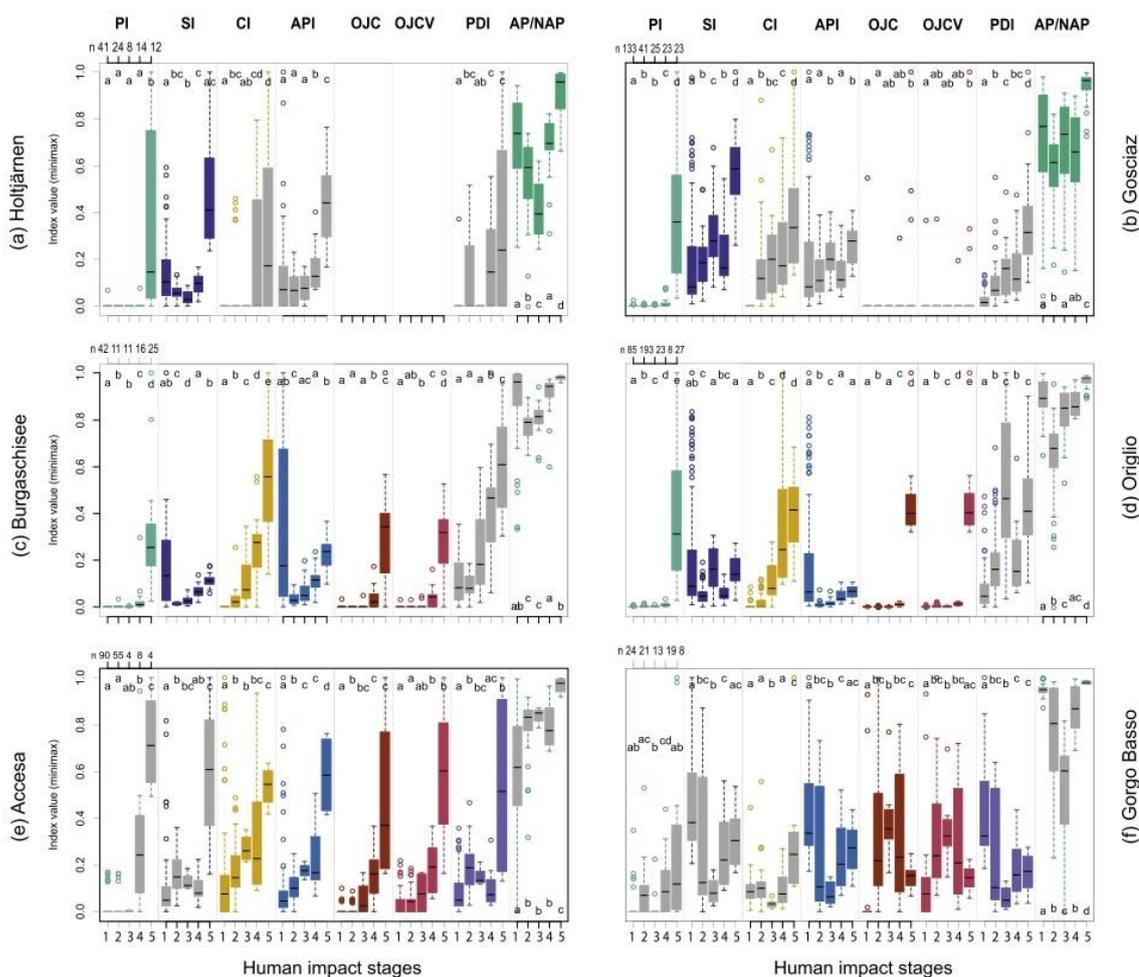


Fig. 5. Boxplots comparing the distributions of the values of the different indices classified according to the different stages of human impact: 1 = No detectable/Very low, 2 = low, 3 = moderate, 4 = high, 5 = very high. Minimax transformations were calculated amongst the index values. The Y-axis of the AP/NAP plots was reversed to facilitate comparison with the other indices shown. Indices used outside their intended geographical scope are shown in grey. Different letters indicate statistically significant differences at $P < 0.05$ (nonparametric Mann–Whitney U test) among the human impact stages that according to our hypothesis, will increase its magnitude towards present.

all sites and human-impact stages (Fig. 5). PI is usually biased by the last cultural period, the Modern Era, characterised by very high abundances of cereal pollen particularly in central and northern European sites (Fig. 5a–d). Indices based on secondary indicators like SI and API often show unrealistically high values in the oldest archaeological periods, which includes the Palaeolithic and the Mesolithic. On the other hand, OJC and OJCV are absent or extremely rare in northern Europe for the entire period (Fig. 5a and b). Similar to PI, the OJC and OJCV indices are biased to the Modern Era in Central Europe and the Southern Alps (Fig. 5c and d), while farther south OJC and OJCV fit to the human impact expectations at the meso-mediterranean site (Accesa; Fig. 5e), but not at the thermo-mediterranean site (Gorgo Basso; Fig. 5f). PDI shows the expected increasing trend north of the Alps (Fig. 5a–c), while south of the Alps, the pattern is unclear (Fig. 5d–f). Finally, the pattern of AP/NAP is unrelated to any gradual increases in human impact through economic stages and archaeological and historical periods.

4. Discussion

4.1. Overall suitability of the anthropogenic indicators

In this study, we tested the suitability of widely used palynological indices based on anthropogenic pollen indicators for different European biomes. We compared the results obtained by the indices with human-impact stages, as derived from human population density growth and the related land use caused by the increasing carrying capacity of agriculture throughout different historical epochs (Kremer, 1993; Lemmen et al., 2011; US Census Bureau, 2018). The analysed indices do not always show a general increase since the Neolithic, and they also show disagreements among them on the extent and timing of land-use-related human impacts. In contrast, the human population experienced linear, exponential or logarithmic growth through the millennia with only episodic interruptions or reversed trends during environmentally caused production crises such as volcanic eruptions, mass migrations, and climatic reversals (e.g. Little Ice Age; Bentley, 2013). In this context, we identify indices as the lowest performing if they show trends that are opposite to those expected from the prehistorical and historical evidence used to model human population dynamics (Fig. 5). For instance, such dissimilarities occur in the case of high SI and API values before the Neolithic (i.e. stage 1) at several sites and in AP/NAP at all sites. Likewise, unexpected decreases in OJC and OJCV at Gorgo Basso between stages 3, 4, and 5, and in PDI, between stages 2 and 3 are seemingly inconsistent with agricultural intensification (Fig. 5). Best performance in terms of monotonic increasing trends across the human-impact stages are generally provided by indices using a few specific pollen indicators such as PI and CI. Although both PI and CI performed best among all indices at Gorgo Basso, they did not fully match population growth expectations. Similarly, SI has a good performance from the second human-impact stage onwards (except in the southern sites; Fig. 5). Changes in PI at Holtjärnen are limited to human-impact stage 5, which prevents an assessment of increasing trends (Fig. 5), but likely reflects the remoteness of the northernmost site in regard to arable farming.

In general, pollen indicator approaches perform best in the regions in which they were developed (Figs. 4 and 5). Specifically, most of the considered indicator species approaches show increasing human impacts between sequential human-impact stages outside the Mediterranean realm (e.g. PI and CI at Burgäschisee and Lago di Origgio; PI at Gosciąz), where this technique was originally developed (Behre, 1981), plant diversity is lower (Mutke et al., 2010), and wild relatives of (southwest Asian Neolithic) crops

and weeds are rare (Zohary et al., 2012). Nevertheless, certain indices may perform well in regions different than the one where they were conceived. For instance, the PDI pastoral index developed in northern Greece performed reasonably well in tracking anthropogenic vegetation change in Holtjärnen (southern Sweden), particularly from the Iron Age onwards (Fig. 4). Such episodic good performances may however be coincidental. Indeed, the Holtjärnen record also provides reason for caution. An early incidence of forest opening at Holtjärnen dated around 3700 cal. BC, which caused PDI to increase, probably resulted from a shift in atmospheric circulation that naturally affected forests and not from human impacts (Hammarlund et al., 2002; Giesecke, 2005).

A given index may vary in performance among different human-impact stages when applied to the entire Holocene (e.g. Behre, 1981). In most of our cases, the AP/NAP and SI indices have a high potential in detecting deforestation at the Neolithic/Bronze Age transition. This transition is easy to infer because the development of more advanced farming techniques during the Bronze Age likely resulted in a permanent ecosystem shift, in contrast to earlier transient forest clearances that were followed by forest regeneration (Lang, 1994; Poska et al., 2004; Rey et al., 2019). Conversely, some indices may fail to identify human impacts at a later, higher technological stage (i.e. stages 3–4, Fig. 5), specifically at southern sites such as Accesa and Origgio. The cause might be a reduction of deforestation rates and an increased efficiency in farming practices during the Roman Imperial Period, for instance (Howatson, 2011). In addition, several centuries-long crises (e.g. migration period, Little Ice Age) are documented in archaeological and historical records (e.g. Maisie, 1998) and by temporally well resolved palaeoecological records (Lotter, 1999; Tinner et al., 1999; Rey et al., 2017). These crises may not be evident in our comparisons among human-impact periods (Fig. 5), which were designed to assess the impacts of long-term trends in human population growth.

4.2. Direct indicators

The indices based on direct indicators (i.e. crops and strict adventives, CI and PI; Lang, 1994) showed an overall good performance at the temperate sites (Fig. 5a–d). In temperate environments, PI and CI were sensitive enough to detect initial stages of human impacts on the landscape when they were used in the appropriate setting, such as the early Neolithic farming (ca. 3800 BC; Cortaillod typochronological unit) at Burgäschisee (Rey et al., 2017). Similarly, CI was used to trace the major milestones in the history of human occupation around Lago di Origgio, such as Neolithisation and the establishment of permanent settlements during the Bronze Age (Tinner et al., 1999). Likewise, CI tracks the main economic changes at Lake Gosciąz since the Neolithic (Ralska-Jasiewiczowa and van Geel, 1992), whereas PI shows inconclusive evidence until the Iron Age (Fig. 4b). In boreal environments, CI performed better than PI (Holtjärnen), while PI was superior at Mediterranean sites (Lago dell'Accesa and Gorgo Basso). The reduced performance of PI in boreal environments might be connected to the prevalence of pastoral activities (Morris et al., 2014), as also revealed by the good agreement with PDI (Fig. 4). Conversely, the reduced performance of CI in the Mediterranean probably relates to the supposed natural occurrence of *Plantago lanceolata*-type. Indeed, Tinner et al. (2009) concluded that intense agriculture around Gorgo Basso prior to the early Neolithic (ca. 6000 BC) would be unrealistic. To overcome this issue, the authors relied on the combined evidence of crops (e.g. Cerealia-t., *Ficus carica*) and weeds to track the onset of Neolithic farming (Tinner et al., 2009). Here, we cannot assess to what extent the natural

occurrence of cereal species may affect the interpretation of Mediterranean pollen records (Roberts et al., 2011). A way to overcome this difficulty and to unambiguously identify arable farming is to associate Cerealia-type pollen with that of other crops (e.g. figs), adventives and/or apophytes (Tinner et al., 2009). Our results emphasize that the indicative power of single taxa should not be considered in absolute terms but rather within the ecological context (reflected in the pollen assemblages) in which it was growing.

Other important direct indicators according to Behre (1981) such as *Fagopyrum* and *Linum usitatissimum* were completely absent or recorded just in modern samples at our study sites and did thus in general not contribute to the index values. The only exception is a single pollen grain of *Linum usitatissimum* found at the end of the Mesolithic (ca. 3700 BC) in the Burgäschisee pollen sequence.

An additional issue related to the use of indices based on direct pollen indicators such as the PI as quantitative proxies for human impact is the possible bias introduced by agro-industrial practices. This is the case for instance in Origlio during the stage of very high human impact (i.e. stage 5, last 1000 years) when *Cannabis*-type pollen became strikingly abundant in the sediment samples as a result of water-retting of hemp for fiber extraction (Bradshaw et al., 1981). These practices caused a marked rise in *Cannabis*-type pollen abundance (from ca. 2–40% of the terrestrial pollen sum) and an overrepresentation of this pollen type in the PI index values (up to 98.6%).

4.3. Indirect indicators

Our results show that the environmental context is determinant for the interpretation of indices based on secondary indicators such as SI, API and PDI. At all the study sites, but more strongly in the Mediterranean realm (i.e. Lago dell'Accesa and Gorgo Basso), these indices, particularly SI and API, suggest strong human impact during the Palaeolithic and the Mesolithic (before 9000–8000 BC; Figs. 4 and 5), which is inconsistent with archaeological evidence (Bietti Sestieri, 2013a, 2013b). The underlying reason is that several of the pollen types included in SI, API and PDI (Table 1) correspond to disturbance-tolerant plant taxa that have benefitted from anthropogenic activities. For instance, *Artemisia* was particularly abundant in the steppic communities that dominated the European landscape during the cold and dry stages of the last deglaciation (ca. 19 to 11.7 ka BP; Lang, 1994; Nolan et al., 2018). Indeed, *Artemisia* accounts for a large proportion of API index values during the first stage of human impact at Origlio and Burgäschisee. In agreement, the SI index values during the post-glacial steppic environment in Burgäschisee are almost entirely related to *Artemisia* and *Juniperus*-type pollen abundances. To account for this and also for the natural occurrence of these taxa in the local flora, Roberts et al. (2019) recommended caution when interpreting their occurrence in Mediterranean landscapes during the Holocene. Furthermore, these pollen types have sometimes been excluded from the calculations of the anthropogenic indices in dry Mediterranean settings (e.g. Cheddadi et al., 2019). As a consequence, API clearly fails to recognize low or absent human impact before the mid-Holocene, while subsequently it follows the more reliable direct indicators such as PI and CI at sites with temperate (i.e. Burgäschisee and Lago di Origlio) and meso-mediterranean vegetation (i.e. Lago dell'Accesa, Fig. 4c–e, 5c–e). In general, SI and API show similar performances (Figs. 4 and 5). Last but not least, these indices would probably benefit from more detailed taxonomic resolution in pollen identification to enhance the value of indicator species. For instance, the API index merges several well-characterised pollen

types such as *P. lanceolata*-type, *P. major*-type, *P. media*-type, *P. maritima*, *P. tenuiflora*, and *P. coronopus*-type (according to Moore et al., 1991) into the genus *Plantago*. Such coarse taxonomic resolution causes a large loss in ecological information, directly affecting human-impact reconstructions (e.g. *P. lanceolata* is likely adventive north of the meso-mediterranean and thermo-mediterranean vegetation types).

Other indirect indicators of human impact (Behre, 1981; Lang, 1994) displayed a very low contribution to the SI sum (e.g. *Polygonum aviculare*-type in all cases except for Höljtjärnen and Accesa, where it was absent) or occurred regularly throughout the core (e.g. *Rumex acetosa*-type in all cases, with smaller percentages for Accesa and Gorgo Basso), even at stages of high human impact. These results suggest that some taxa may be used as qualitative indicators (presence – absence) more than quantitatively (i.e. with abundance values).

4.4. Woody crops

The performance of the indices based on woody crops, i.e. OJC and OJCV, was generally low across the selected study sites (Figs. 4 and 5), with only one exception in the meso-mediterranean vegetation (Accesa), where these indices were originally conceived (Fig. 4e and f, 5e–f). The native status in the Mediterranean region of the constituent species (i.e. *Olea europaea*, *Juglans regia*, *Castanea sativa*), along with their relatively recent and often massive cultivation, potentially implies the coexistence of wild and domesticated trees in certain periods (Conedera et al., 2004; Pollegioni et al., 2017; Langgut et al., 2019), in addition to biased indication power (Roberts et al., 2019) when applying these methodologies. For instance, strikingly high values of OJC in thermo-mediterranean Sicily (Fig. 4f) during the Neolithic are very likely due to abundant *Olea europaea* pollen from wild populations (*Olea europaea* var. *oleaster*, see discussion in Tinner et al., 2009). Indeed, the archaeological evidence places the origins of olive tree domestication in the Mediterranean Levant during the Chalcolithic at ca. 4000 BC and tree cultivation likely arrived in Sicily at the beginning of the Bronze Age at ca. 2000 BC (Besnard et al., 2018; Langgut et al., 2019). Furthermore, an OJC drop in Sicily during Roman Times (Fig. 4f) is inconsistent with the agricultural intensification inferred from archaeological evidence during that human-impact stage. OJC values are largely driven by *Olea* pollen percentages throughout the record and primarily reflect the demise of Mediterranean mixed evergreen broadleaved woodlands related to land-use intensification (Tinner et al., 2009), rather than the collapse of olive plantations (Fig. 5f). Thus, only the later medieval increase in OJC, driven by *Olea* pollen abundance, should be attributed to broad-scale olive cultivation in the area (Fig. 4f; Tinner et al., 2009). Palaeobotanical evidence also supports the native status of *Castanea sativa* to several Mediterranean areas including the sub-mediterranean Italian Peninsula, where it may have survived the harshest periods of the last glaciation (Krebs et al., 2004, 2019). Indeed, when the OJC index was proposed, Mercuri et al. (2013b) warned about the need for independent archaeological information and the use of other pollen indicators to support inferences based on this index. The incorporation of *Vitis* to the index (i.e. OJCV) faces the same issues because *Vitis* is also native to the Mediterranean Basin (Morales and Ocete, 2015), and *Vitis* pollen shows regular occurrences in many Mediterranean and sub-Mediterranean palynological sequences throughout the Holocene, probably related to *Vitis vinifera* subsp. *sylvestris* (e.g. at Lago di Origlio; Tinner et al., 1999). Despite these issues, these indices may help to corroborate intensified land use where any of the included taxa constituted a relevant food source: e.g. *Juglans regia* on the Swiss Plateau, *Castanea*

sativa in the Southern Alps, and *Olea europaea* under sub-humid meso-mediterranean conditions (Tinner et al., 1999; Colombaroli et al., 2008; Rey et al., 2017). In summary, the suitability of tree crop taxa as anthropogenic indicators is highly context-dependent (both geographical and historical), as clearly highlighted by the large dominance of single pollen types in the composition of the OJC/OJCV depending on the site and historical period considered (see above). In this regard, similar to API and SI, OJC/OJCV may be best interpreted as a summary of pollen types of indirect value than a human impact index *sensu strictu* (Behre, 1981).

5. Conclusions

Disentangling anthropogenic and natural drivers of vegetation change is of paramount importance in palaeoecology. The most widely used method continues to be the long-standing species indicator approach, although alternative methodologies and proxies have been developed more recently (e.g. Sugita, 2007; Fyfe et al., 2010). In particular, systematic approaches and standardized tools assisting pollen-based reconstructions of land use are still lacking. In this context, detailed and region- or site-specific assessments of the native plant range and the definition of apophytic and adventive anthropogenic pollen indicators (e.g. following a probabilistic approach as proposed by Krebs et al., 2019) is crucial to improve the performance of the existing indices to track changes in land-use intensity. Although the effects of the taxonomic resolution in the identification of human indicators has not been addressed in detail so far, enhanced taxonomic resolution allowing stricter selection of the anthropogenic pollen indicators may also play a role in improving estimates of human impact through long timescales, as the indices with low taxonomic resolution may not perform well even in their scope area. Future research on this topic should therefore aim to develop more detailed and articulated algorithms for assessing human impacts based on multi-proxy palaeoecological data. In particular, we stress the importance of developing a generalized context-dependent approach that considers the geographic area of reference and analyses the accompanying taxa in the corresponding stratigraphic levels of the pollen assemblage when assessing the indicative power. Finally, for a more precise and accurate independent validation of long-term vegetation dynamics using archaeology, it will be crucial to synthesize the available archaeological evidence (e.g. radiocarbon dates and their material culture context) to better infer major technological innovations, economic changes, land use, and population densities.

Author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Influence of taxonomic resolution on the value of anthropogenic pollen indicators

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Keywords: Anthropogenic indicators – Land use – Human impact – Taxonomic resolution – Palaeoecology – Europe

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Influence of taxonomic resolution on the value of anthropogenic pollen indicators

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Abstract

The taxonomic resolution of palynological identification is determined by morphological criteria that are used to define pollen types. Different levels of taxonomic resolution are reached in palynology, depending on several factors such as the analyst's expertise, the palynological school, the aim of the study, the preservation of the pollen grains, the reference collections and the microscope facilities. Previous research has suggested that attaining pollen records with high taxonomic resolution is important to reconstruct correctly past land use and human impact. This is in turn central to disentangling past human activities from other drivers of long-term vegetation dynamics such as natural disturbance or climate variability. In this study, we assess the impact of taxonomic resolution on the indicative capacity of anthropogenic pollen types. To achieve this, we attribute the pollen types of sixteen sedimentary records, located along a latitudinal gradient spanning from Switzerland to Italy, to three levels of taxonomic resolution previously proposed at the European scale. Our results show that higher taxonomic resolution improves the identification of human impact by enhancing the indicative power of important pollen indicators widely used in the research field. Our results may contribute to the improvement of palynological reconstructions of land use and human impact by identifying key pollen types whose determination requires particular attention.

Keywords Anthropogenic indicators · Land use · Human impact · Taxonomic resolution · Palaeoecology · Europe

Introduction

The classification of fossil pollen grains into taxonomic groups (i.e. pollen types) is the foundation of palynological research (Birks and Birks 1980). The precision of this

identification, mostly based on morphological criteria, constrains the taxonomic resolution reached (Rull 2012). Pollen data often suffer from poor taxonomic resolution (Louys 2012), as some types are identifiable to species level but most of them only to genus or even higher taxonomic levels (e.g. family; Huntley and Webb 1988). In contrast, a sound taxonomy is one of the main requirements for palaeoecological reconstructions of environmental change (Mitchell et al. 2014), as taxonomic precision may influence the ability of pollen data to track plant and vegetation dynamics (Huntley and Webb 1988).

When reconstructing environmental changes through palaeoecology, identification to species level should always be the ultimate goal, because ecological and environmental requirements are far better defined and more precise for species than for higher taxonomic categories, and this in turn often results in more robust, accurate and reliable palaeoecological reconstructions (Birks and Birks 1980). However, taxonomic uncertainty is commonly discarded as a source of error in analogue studies, which assume that the pollen assemblages will include at least a few diagnostic taxa with

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high taxonomic precision (Jackson and Williams 2004). Furthermore, the taxonomic resolution attained as well as the nomenclature used vary greatly among palynologists, depending on the used palynological keys and atlases, the palynology school, the research aims, the environmental setting and the taphonomy of the pollen analysed. Moreover, some pollen analysts may not try to reach more precise identifications (e.g. to species level when possible) because they perceive that the taxonomic refinements will not substantially improve the palaeoenvironmental reconstructions (Finkelstein et al. 2006). Consequently, when dealing with datasets produced by different analysts, pollen data require a process of taxonomic harmonization where the nomenclature is standardized by identifying all the synonyms used to refer to the same morphological type (e.g. Giesecke et al. 2019). As taxonomic harmonization is increasingly common due to the growing availability of palynological datasets and big data analyses, the effects of potential information losses due to the reduction of taxonomic resolution must be well understood.

These problems are becoming particularly evident when reconstructing past land use based on anthropogenic pollen indicators (e.g. Behre 1981; Lang 1994; Deza-Araujo et al. 2020). Although these anthropogenic pollen indicators have been established based on the modern occurrence of their plant equivalents in farming contexts (Behre 1981), they are defined at different levels of taxonomic resolution depending on the ease of their identification and the authorship of the methodology (Behre 1981, 1990; Mercuri et al. 2013a; Deza-Araujo et al. 2020) (Table 1). Indeed, only a few cultivated plants can be unambiguously identified by pollen to species level (e.g. *Pisum sativum* L.; Reille 1999). Furthermore, several families or subfamilies including a number of domesticated species (e.g. Brassicaceae, Cichorioideae) bear very uniform pollen morphology and are thus commonly identified only to (sub) family level (Blackmore 1984; Beug 2004). This problem is usually circumvented by examining the synchronous occurrence of different pollen types

indicative of human-modified landscapes, often involving the use of human indicator indices (e.g. OJC, OJCV, CI; Deza-Araujo et al. 2020).

Previous research has suggested that the identification of anthropogenic land use and its separation from other drivers of vegetation change such as climate would largely benefit from high taxonomic resolution of the pollen types used as human indicators (Tinner et al. 1996). Such refinement may concern the identification of introduced crops and weeds (Brun 2011; Rösch and Lechterbeck 2016). Further, achieving a good pollen taxonomic resolution is relevant to pollen richness estimates, and biodiversity change is in turn related to major land use strategies (Brun 2009; Feurdean et al. 2013). However, studies explicitly conceived to understand the effects of taxonomical resolution on anthropogenic pollen indicators are so far lacking, while other palaeoenvironmental proxies have only been rarely examined in this respect, with dissimilar results. For instance, decreasing taxonomic resolution had a relatively limited effect on reconstructed depth to water table based on testate amoebae, probably due to ecological redundancy (Mitchell et al. 2014). In contrast, chironomid-based summer air temperature reconstructions were either sensitive or not to taxonomic resolution, with the magnitude of such variation largely depending on the study site (Heiri and Lotter 2010). Regarding palynological research, studies on the effects of taxonomic precision have so far focused on biogeographical and biodiversity issues, highlighting the need for improved taxonomic resolution (Finkelstein et al. 2006) or suggesting a not always straightforward relationship between pollen richness and plant diversity (Giesecke et al. 2019; Reitalu et al. 2019). Birks (1994) also found that datasets with more detailed taxonomy notably improved quantitative reconstructions of soil pH using pollen. Similarly, low taxonomic resolution can hamper the indicative value of pollen data in palaeoclimatic reconstructions. For instance, the use of *Podocarpus* as a proxy for cool temperatures is ineffectual, as its pollen cannot be identified beyond the genus level and

Table 1 Original taxonomical resolution of the most used anthropogenic pollen indicators in central Europe and Mediterranean region in the literature (i.e. Behre 1981; Mercuri et al. 2013b) and in the study datasets

Anthropogenic indicator	Taxonomic resolution	Reference
<i>Linum usitatissimum</i> , <i>Vicia faba</i> , <i>Centaurea cyanus</i> , <i>Fallopia convolvulus</i> , <i>Sceleranthus annuus</i> , <i>Spergula arvensis</i> , <i>Rumex acetosella</i> , <i>R. acetosa</i> , <i>Polygonum aviculare</i> , <i>P. persicaria</i> , <i>Trifolium repens</i> , <i>Plantago lanceolata</i> , <i>P. major</i> , <i>P. media</i> , <i>Succisa pratensis</i> , <i>Calluna vulgaris</i> , <i>Juniperus (communis)</i> , <i>Melampyrum pratense</i> , <i>Pteridium aquilinum</i> , <i>Polypodium vulgare</i> , <i>Artemisia (vulgaris)</i> , <i>Ficus carica</i>	Species (including synonyms)	Behre (1981, 1990)
<i>Secale</i> , <i>Hordeum</i> , <i>Triticum</i> , <i>Avena</i> , <i>Fagopyrum</i> , <i>Cannabis</i> , <i>Lychnis-Agrostemma</i> , <i>Jasione-Campanula</i> , <i>Urtica</i> , <i>Pistacia</i> , <i>Olea</i> , <i>Juglans</i> , <i>Castanea</i> , <i>Vitis</i>	Genus	Behre (1981); Berger et al. (2019); Mercuri et al. (2013b)
Cichorioideae, Asteroideae, Chenopodiaceae, Caryophyllaceae, Brassicaceae, Poaceae, Ranunculaceae, Cyperaceae, Apiaceae	Subfamily/Tribe/Family	Behre (1981)

its constituent species have considerably variable bioclimatic preferences (Punyasena et al. 2011).

To overcome this knowledge gap and to test the effects of taxonomic resolution on land-use reconstructions, we analysed the anthropogenic pollen indicators in sixteen postglacial palynological datasets along a latitudinal gradient between Alpine summits close to the snow line and subtropical coastal Sicily at different taxonomic resolutions. This altitudinal and latitudinal gradient analysis allows the assessment of the occurrence of biogeographical differences affecting human pollen indicators, as it embraces the Mediterranean realm, where many wild relatives of (South-West Asian Neolithic) crops and weeds are native (Zohary et al. 2012) and Central Europe, where wild relatives of crops and weeds are rare (Deza-Araujo et al. 2020). Specifically, wild relatives of crops and weeds might be palynologically indistinguishable from cultivars and adventives and thus markedly affect human impact reconstructions.

The palynological datasets concerned have been produced by the same palynology school at a rather detailed and consistent taxonomy. Drawing on these records and using comprehensive harmonization tables at the European scale (Giesecke et al. 2019), we simulate datasets at lower hierarchical levels and assess the impact of this change in taxonomical resolution on the anthropogenic pollen curve and its interpretation. We use specialized literature to define anthropogenic pollen indicators at higher taxonomic resolution level than the one used routinely and to assign them to the categories of primary (crops) or secondary (introduced or opportunistic weeds) indicators. We hypothesize that reducing the taxonomic resolution will cause a decrease in the specificity and sensitivity of the pollen indicators for detecting and quantifying anthropogenic land use, with different pollen types having more or less influence on this change according to the biogeographical region. Further, we also hypothesize that lowered taxonomic levels in pollen identification will result in misleading reconstructions of past anthropogenic land use.

Materials and methods

Study area

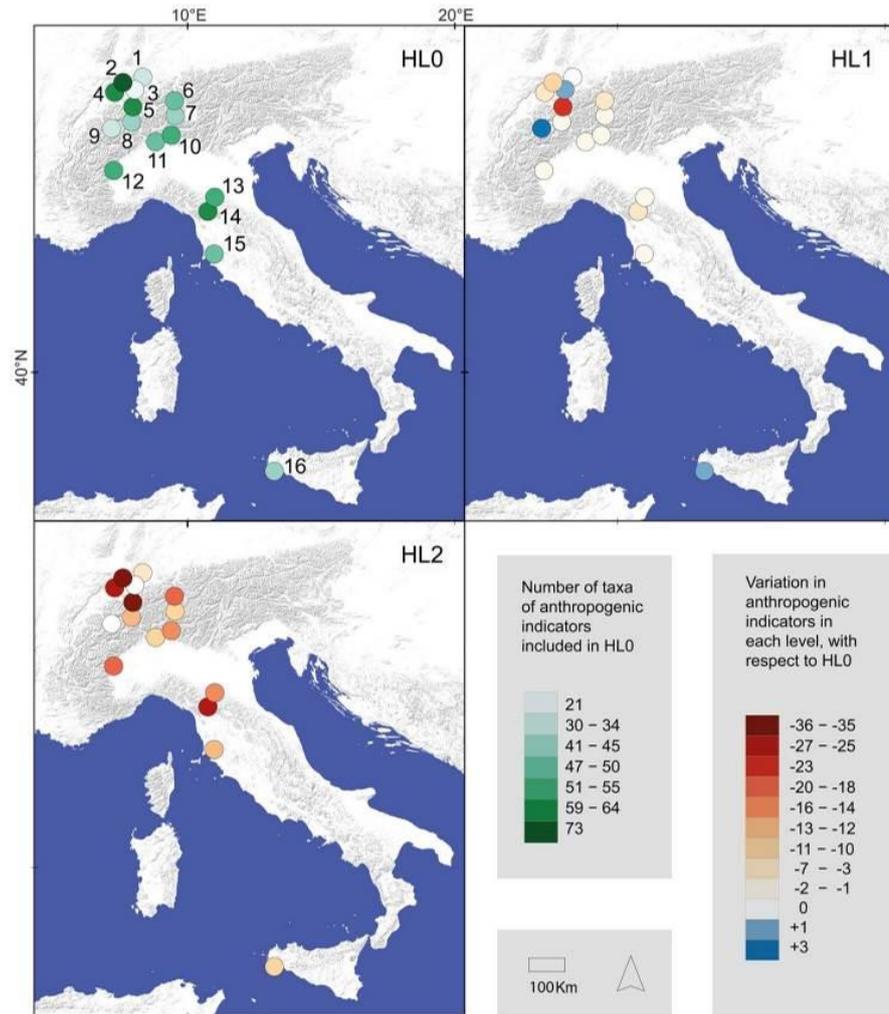
We selected sixteen postglacial palaeoecological sequences along a latitudinal gradient encompassing from northern Switzerland to southern Italy (Sicily; Fig. 1), located at various altitudes (Table 2). These sequences were produced at the Palaeoecology Section of the University of Bern, thus allowing for consistent and high taxonomic resolution. The pollen datasets were obtained from the Alpine Palaeoecological Database (ALPADABA) via Neotoma (Williams et al. 2018).

Taxonomic resolution of human pollen indicators

A bibliographic search yielded a list of plants which are associated with farming: primary indicators (plants cultivated in fields, orchards and gardens) and secondary indicators (weeds) classified into adventives and apophytes (ESM 1; Behre 1990; di Castri et al. 1990; Lang 1994; Chytrý et al. 2008; Sökand and Kalle 2015). Adventives are non-native plants that were introduced with the agriculture (or locally very rarely before agriculture), whereas apophytes are native plants that were favored by human land use (Behre 1981; Lang 1994). This concept also applies to the crops. Some crops are native to Europe, while others were introduced. Here we apply the concept of adventive plants only to the weeds, but pay particular attention to whether a crop was native or not to the area. Indeed, most European crops originate from Southern Europe (e.g. fruit trees or lianas such as *Castanea sativa*, *Juglans regia*, *Olea europaea* or *Vitis vinifera*). By assembling this species list, we aimed to refine the anthropogenic pollen types traditionally used at lower taxonomic resolution such as at genus or family level (Table 1; Behre 1981). From the pollen types in our datasets, we selected all those that corresponded to anthropogenic pollen indicators at different taxonomic resolutions (see Table 1), resulting in a list of potential pollen indicators (ESM 2).

The nomenclature of the potential pollen indicators was first standardized according to the accepted pollen type names of the European Pollen Database (Giesecke et al. 2019). The starting point is a list of all the pollen type names accepted in the EPD (once synonymies were solved), assigned by Giesecke et al. (2019) to the base hierarchical level HL0. This level represents the highest taxonomic resolution currently attainable using sophisticated light microscopy (e.g. 1,000× magnification, phase contrast), generally referring to genera, groups of closely related genera, families or, more rarely, species or groups of species. Based on HL0, Giesecke et al. (2019) constructed two hierarchical levels (HL1, HL2) that rely on pollen-morphological features and possess a decreasing taxonomic resolution. The first level (HL1) provides a list of morphologically similar pollen types identified when a good reference collection is available. The second hierarchy level (HL2) combines types with distinctive, mainly readily identifiable features often corresponding to groups of related plant genera or to families. HL2 combines pollen types that can be easily identified but are differently used in palaeoecology. For instance, it is widely used for *Plantago* but rarely for Poaceae-type, which includes also Cerealia-type at HL2. We selected the anthropogenic pollen indicators to be included in each simulated dataset according to the respective taxonomic level of harmonization HL0 to HL2 (e.g. for *Plantago* see Fig. 2a). At each taxonomic hierarchical level, pollen types deriving from

Fig. 1 Location of the study sites and number of anthropogenic pollen types included in the hierarchical levels after harmonization (HL0-HL2) for each study site. 1—Egelsee (Menzingen), 2—Burgäschisee, 3—Soppensee, 4—Moossee, 5—Bachalpsee; 6—Lej da San Murezzan, 7—Lej da Champfèr, 8—Lengi Egga, 9—Gouillé Rion, 10—Lago di Origlio, 11—Lago di Muzzano, 12—Lago Piccolo di Avigliana, 13—Pavullo nel Frignano, 14—Lago del Greppo, 15—Lago dell’Accesa, 16—Gorgo Basso



plants that are not cultivated or not considered as adventives or apophytes were disregarded because of their diagnostic irrelevance for land use detection (ESM 2). The harmonization was performed using the packages “tidyverse” version 1.3.0 (Wickham et al. 2019a) and “readxl” version 1.3.1 (Wickham et al. 2019b) running in the R environment (R Core Team 2018), and resulted in two simulated datasets for each study site. Figure 1 reports the number of taxa and their variations in each hierarchical level with respect to the base level (HL0) for each considered site and taxonomic hierarchical level.

Within each harmonized sequence, we assigned a category of indicative capacity according to the synanthropic status found in literature (ESM 1). Introduced (or partly introduced) primary indicators have the highest indicative capacity, followed by plants considered to be adventives, and finally, the apophytes (Behre 1981, 1990; Lang 1994, ESM 2). When decreasing taxonomic precision

changed the constitutive taxa of a given pollen type, we also lowered its indicative capacity. For instance, *Plantago lanceolata*-type and *P. major*-type are considered adventives at the highest taxonomic resolution levels HL0 and HL1. However, at level HL2 these pollen types are merged with other *Plantago* pollen types with no human indicator capacity into *Plantago*, which is thus regarded as an apophyte (Fig. 2).

Statistical analysis

Pollen percentage calculation and Wilcoxon test

Pollen percentages were calculated with respect to a reference sum that included the pollen of trees, shrubs and upland herbs, and the spores of terrestrial ferns. We included fern spores in the reference sum because *Pteridium aquilinum* and *Polypodium* are both considered secondary human

Table 2 Main features of the palynological records considered in this study

Site	Lat (°N), Long (°E)	Elevation (m a.s.l.)	Area (ha)	Age range (cal yr BP)	MAT (°C) (Fick and Hijmans 2017)	Reference
1. Egelsee (Menzingen)	47.183480, 8.582379	770	1.2	50–16,200	8.7	Wehrli et al. (2007)
2. Burgäschisee	47.148056, 7.658333	465	21	– 50–18,700	8.9	Rey et al. (2019a, b)
3. Soppensee	47.090421, 8.080115	596	22.7	– 50–14,200	8.6	Hajdas and Michezyski (2010); Lotter (1999)
4. Moossee	47.021944, 7.480278	521	31	3,850–7,100	9	Rey et al. (2019a, b)
5. Bachalpsee	46.670356, 8.023247	2,265	8	– 50–12,900	0.2	Lotter et al. (2006); van der Knaap et al. (2000)
6. Lej da San Murezzan	46.495168, 9.845067	1,768	78	– 50–11,900	1.9	Gobet et al. (2003, 2005); Henne et al. (2011)
7. Lej da Champfêr	46.471268, 9.807297	1,791	50	– 50–11,850	1.8	Gobet et al. (2003, 2005)
8. Lengi Egga	46.396840, 7.980020	2,557	2.89	10–12,600	– 0.6	Tinner and Theurillat (2003)
9. Gouillé Rion	46.157222, 7.362778	2,343	0.16	– 50–11,950	1.0	Tinner et al. (1996)
10. Lago di Origlio	46.060435, 8.942306	416	8	– 50–18,900	10.6	Tinner et al. (1999)
11. Lago di Muzzano	45.996621, 8.928177	337	22	– 50–15,150	11.5	Gobet et al. (2000); Tinner et al. (1999)
12. Lago Piccolo di Avigliana	45.050000, 7.383334	356	60	320–19,350	11.8	Vescovi et al. (2007)
13. Pavullo nel Frignano	44.318335, 10.837500	675	ca. 20	100–16,300	12.6	Vescovi et al. (2010b)
14. Lago del Greppo	44.119722, 10.683055	1,442	0.018	– 50–14,950	6.7	Vescovi et al. (2010a)
15. Lago dell'Accesa	43.059388, 10.898260	157	16	50–11,600	14.2	Colombaroli et al. (2008); Fins- inger et al. (2010)
16. Gorgo Basso	37.609174, 12.654939	6	3	– 55–10,200	18.1	Tinner et al. (2009)

indicators (Table 1; Behre 1981). The sum of pollen percentages of human indicators at each hierarchical level and each category of indicative capacity was plotted against time (Fig. 3).

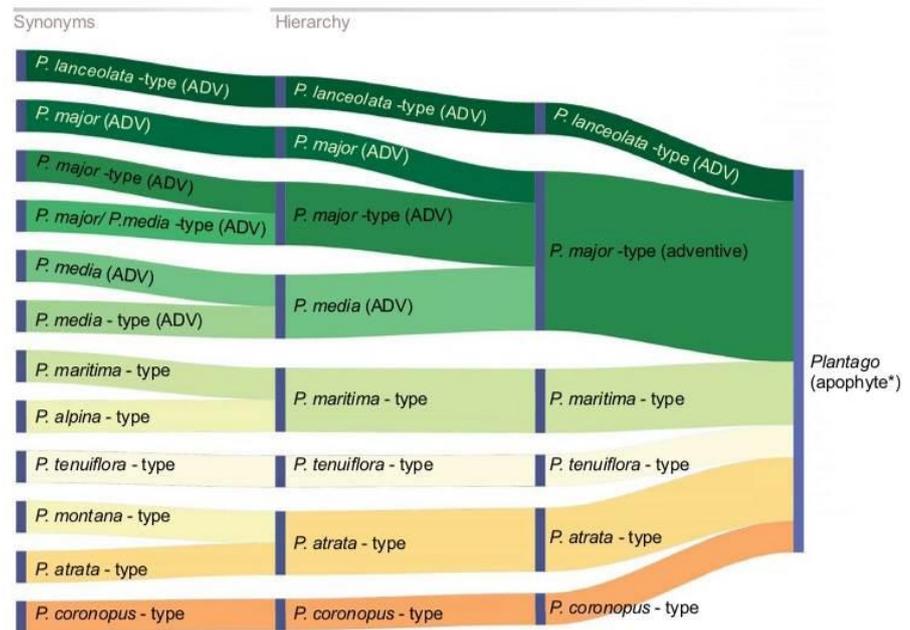
Our null hypothesis (H_0) is that the abundance of human pollen indicators does not depend on the taxonomic hierarchical level (HL0 to HL2), meaning that decreasing taxonomic resolution does not bring any information loss. To test this hypothesis, in a first step we plotted the Kernel density (Sheather and Jones 1991) of anthropogenic pollen percentages between the base resolution level HL0 and the subsequently lower resolution levels HL1 and HL2 for each category of indicative capacity, i.e. primary indicators, adventives and apophytes. In a second step, we ran Wilcoxon signed-rank paired tests (Wilcoxon 1945) between them (Fig. 4). For these analyses, we used the R package “plyr” version 1.8.4 (Wickham 2011).

‘Distantia’ analyses

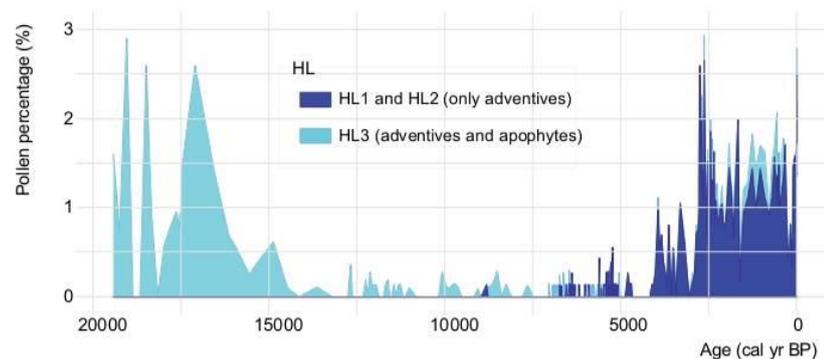
To quantify the influence of the decrease in the taxonomic resolution of human indicators on their indicative value, we calculated the dissimilarities between the assemblages of anthropogenic pollen types (pollen percentages with respect to the reference sum defined above) among HL sequences with the R package “distantia” version 1.0.2 (Benito and Birks 2020). This package computes the dissimilarity measure Ψ or psi (Gordon and Birks 1974) between two multivariate ecological time-series (METS). Given two METS (A and B, with lengths m and n), the dissimilarity measure Ψ is calculated as the sum of distances between their respective samples (AB_{between}), normalized by the sum of distances between the consecutive samples within each sequence (AB_{within}), plus 1 (in the case of including diagonals in the calculation to find the least-cost path):

Fig. 2 **a** Pollen type synonyms (Var.) and hierarchical levels of taxonomic resolution (HL0-HL2) and their relationship as in Giesecke et al. (2019). Example for *Plantago* and its constituent pollen types found in our study sites. Discontinuous line denotes exclusion of the pollen type as a human indicator in that harmonization level. (*) *P. lanceolata*-type and *P. major/media*-type are considered as adventives (ADV), but move to the apophyte category (APO) when they are merged with the other pollen types (e.g. *P. maritima*-type, *P. atrata*-type) into *Plantago*-type. **b** Results of the harmonization to different HL levels for *P. lanceolata*-type at the site Origlio (Tinner et al. 1999). Here, *P. lanceolata*-type is an (independent) adventive with high human-impact value at the levels HL0 and HL1 but moves together with other pollen types (e.g. *P. alpina*-type, *P. montana*-type) into the far less diagnostic apophyte category *Plantago*-type at the level HL2 (see high natural abundances at HL2 before agriculture started at ca. 7,500 cal BP). All levels used and included in the analysis are found in ESM 2

(a) Synonyms and Hierarchical Levels of harmonization (HL) for *Plantago*



(b) *Plantago lanceolata*-type harmonization in Origlio



$$\psi = ((AB_{\text{between}} - AB_{\text{within}}) / AB_{\text{within}}) + 1.$$

The computation of the distance between their respective samples (AB_{between}) and between consecutive samples (AB_{within}) was made using the Euclidean method. In a first step, we quantified the influence of taxonomic resolution of anthropogenic pollen types on the dissimilarity among the three sequences HL0-HL2 (Table 3). This first dissimilarity analysis was based on the variables “anthropogenic pollen types” and the sequences were ordered along “depth/age”.

In a second step, we ordered the sequences along pollen-types and ran an analysis based on the variable “time intervals” with the goal of identifying the periods and taxa responsible for the dissimilarity. This second dissimilarity

analysis was made to disclose the relevance of removed time intervals on the overall dissimilarity between hierarchical levels HL0-HL1 at a specific site. This analysis focused on HL0-HL1 because the lowest level HL2 is only moderately used by palynologists (e.g. for *Plantago*). The values of the variables “time intervals” were calculated by grouping pollen percentages into 500-year bins (average considering only non-zero values). The results are plotted as percentage drop in psi values for the remaining time variables, graphically allocated to the removed period (Fig. 5). Once a high drop in psi values was detected for a specific time interval with the analysis, we could identify in the pollen diagrams which were the taxa responsible for that change.

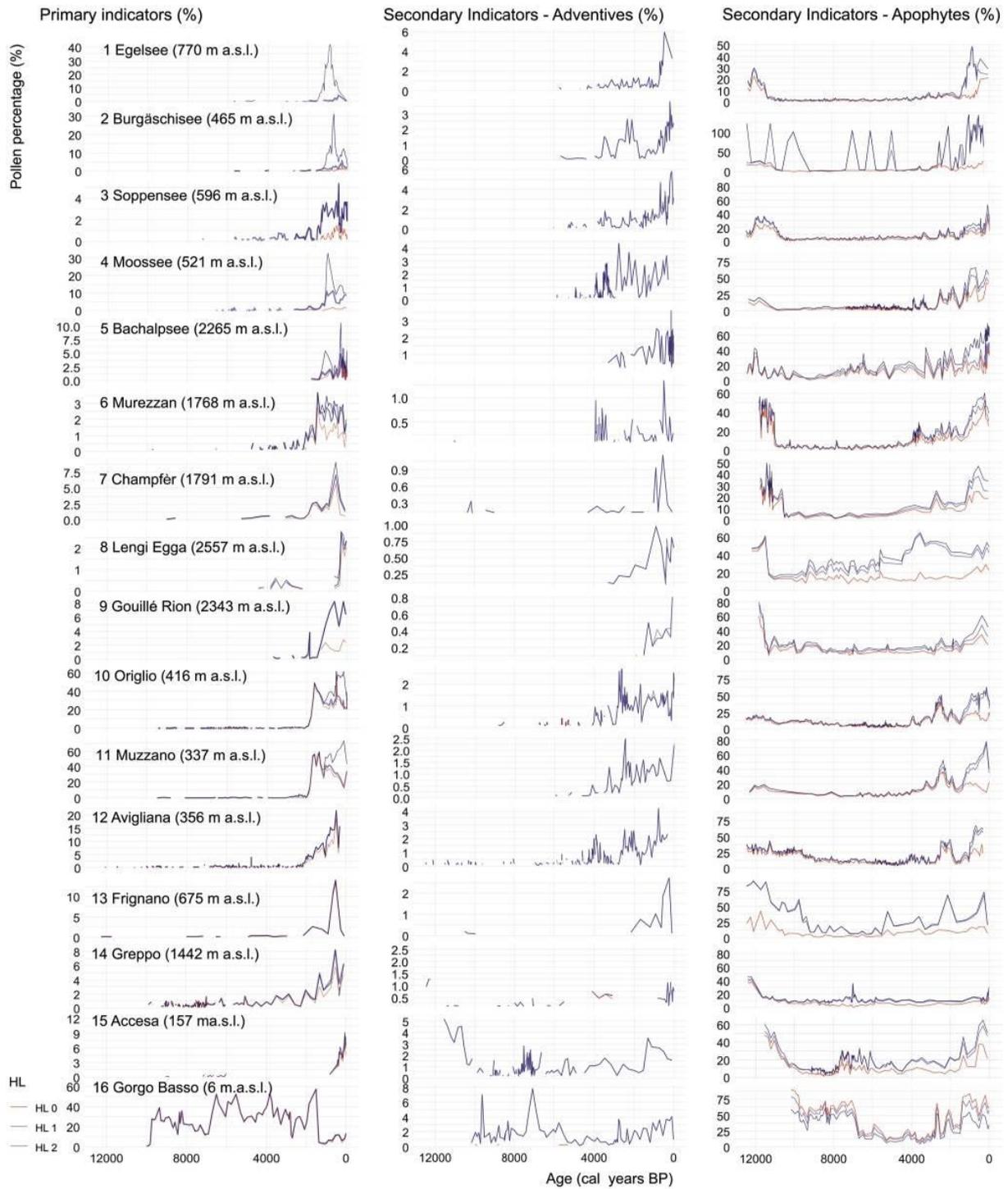


Fig. 3 Anthropogenic pollen curves (as percentages of the reference sum including terrestrial pollen and fern spores) in each study site at the different hierarchical levels of harmonization (HL0 to HL2, with HL0 representing the highest and HL2 the the lowest level of taxonomic resolution) for each category of indicative capacities: Primary

Indicators refer to crops and Secondary Indicators to weeds; adventives are plants that were involuntarily introduced alongside farming; apophytes are synanthropic species that are native in origin. In parenthesis, the altitude of the site; note the different scales in the y-axes; all graphics are constrained to the last 12,000 calendar years

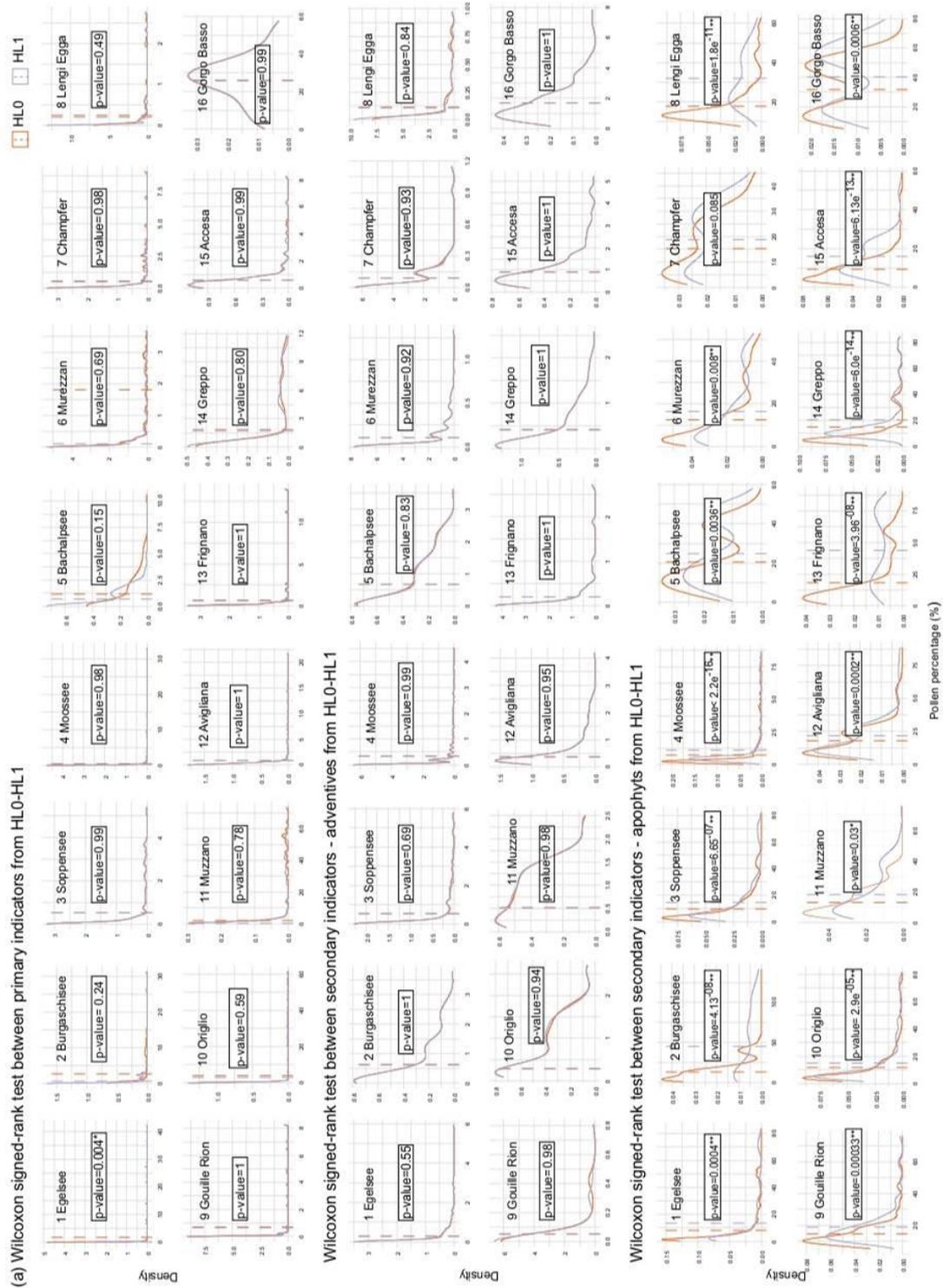


Fig. 4 Kernel density (Sheather and Jones 1991) of anthropogenic pollen percentages in each study site, comparing the base level (HLO) sequences and the others: **a** HLO-HL1; and **b** HLO-HL2. The mean is shown for each curve. Each graph shows the statistical significance (p value) between the two hierarchical levels using Wilcoxon signed-

rank paired test (Wilcoxon 1945). Statistically significant differences at $p < 0.05$ and $p < 0.01$ are denoted with * and **, respectively. Graphs not showing a p value correspond to the ones with no data at HL2

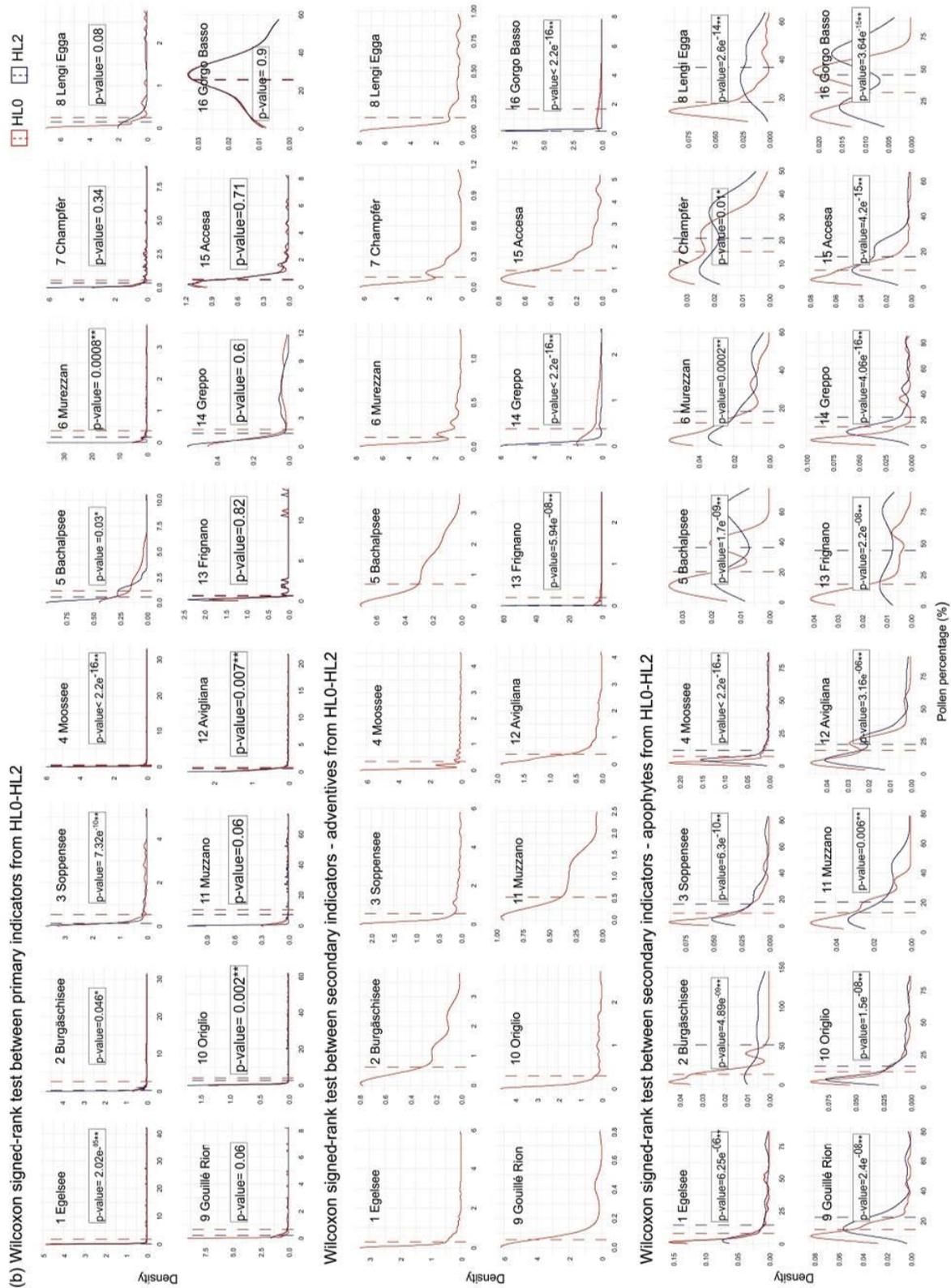


Fig. 4 (continued)

Table 3 Dissimilarity measure Ψ or psi values between pairs of HL sequences (Benito and Birks 2020)

Site	HL0-HL1	HL0-HL2	HL1-HL2
1. Egelsee (Menzingen)	1.212	1.244	0.198
2. Burgäschisee	2.296	2.024	0.220
3. Soppensee	1.443	1.531	0.368
4. Moossee	1.269	1.289	0.209
5. Bachalpsee	0.405	0.885	0.744
6. Lej da San Murezzan	0.865	0.932	0.356
7. Lej da Champfer	0.514	0.624	0.290
8. Lengi Egga	2.780	2.826	0.439
9. Gouillé Rion	0.930	1.063	0.499
10. Lago di Origlio	0.563	0.617	0.258
11. Lago di Muzzano	0.444	0.552	0.330
12. Lago Piccolo di Avigliana	0.872	0.912	0.229
13. Pavullo nel Frignano	2.021	2.019	0.067
14. Lago del Greppo	1.137	1.367	0.818
15. Lago dell'Accesa	1.584	1.712	1.846
16. Gorgo Basso	0.493	0.553	0.278

This analysis quantifies the influence of the taxonomic resolution of anthropogenic pollen types on the dissimilarity among the three sequences HL0 to HL2. For each site throughout the entire time sequence, higher values indicate higher dissimilarities

Change point analyses

To investigate long-term variations in the cumulative curve of all anthropogenic pollen taxa between the HL sequences, we used the “*changepoint*” v1.1.5 package of R (Killick and Eckley 2014; R Core Team 2018) to determine the time of significant human (and environmental) changes by each taxonomic hierarchical level (Killick et al. 2012). The change point analysis considers the variations between HL0, HL1 and HL2 concerning the mean and variance of the summary anthropogenic pollen records. We defined a maximum number of four change points to search for and constrained the datasets to the last 12,000 years to enhance inter-site comparison (ESM 3), applying the binary segmentation method (Scott and Knott 1974). This method is an iterative search method that tests if a change point at position τ exists that separates an ordered sequence of data ($y_1:n = (y_1, \dots, y_n)$) into two segments ($y_1:\tau = (y_1, \dots, y_\tau)$, $y_{\tau+1:n} = (y_{\tau+1}, \dots, y_n)$) at each iteration. A change point is taken in a given interaction when a cost function applied to the entire sequence ($\Omega_1:n$) is larger than the sum of the cost functions applied separately to the two segments plus a penalty β to guard against overfitting ($\Omega_1:\tau + \Omega_{\tau+1:n} + \beta$), until no change points that meet this condition are detected (Killick et al. 2012). Change point analysis is a method increasingly used in palaeoecology to determine major shifts in time-series (e.g. Giesecke et al. 2014; Rius et al. 2014; Finsinger et al. 2018).

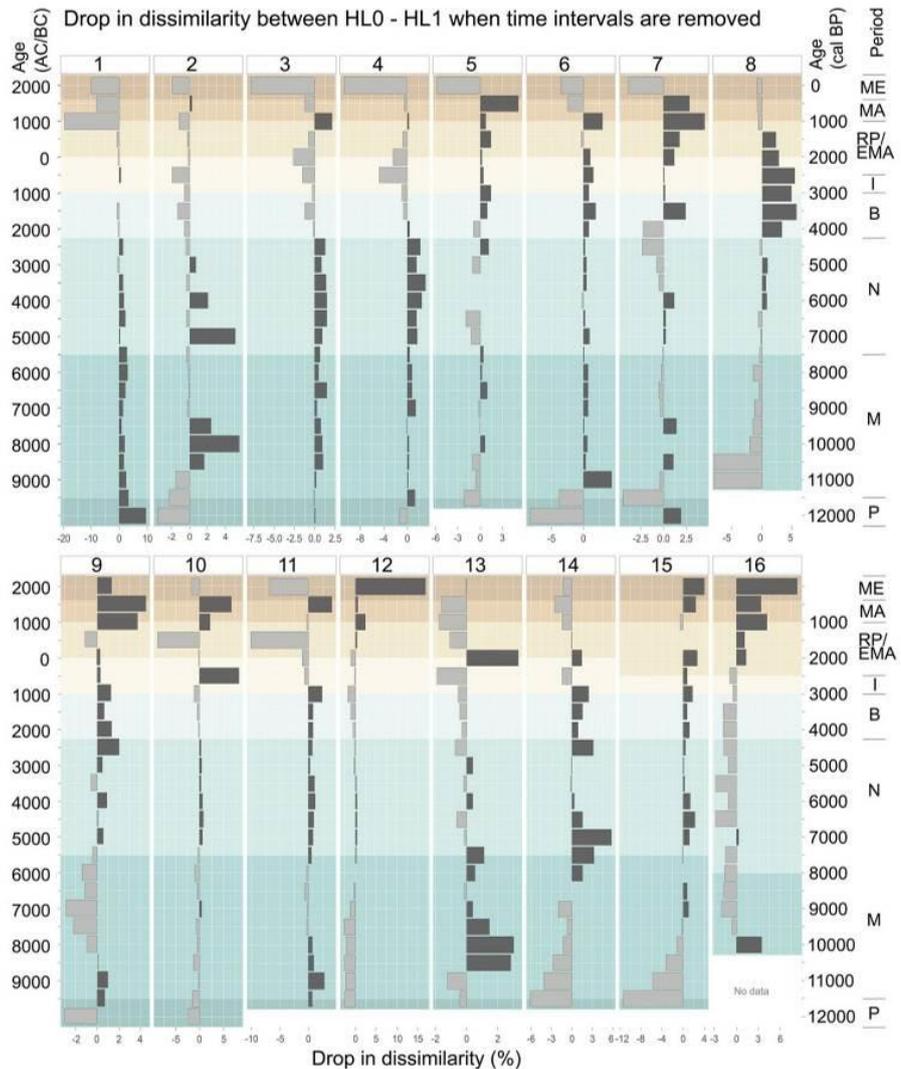
Results

Effect of HL harmonization in each site and pollen type

The harmonization process resulted in a variation of the number of indicative taxa among all study sites (Fig. 1). At the base level HL0, a slight latitudinal increase of anthropogenic taxa towards the southern sites was found, although this trend is blurred by the specific characteristics of each site (mainly altitude) and the resolution achieved in the dataset. Taxonomic harmonization at the three hierarchical levels shows a significant reduction in the total number of potential anthropogenic pollen types from HL0 to HL2 (179 in HL0, 121 in HL1, and 49 in HL2 (ESM 2)). Similarly, the overall number (all sites) of pollen types with indicative value for anthropogenic impact used in the simulated datasets dropped from HL0 to HL2 (80 in HL0, 63 in HL1, and 42 in HL2). The total number of anthropogenic indicator taxa remains mostly constant at site level between HL0 and HL1 but shows a dramatic drop in HL2 at most sites (Fig. 1).

A first group of anthropogenic pollen types with indicator capacity was totally independent from the harmonization and consisted of easily identifiable taxa (even at the lowest HL2) such as *Artemisia*, *Adonis*, *Caltha*-type, *Ranunculus arvensis*-type (apophytes), *Nigella* (adventive), *Fagopyrum*, *Olea europaea*, *Castanea sativa*, *Ficus carica*, *Vitis* and *Pistacia* (introduced or native primary indicators). On the other hand, the indicative value of a numerous array of pollen types clearly depends on the taxonomic resolution attained, although the magnitude of this effect is variable. At the lowest degree of dependence, the following group of taxa bear constant indicative capacity through HL0 and HL1 levels since their precise identification (at species or genus level) is often achieved, although a decrease in indicative power at HL2 must be noted. These taxa are the primary indicator *Linum usitatissimum* and most of the secondary adventives (*Agrostemma githago*, *Fallopia*, *Persicaria maculosa*-type, *Plantago lanceolata*-type, *P. major*-type, *P. media*-type, *Polygonum aviculare*-type, *Scleranthus*, *Torilis japonica*); in this group we also have important taxa such as *Rumex acetosa*-type and *R. acetosella*-type, which do not change their indicative value with varying taxonomical resolution (they are both apophytes), but do change the inferred type of human land use (*R. acetosa*-type is a herb indicator of grasslands and *R. acetosella*-type is indicative of ruderal vegetation). With a moderate degree of dependence from harmonization, we have the primary indicator *Cannabis sativa*-type and adventive *Centaurea cyanus*-type. In contrast, the group most strongly affected by the harmonization in terms of indicator value included principally human pollen types originally defined at low taxonomic resolution

Fig. 5 Drop in dissimilarity measure Ψ or psi values, in percentages, when the given time interval is removed from the dissimilarity analysis between HL0-HL1 hierarchical levels. This analysis was done with the purpose of quantifying the influence of certain periods on the dissimilarity between HL0 and HL1 sequences. Time intervals are 500 years. Large positive numbers (dark grey) indicate increase in similarity when the given time interval is removed, disclosing the relevance of the time interval for dissimilarity between both hierarchical levels (HL0-HL1). Negative values (light grey) indicate an increase in dissimilarity between the hierarchical levels when the time interval is dropped. The numbers in the graphics follow the nomenclature of sites in Fig. 1 and Table 2. Archaeological and historical periods: P—Palaeolithic, M—Mesolithic, N—Neolithic, B—Bronze Age, I—Iron Age, RP—Roman Imperial Period, EMA—Early Middle Ages, MA—Middle Ages, ME—Modern Era. Note the different scales in the X-axes. All graphics are constrained to the last 12,000 cal years



such as Cerealia-type, Poaceae, Brassicaceae, Cyperaceae and *Plantago* (Fig. 6).

Effect of the harmonization on the cumulative curves of anthropogenic indicators

The cumulative curves of anthropogenic pollen according to their category of indicative capacity showed differences resulting from the harmonization process (Fig. 3). However, when comparing HL0 and HL1 only the curves of apophytes were significantly different, unlike those of all the primary indicators and the adventives (Fig. 4). The influence of the harmonization was stronger when considering HL0 and HL2, particularly on the abundances of secondary (both adventives and apophytes) and primary human indicator types, mostly in the northern sites (Fig. 4). However, at most

sites adventives were lacking at HL2 because they were re-assigned to the apophyte category (Figs. 2, 3 and 4).

The largest dissimilarity values (Ψ or psi values) in the assemblages of anthropogenic pollen indicators were found between the base level HL0 and the lowest level of resolution HL2, except at Burgäschisee (site #2), which was originally produced at particularly high taxonomic resolution (73 anthropogenic taxa in HL0 compared to 63 in HL1), at Pavullo nel Frignano (site #13), where the outstanding abundance of Cyperaceae pollen in HL1 enhances the HL0-HL1 dissimilarity, and at Accesa (site #15), where the change in the number of taxa is even more drastic between HL1 (46 taxa) and HL2 (34 taxa; Table 3).

Resolution	Classification	Indicative	Anthropogenic	Best resolution achieved when the pollen type can be			
HL2	Pollen types totally independent from the harmonization	PI ²	<i>Castanea sativa</i>	(Best resolution achieved already at the lowest level)			
			<i>Fagopyrum</i>				
			<i>Ficus carica</i>				
			<i>Olea europaea</i>				
			<i>Pistacia</i>				
			<i>Vitis</i>				
		SI	ADV		<i>Nigella</i>		
					APO	<i>Adonis</i>	
						<i>Artemisia</i>	
						<i>Caltha</i> -type	
						<i>Melampyrum</i>	
						<i>Polypodium</i>	
						<i>Pteridium</i>	
<i>Ranunculus</i>							
HL1	Pollen type with moderate degree of dependence from harmonization	PI ²	<i>Linum</i>	<i>Linum catharticum</i> -type (SI, APO)			
			SI	ADV	<i>Persicaria</i>	<i>Polygonum</i> (pericolpate/periporate) (SI, APO)	
		<i>Plantago</i>			<i>Plantago</i> (e.g. <i>P. major</i> -type (SI, ADV), <i>P. maritima</i> -type, <i>P. tenuiflora</i>)		
		<i>P. major</i> -type					
		<i>P. media</i> -type					
		<i>Polygonum</i>		<i>Polygonum</i> -type (tricolpate), <i>Bistorta officinalis</i> -type, <i>Fallopia</i> (SI, ADV)			
		<i>Fallopia</i>					
		APO	<i>Agrostemma</i>	Caryophyllaceae (periporate excl. Paronychioideae) (incl. <i>Sagina</i> , <i>Silene</i> -type (SI, APO), <i>Stellaria holostea</i> , <i>Gypsophila repens</i> -type, <i>Dianthus/Petrorhaghia</i> , <i>Moehringia</i> -type)			
			<i>Scleranthus</i>				
		APO	<i>Torilis japonica</i>	Apiaceae (SI, APO) (e.g. <i>Pimpinella major</i> -type (SI, APO), <i>Peucedanum</i> -type, <i>Anthriscus sylvestris</i> -type (SI, APO), <i>Astrantia</i> -type, <i>Pleurospermum</i> -type, <i>Cicuta virosa</i> , <i>Daucus</i> (SI, APO), <i>Oenanthe</i> , <i>Eryngium</i> , <i>Meum</i> -type, <i>Chaerophyllum hirsutum</i> -type)			
			<i>Rumex acetosa</i> - <i>Rumex acetosella</i> - type*	<i>Rumex/Oxyria</i> (SI, APO) (<i>R. acetosa</i> -type (SI, APO), <i>R. acetosella</i> -type (SI, APO), <i>R. obtusifolius</i> -type (SI, APO), <i>R. alpinus</i> -type)			
		HL0	Pollen type with high degree of dependence from the harmonization	PI ¹	<i>Cannabis sativa</i> -type	<i>Humulus lupulus</i> -type, <i>Cannabis/Humulus</i> -type	
					<i>Avena</i> -type <i>Hordeum</i> -type <i>Secale cereale</i> <i>Triticum</i> -type <i>Zea mays</i>	Poaceae (no Cerealia-type)	
SI	ADV				<i>Centaurea cyamus</i> -	<i>Centaurea montana</i> -type	
HL0	Pollen types totally dependent from the harmonization				PI ¹	Cerealia-type	Poaceae (no Cerealia-type)
N/A	Pollen types totally dependent from the harmonization				SI	ADV	<i>Plantago</i> **
		APO	Brassicaceae**				
			Cyperaceae**				
		Poaceae**					

PI¹ =primary indicators non-native to Europe; PI² =primary indicators native to Europe; SI= Secondary indicator; ADV= Adventive;

APO= Apophyte

* denotes pollen types that do not decrease their indicative capacity, but change the inferred type of human land use

** denotes some of the pollen types traditionally used at a low taxonomic resolution, which use we advise against

Fig. 6 Classification of main anthropogenic pollen types by the degree of effect that the taxonomic harmonization had on its indicative capacity. Pollen types totally independent from harmonization did not change their anthropogenic indicative capacity at any level

(HL0-HL1-HL2). For each anthropogenic indicator, we indicate the highest resolution level, so that it is not confused with other pollen types with different indicative capacity. For a detailed explanation of the taxonomic harmonization list, see ESM 2

Time variations of human pollen types due to HL harmonization

Estimation of the land use impact tends to be higher at lower levels of resolution. When the dissimilarity was estimated on the basis of time intervals and the contribution of each time interval to dissimilarity was calculated, the highest levels of dissimilarity between the HL0 and HL1 sequences were found mainly during the Mesolithic and Neolithic (Fig. 5). At Egelsee (site #1), Soppensee (site #3), and Muzzano (site #11), while the dissimilarity is slightly higher in periods such as the Paleolithic when land use is not detectable or minimal. In other cases, and especially at high altitude sites, the highest dissimilarity occurs after the Bronze Age due to Cyperaceae, Poaceae, Brassicaceae and Ericaceae (tetrads) included in HL1, as at Murezzan (site #6 at 1,768 m a.s.l.), Champfer (site #7 at 1,791 m a.s.l.) and Lengi Egga (site #8 at 2,557 m.a.s.l.). The dissimilarity at Egelsee (site #1) is also very high (up to 10%) in the Modern Era. Within the Mediterranean sites, at Gorgo Basso (site #16) the dissimilarity is concentrated at the beginning of the record during the Mesolithic [due to Poaceae, Ericaceae (tetrads) and Brassicaceae in the older samples] and after the early Middle Ages, with up to 4% of dissimilarity change mainly due to Apiaceae. The change point analysis of the anthropogenic pollen indicators (ESM 3) identified mainly the environmental change at the onset of the Holocene, the human-induced vegetation change around the Neolithic, and the land use intensification around the Bronze Age. Overall, the detected changes coincide in time, with some rare exceptions. For instance, at Lengi Egga (site #8 at 2,557 m a.s.l.) the highest resolution HL0 displays a later change point in land-use intensification with respect to HL1 and HL2. At other sites, HL0 presented earlier change points than HL1 and HL2 at the onset of the Holocene, as at Lago Piccolo di Avigliana (site #12) and Lago del Greppo (site #14).

Discussion

Pollen-inferred reconstructions of human activity rely on the relationship between agricultural crops or weeds and their imprint in pollen assemblages (Behre 1981). Previous studies showed that high taxonomic resolution is important for the reconstruction of human impact from pollen records (Tinner et al. 1996; Seppä and Bennett 2003). Specifically, an accurate and precise pollen taxonomy is key to correctly identifying crops or weeds associated with land use and in defining diagnostic human-impact indices (Giesecke et al. 2014). Attaining the high taxonomic resolution needed may be time consuming and require a significant analytical effort, including consulting reference slides and using microscopes equipped with 1,000× magnification (using immersion oil)

and phase contrast (Tinner et al. 2007; Beug 2004; Rey et al. 2017). However, such additional work is worthwhile when aiming at detailed reconstructions of arable farming activities in prehistoric times, as the determination of different pollen types of cereals (e.g. *Avena*-type, *Hordeum*-type, *Triticum*-type) may deliver relevant information in this regard (Beug 2004; Rey et al. 2017). Likewise, it becomes essential to understand the possible effects of taxonomical losses related to the harmonization practices inherent in big data analysis, the use of diversity at higher taxonomic ranks (e.g. genus, family) as a surrogate for species diversity (Bevilacqua et al. 2012), as well as the use of functional types for compensating for existing taxonomic imprecisions (Gajewski 2008), particularly considering the prominence that these topics are reaching in recent times.

Here, we show that decreasing taxonomic resolution has noticeable effects when moving from highest to high (i.e. HL0–HL1) and from highest to intermediate (HL0–HL2) levels (Table 3, Figs. 3 and 4). Further, our results show that aiming at the highest possible taxonomic resolution level is important in distinguishing between adventive and apophyte taxa, i.e. in separating introduced crops and weeds from native plants. This distinction is important for disentangling the role of human impact from other natural drivers of vegetation change like climatic variability, fire disturbance or herbivory. Indeed, if all human indicators are put together at sites originally produced with high taxonomical resolution, the dissimilarity values are already remarkable between the base level HL0 and the immediately lower harmonization level HL1 (Table 3).

As agricultural crops are the foundation of farming economies, primary human indicators have the highest indicative value (Behre 1981). Caution is however needed in the interpretation of primary indicators that are native to an area (e.g. *Olea europaea* and *Vitis vinifera* in southern Europe). Here we show that primary indicators are mostly well recognized at the high levels HL0 and HL1 but might be overlooked at lower taxonomic resolution (HL2; see ESM 3). The highest loss in the indicative capacity of anthropogenic pollen indicators may occur when the pollen of primary indicators such as cereals cannot be distinguished from the pollen of wild grasses. In regard to the secondary indicators, adventives are particularly important because these taxa were introduced with agriculture. These plants therefore depend on human activities to thrive and are not naturally present in the vegetation, which makes them particularly well suited as indicators of human activity (Behre 1990; Lang 1994; Tinner et al. 2007), in contrast to apophytes. Remarkably, our results also show that the family or sub-family level may lead to confusion of natural and anthropogenic processes in human impact and land use reconstructions, so they should be avoided in such assessments. Low taxonomic resolution actually introduces an overrepresentation and thus

an overestimation of naturally occurring apophytes, consequently reducing the diagnostic value of summary pollen curves of human impact. Such palynological considerations are in agreement with previous studies showing that species level is the most accurate taxonomic rank for bioindication analysis (Nahmani et al. 2006), even if this is seldom reached in reconstructions of past human impact.

The beneficial effect of enhanced taxonomic resolution can be illustrated with *Rumex* and *Oxyria*. Most palynologists do not distinguish the pollen of *Rumex* and *Oxyria*, considering all these grains as *Rumex*-type. This imprecise determination, however, may pose a relevant issue in arctic and alpine landscapes, where the generalised use of *Oxyria* or *Oxyria*-type (because *Oxyria* is a common plant there) may mask the presence/abundance of *Rumex acetosella*-type and *R. acetosa*-type and thus make the identification of human impact difficult. Furthermore, *R. acetosella*-type is considered an apophyte indicative of ruderal vegetation and arable farming and thus has more indicative value than *R. acetosa*-type, a grassland indicator (Behre 1981). Similarly, *Plantago*-type has adventive constituents (e.g. *P. lanceolata*-type) strongly related to land use but also apophytes that occur in natural environments (e.g. *P. alpina*-type, *P. montana*-type; Fig. 2). The determination of *Plantago* pollen at genus level is quite common in practice (Mercuri et al. 2013a) although it may hamper or even prevent the recognition of human impact. Our study also calls for attention to common and usually abundant plant taxa that have so far experienced little progress in their pollen taxonomy such as Poaceae or Cyperaceae. However, some promising technical innovation such as confocal microscopy might help in the future (Seppä and Bennett 2003). Interestingly, *Eriophorum* and *Carex* pollen (both apophytic Cyperaceae) could be amalgamated into *Dulichium*-type (Faegri and Iversen 1975), which might allow tentative reconstructions of land-use regimes (Fjordheim et al. 2018) in the absence of other more specific human indicators. Dissimilarities derived from taxonomic precision were very high (up to 10%) during the Modern Period (after AD 1600; Fig. 5). However, even if apparently minor, low taxonomic precision in the identification of anthropogenic pollen indicators can lead to overestimate human impact when investigating prehistoric periods such as the Mesolithic-Neolithic transition (Fig. 5). Given that in this initial stage crops and weeds were still rare and thus their pollen signature very weak, an accurate application of the human indicator method is crucial (Fig. 5; ESM 3). For instance, in Sicily, primary and secondary indicators of human activity were found during the Neolithic (after 8,000 BP, Fig. 3). Nevertheless, with the exception of *Ficus*, the evidence was ambiguous (Tinner et al. 2009), since plants producing the other anthropogenic pollen types (including Cerealia-type) were present in the Mediterranean natural vegetation prior to the onset of Neolithization ca.

8,000 years ago (Calò et al. 2012). Combining unambiguous and ambiguous pollen indicators of human activities (here the primary indicators *Ficus* and Cerealia-type) may contribute to solving this issue by reducing the probability of wrong attribution to human impact. Woody taxa such as *Juglans regia*, *Vitis vinifera* or *Olea europaea* are important primary indicators in southern Europe. The identification of these pollen indicators is robust and unequivocal, but if imprecise due to bad preservation they are often taxonomically downscaled. For example, Weiberg et al. (2019) grouped Oleaceae with *Olea* and considered it as a primary indicator, whereas other genera of Oleaceae such as *Fraxinus*, *Phillyrea* or *Jasminum* stayed separate. Similarly, the same authors grouped Juglandinae with *Juglans* (to account for sporadic occurrences of *Carya* and *Pterocarya*). Importantly, the use of these taxa as primary indicators needs a thorough control of whether they were part of the native vegetation in the study area prior to the shift to production economy during the Neolithic (e.g. *Olea europaea* is native in thermomediterranean vegetation of Europe; Laggut et al. 2019) or not. Indeed, in the past years, pollen of these fruit trees has been increasingly used to identify human impact in southern Europe (e.g. Mercuri et al. 2013b; Woodbridge et al. 2019). However, these pollen types cannot be separated from their wild European ancestors or relatives even at the highest level of taxonomic resolution.

The integration of plant macrofossil analysis in archaeological settings (e.g. Tserendorj et al. 2021) may overcome issues related to wild and cultivated varieties producing the same pollen type as it allows the identification of cultivars of these species (Terral et al. 2004) and is particularly well suited for exploration of the transition from wild to cultivated varieties (Valamoti et al. 2020). The introduction of fruit trees occurred usually significantly later than that of basic crops such as cereals. Usually, fruit trees boost the human impact curves since the Iron or Roman Age (Fig. 3), when they were introduced in non-Mediterranean areas (Conedera et al. 2004; Pollegioni et al. 2017). In contrast to *Vitis vinifera* and *Olea europaea*, which were widespread in southern Europe before the onset of farming, the natural rarity of *Castanea sativa* and *Juglans regia* (Krebs et al. 2019) make them good indicators of post-Neolithic human impact all over Europe.

Difficulties may arise when an indicator species is native to an area but adventive in another (Moore et al. 1991; Deza-Araujo et al. 2020), specifically in supra-regional syntheses. The different status of a pollen type in different regions implies that pollen-based reconstructions of human impact should always account for the specific local to regional conditions. Specifically, pollen types which are good proxies for anthropogenic disturbance in temperate or boreal Europe north of ca. 45°N are less reliable when applied in southern Europe, where many pollen types (e.g.

Ammi, *Anemone*, *Apium*, *Bupleurum*, *Cardamine*, *Centaurea montana*-type, *Clematis*, *Delphinium*, *Filago*-type, *Gnaphalium*-type, *Jasione montana*, *Linum austriacum*-type, *Matthiola*, *Secale*, *Scabiosa*, *Silene*) derive from both anthropogenically introduced and natural species. As in the temperate and boreal areas of Europe, the ambiguity of pollen interpretation is highest when considering families with poorly differentiated pollen types such as Apiaceae, Brassicaceae, Caryophyllaceae and Poaceae, all very diversified in the Mediterranean region. Extreme cases are represented by Amaranthaceae, including many shrubs linked to salty and seasonally inundated clayey soils (e.g. *Suaeda*, *Halocnemum*, *Salsola*, *Salicornia* s.l., *Atriplex* s.l.) growing in the coastal marshes or colonizing the inland badlands. Here, the problems derived from palynological taxonomical imprecision may be mitigated by the inclusion of other palaeoecological proxies such as sedimentary ancient DNA and molecular biomarkers. These novel approaches are particularly useful when refined resolution is not possible through pollen analysis (Dubois and Jacob 2016). For instance, cannabinol (an organic molecule specific to hemp) allows the distinction of *Cannabis* from *Humulus* (Lavrieux et al. 2013) two taxa that in palynology have some taxonomic overlaps (Moore et al. 1991).

Conclusions

The use of taxonomically poorly resolved anthropogenic indicators is a widespread practice in palaeoecology. Such taxonomic imprecision may bias the determination of human impact on past environments, given that natural species might be considered as anthropogenic and vice-versa. Moreover, the nature of land use activities might not be recognized correctly (e.g. different crops and weeds associated with arable and pastoral farming). In general, pollen datasets at low taxonomical resolution tend to overestimate land use and to produce false positives in detecting human presence during periods of very low or insignificant human impact. To overcome these difficulties, we provide a detailed list of key pollen types that require adequate taxonomic resolution for the identification of human impact (Fig. 6). Where an accurate pollen identification is not possible, questions related to human impact identification may remain open. To some extent, this is also true for the highest taxonomic resolution that can be reached today with palynology. Given that the diagnostic capacity depends on the identification of species or even varieties of plants, further studies refining the taxonomic level of important taxa are in any case needed. Substantial improvements may derive from taxonomic enhancements related to new techniques, such as biochemical analyses and sedimentary ancient DNA. Our study also has implications for multidisciplinary research in this

topic, for instance we expect further progress from a better integration of palaeoecological, archaeobotanical, archaeological and historical approaches. Future multi-proxy studies focusing on increasing the taxonomic level of determination of crops and adventives may provide new insights on the land use history of Europe.

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Supplementary Information 1

ESM 1 Plant species with anthropogenic indicative capacity in palaeoecological studies, according to their relative importance in archaeological/ historical periods. Evidence of selected species by macro-remains and pollen records in the different cultural epochs. After Lang (1994), Willerding (1986) and Knörzer (2007). (*) species that were not present in our study records. (**) plant taxa that belong to human indicators traditionally defined at lower taxonomic resolution (family, subfamily)

Human indicator	Family	Origin	Neolithic	Bronze Age	Pre-Roman Iron Age	Roman Period	Middle Ages	Older modern Times	Younger modern Times (after 1800 AD)
PRIMARY INDICATORS (Cultivated crops)									
CARBOHYDRATE PLANTS									
<i>Triticum aestivum/durum</i>	Poaceae**	W.As	○	○	○	○	○	○	○
<i>Triticum dicoccum</i>	Poaceae**	W.As	○	○	○	○	○	○	○
<i>Triticum monococcum</i>	Poaceae**	W.As	○	○	○	○	○	○	○
<i>Triticum spelta</i>	Poaceae**	W.As	○	○	○	○	○	○	○
<i>Hordeum vulgare</i>	Poaceae**	W.As	○	○	○	○	○	○	○
<i>Avena sativa</i>	Poaceae**	W.As		○	○	○	○	○	○
<i>Panicum miliaceum*</i>	Poaceae**	C.As	○	○	○	○	○	○	○
<i>Setaria italica</i>	Poaceae**	As	○	○	○	○	○	○	○
<i>Secale cereale</i>	Poaceae**	W.As			○	○	○	○	○
<i>Zea mays</i>	Poaceae**	C.Am						○	○
<i>Fagopyrum esculentum</i>	Polygonaceae	E.As					○	○	○
<i>Solanum tuberosum*</i>	Solanaceae	S.Am						○	○
PROTEIN PLANTS									
<i>Pisum sativum</i>	Fabaceae	W.As	○	○	○	○	○	○	○
<i>Lens culinaris*</i>	Fabaceae	W.As	○	○	○	○	○	○	○
<i>Vicia faba</i>	Fabaceae	W.As		○	○	○	○	○	○

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<i>Phaseolus vulgaris</i> *	Fabaceae	C.+S.Am						○	○
<i>Cicer arietinum</i>	Fabaceae	W.As	○	○	○	○	○	○	○
OIL AND FIBRE PLANTS									
<i>Linum usitatissimum</i>	Linaceae	Eur,W.As	○	○	○	○	○	○	○
<i>Cannabis sativa</i>	Cannabaceae	C.As			○	○	○	○	○
<i>Papaver somniferum</i> *	Papaveraceae	?	○	○	○	○	○	○	○
<i>Camelina sativa</i> *	Brassicaceae**	E.Med	○	○	○	○	○	○	○
<i>Brassica rapa</i> *	Brassicaceae**	Eur	○	○	○	○	○	○	○
VEGETABLES									
<i>Cucumis sativus</i> *	Cucurbitaceae	S.As			○	○	○	○	○
<i>Cucumis melo</i> *	Cucurbitaceae	S.As,Afr			○	○	○	○	○
<i>Lycopersicon esculentum</i> *	Solanaceae	C.+S.Am						○	○
<i>Beta vulgaris</i> *	Amaranthaceae*	Med,Atl			○	○	○	○	○
DYE PLANTS									
<i>Reseda luteola</i> *	Resedaceae	Med	○		○	○	○	○	○
<i>Isatis tinctoria</i> *	Brassicaceae**	W.As			○	○	○	○	
<i>Rubia tinctorum</i> *	Rubiaceae	SW.As			○	○	○	○	○
FRUIT TREES AND NUTS									
<i>Olea europaea</i>	Oleaceae	Med	○	○	○	○	○	○	○
<i>Juglans regia</i>	Juglandaceae	E.M,W.As		○	○	○	○	○	○
<i>Castanea sativa</i>	Fagaceae	W.As		○	○	○	○	○	○
<i>Ficus carica</i>	Moraceae	Med	○	○	○	○	○	○	○
<i>Citrus div. spec.</i> *	Rutaceae	SE.As			○	○	○	○	○
<i>Malus domestica</i> *	Rosaceae	Eur	○	○	○	○	○	○	○
<i>Prunus avium</i> *	Rosaceae	Eur	○		○	○	○	○	○
<i>Prunus domestica</i> *	Rosaceae	W.As	○	○	○	○	○	○	○

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<i>Vitis vinifera</i>	Vitaceae	Eur	○	○	○	○	○	○	○
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APOPHYTES AND ARCHAEOPHYTES IN THE WEED AND RUDERAL VEGETATION OF CENTRAL EUROPE

		APO	NL	BA	IA	RP	MA
<i>Aegopodium podagraria</i> *	Apiaceae**	?	.	.	0	0	0
<i>Carduus nutans</i> *	Asteraceae	0	.	.	0	0	0
<i>Cirsium arvense</i> *	Asteraceae	0	0	0	0	0	0
<i>Euphorbia cyparissias</i> *	Euphorbiaceae	0	.	0	.	0	0
<i>Lamium album</i> *	Lamiaceae	0	0	.	0	0	0
<i>Linaria vulgaris</i> *	Plantaginaceae	0	0	.	0	0	0
<i>Malva sylvestris</i> *	Malvaceae	0	0	0	0	0	0
<i>Mentha arvensis</i> *	Lamiaceae	0	0	0	0	0	0
<i>Plantago lanceolata</i>	Plantaginaceae	?/.	0	0	0	0	0
<i>Plantago major</i>	Plantaginaceae	0/.	0	0	0	0	0
<i>Plantago media</i>	Plantaginaceae	0/.	.	0	0	0	0
<i>Potentilla anserina</i> *	Rosaceae	0	.	.	0	0	0
<i>Potentilla argentea</i> *	Rosaceae	?	0	.	.	0	0
<i>Ranunculus repens (other)</i> *	Ranunculaceae**	0	0	0	0	0	0
<i>Rumex acetosella</i>	Polygonaceae	0	0	0	0	0	0
<i>Stellaria graminea (other)</i> *	Caryophyllaceae**	0	0	0	0	0	0
<i>Urtica dioica</i>	Urticaceae	0	0	0	0	0	0
<i>Alliaria petiolata</i> *	Brassicaceae**	.	0	.	.	0	0
<i>Arctium lappa</i> *	Asteraceae	.	0	0	.	0	0
<i>Arctium minus</i> *	Asteraceae	.	0	0	0	0	0
<i>Artemisia vulgaris</i>	Asteraceae (Asteroideae)**	.	0	.	.	.	0
<i>Carduus crispus</i> *	Asteraceae	.	0	.	0	0	0
<i>Chenopodium bonus-henricus</i> *	Amaranthaceae**	.	0	0	0	0	0
<i>Cirsium vulgare</i> *	Asteraceae	.	0	.	0	0	0

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<i>Echium vulgare</i> *	Boraginaceae	.	0	0	0	0	0
<i>Lapsana communis</i> *	Asteraceae	.	0	0	0	0	0
<i>Malva moschata</i> *	Malvaceae	.	0
<i>Melilotus officinalis</i> *	Fabaceae	.	0	.	.	.	0
<i>Nepeta cataria</i> *	Lamiaceae	.	0	.	0	0	0
<i>Picris hieracioides</i> *	Asteraceae (Cichorioideae)**	.	0	0	0	0	0
<i>Saponaria officinalis</i>	Caryophyllaceae**	.	0	0	.	0	0
<i>Verbena officinalis</i> *	Verbenaceae	.	0	0	0	0	0
<i>Veronica serpyllifolia</i> *	Plantaginaceae	.	0	.	0	0	.
<i>Ballota nigra</i> *	Lamiaceae	.	.	0	0	0	0
<i>Barbarea vulgaris</i> *	Brassicaceae**	.	.	.	0	0	0
<i>Dipsacus fullonum</i> *	Caprifoliaceae	.	.	.	0	0	0
<i>Cichorium intybus</i> *	Asteraceae (Cichorioideae)**	0	0
<i>Potentilla reptans</i> *	Rosaceae	0	0
<i>Reseda lutea</i> *	Resedaceae	0	0
<i>Bunias orientalis</i> *	Brassicaceae**	0
<i>Cardaria draba</i> *	Brassicaceae**	0
<i>Leonurus cardiaca</i> *	Lamiaceae	0
<i>Marrubium vulgare</i> *	Lamiaceae	0
<i>Muscari comosum</i> *	Liliaceae	0
ANNUALS							
<i>Atriplex patula</i> *	Amaranthaceae**	0	0	0	0	0	0
<i>Bidens cernua</i>	Asteraceae (Asteroideae)**	0	0	0	0	0	0

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<i>Centaurea cyanus</i>	Asteraceae	0/.	0	0	0	.	0
<i>Cerastium arvense</i>	Caryophyllaceae**	0	.	.	0	.	0
<i>Chenopodium album*</i>	Amaranthaceae**	0	0	0	0	0	0
<i>Euphorbia peplus*</i>	Euphorbiaceae	0	.	.	.	0	0
<i>Fallopia convolvulus</i>	Polygonaceae	0/.	0	0	0	0	0
<i>Galeopsis tetrahit*</i>	Lamiaceae	0	0	0	0	0	0
<i>Persicaria hydropiper*</i>	Polygonaceae	0	0	0	0	0	0
<i>Persicaria lapathifolia*</i>	Polygonaceae	0	0	0	0	0	0
<i>Persicaria maculosa</i>	Polygonaceae	0/.	0	0	0	0	0
<i>Persicaria minor*</i>	Polygonaceae	0	0	0	0	0	0
<i>Persicaria mitis*</i>	Polygonaceae	0	0	.	0	0	0
<i>Polygonum aviculare</i>	Polygonaceae	0/.	0	0	0	0	0
<i>Rumex maritimus (other)*</i>	Polygonaceae	0	.	.	0	0	0
<i>Stellaria media (other)</i>	Caryophyllaceae**	0	0	0	0	0	0
<i>Viola arvensis</i>	Violaceae	0	0	0	0	0	0
<i>Aethusa cynapium*</i>	Apiaceae**	.	0	0	0	0	0
<i>Agrostemma githago</i>	Caryophyllaceae**	.	0	0	0	0	0
<i>Anagallis arvensis*</i>	Primulaceae	.	0	0	0	0	0
<i>Aphanes arvensis*</i>	Rosaceae	.	0	.	0	0	0
<i>Arabidopsis thaliana*</i>	Brassicaceae**	.	0
<i>Arenaria serpyllifolia</i>	Caryophyllaceae**	.	0	0	0	0	0
<i>Avena fatua</i>	Poaceae**	.	0	0	0	0	0
<i>Bromus arvensis</i>	Poaceae**	.	0	0	0	0	0

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<i>Bromus secalinus</i>	Poaceae**	.	0	0	0	0	0
<i>Bromus sterilis</i>	Poaceae**	.	0	0	0	0	0
<i>Capsella bursa-pastoris*</i>	Brassicaceae**	.	0	0	0	0	0
<i>Chenopodium ficifolium*</i>	Amaranthaceae**	.	0	0	0	0	0
<i>Chenopodium polyspermum*</i>	Amaranthaceae**	.	0	0	0	0	0
<i>Convolvulus arvensis*</i>	Convolvulaceae	.	0	0	0	0	0
<i>Descurainia sophia*</i>	Brassicaceae**	.	0	.	0	0	0
<i>Digitaria ischaemum*</i>	Poaceae**	.	0	0	0	0	0
<i>Echinochloa crus-galli*</i>	Poaceae**	.	0	0	0	0	0
<i>Fumaria officinalis*</i>	Papaveraceae	.	0	0	0	0	0
<i>Galium aparine*</i>	Rubiaceae	.	0	0	0	0	0
<i>Galium spurium*</i>	Rubiaceae	.	0	0	0	0	0
<i>Geranium dissectum*</i>	Geraniaceae	.	0	0	.	0	0
<i>Hordeum murinum</i>	Poaceae**	.	0	.	0	.	0
<i>Hyoscyamus niger*</i>	Solanaceae	.	0	0	0	0	0
<i>Lamium purpureum*</i>	Lamiaceae	.	0	0	0	0	0
<i>Lithospermum arvense*</i>	Boraginaceae	.	0	0	0	0	0
<i>Lolium temulentum*</i>	Poaceae**	.	0	0	0	0	0
<i>Malva pusilla*</i>	Malvaceae	.	0	0	0	0	0
<i>Matricaria recutita</i>	Asteraceae (Asteroideae)**	.	0	.	.	0	0
<i>Myosotis arvensis*</i>	Boraginaceae	.	0	0	0	0	0
<i>Papaver argemone*</i>	Papaveraceae	.	0	0	0	0	0
<i>Papaver rhoeas*</i>	Papaveraceae	.	0	0	0	0	0

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<i>Raphanus raphanistrum</i> *	Brassicaceae**	.	0	0	0	0	0
<i>Reseda luteola</i> *	Resedaceae	.	0	.	.	0	0
<i>Scleranthus annuus</i>	Caryophyllaceae**	.	0	0	0	0	0
<i>Setaria pumila</i> *	Poaceae**	.	0		0	0	0
<i>Setaria viridis</i> *	Poaceae**	.	0	0	0	0	0
<i>Silene latifolia</i>	Caryophyllaceae**	.	0	0	0	0	0
<i>Sinapis arvensis</i>	Brassicaceae**	.	0	0	0	0	0
<i>Sisymbrium officinale</i> *	Brassicaceae**	.	0	0	0	0	0
<i>Solanum nigrum</i> *	Solanaceae	.	0	0	0	0	0
<i>Sonchus oleraceus</i> *	Asteraceae (Cichorioideae)**	.	0	0	0	0	0
<i>Spergula arvensis</i> *	Caryophyllaceae**	.	0	0	0	0	0
<i>Thlaspi arvense</i> *	Brassicaceae	.	0	0	0	0	0
<i>Torilis japonica</i>	Apiaceae**	.	0	0	0	0	0
<i>Trifolium arvense</i>	Fabaceae	.	0	0	0	0	0
<i>Urtica urens</i>	Urticaceae	.	0	0	0	0	0
<i>Valerianella dentata</i>	Caprifoliaceae	.	0	0	0	0	0
<i>Valerianella locusta</i>	Caprifoliaceae	.	0	0	0	0	0
<i>Veronica hederifolia</i>	Plantaginaceae	.	0	0	0	0	0
<i>Vicia hirsuta</i>	Fabaceae	.	0	0	0	0	0
<i>Vicia tetrasperma</i>	Fabaceae	.	0	0	0	0	0
<i>Adonis aestivalis</i>	Ranunculaceae***	.	.	0	.	.	0
<i>Anchusa arvensis</i>	Boraginaceae	.	.	0	.	0	0
<i>Anthemis arvensis</i> *	Asteraceae (Asteroideae)**	.	.	0	0	0	0
<i>Bromus tectorum</i>	Poaceae**	.	.	0	0	0	0
<i>Conringia orientalis</i> *	Brassicaceae**	.	.	0	.	.	0
<i>Datura stramonium</i> *	Solanaceae	.	.	0	.	.	0

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<i>Erodium cicutarium</i> *	Geraniaceae	.	.	0	0	0	0
<i>Euphorbia helioscopia</i> *	Euphorbiaceae	.	.	0	0	0	0
<i>Euphorbia platyphyllos</i> *	Euphorbiaceae	.	.	0	.	.	0
<i>Geranium columbinum</i> *	Geraniaceae	.	.	0	.	.	.
<i>Geranium pusillum</i> *	Geraniaceae	.	.	0	.	0	0
<i>Heliotropium europaeum</i> *	Boraginaceae	.	.	0	.	.	0
<i>Mercurialis annua</i> *	Euphorbiaceae	.	.	0	.	0	0
<i>Orlaya grandiflora</i>	Apiaceae**	.	.	0	.	0	0
<i>Rapistrum perenne</i> *	Brassicaceae**	.	.	0	.	.	.
<i>Anthemis cotula</i>	Asteraceae (Asteroideae)**	.	.	.	0	0	0
<i>Digitaria sanguinalis</i> *	Poaceae**	.	.	.	0	0	0
<i>Euphorbia exigua</i> *	Euphorbiaceae	.	.	.	0	0	0
<i>Fumaria vaillantii</i> *	Papaveraceae	.	.	.	0	.	0
<i>Lamium amplexicaule</i> *	Lamiaceae	.	.	.	0	0	0
<i>Malva neglecta</i> *	Malvaceae	.	.	.	0	.	0
<i>Odontites vulgaris</i> *	Orobanchaceae	.	.	.	0	0	0
<i>Odontites verna</i> *	Orobanchaceae	.	.	.	0	0	0
<i>Plantago arenaria</i> *	Plantaginaceae	.	.	.	0	.	.
<i>Poa annua</i> *	Poaceae**	.	.	.	0	0	0
<i>Ranunculus arvensis</i>	Ranunculaceae**	.	.	.	0	0	0
<i>Tripleurospermum perforatum</i> *	Asteraceae (Asteroideae)**	.	.	.	0	0	0
<i>Vicia villosa</i>	Fabaceae	.	.	.	0	0	0
<i>Anchusa officinalis</i> *	Boraginaceae	0	0

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<i>Barbarea intermedia*</i>	Brassicaceae**	0	.
<i>Legousia speculum-veneris*</i>	Campanulaceae**	0	0
<i>Lepidium campestre*</i>	Brassicaceae**	0	0
<i>Lepidium ruderale*</i>	Brassicaceae**	0	0
<i>Neslia paniculata*</i>	Brassicaceae**	0	0
<i>Nigella arvensis</i>	Ranunculaceae**	0	0
<i>Portulaca oleracea*</i>	Portulacaceae	0	0
<i>Silene noctiflora other</i>	Caryophyllaceae**	0	0
<i>Xanthium strumarium</i>	Asteraceae (Asteroideae)**	0	0
<i>Cerinthe minor*</i>	Boraginaceae	0
<i>Cynoglossum officinale*</i>	Boraginaceae	0
<i>Elsholtzia ciliata*</i>	Lamiaceae	0
GRASSES			NL	BA	IA	RP	MA
<i>Anthoxanthum odoratum*</i>	Poaceae**		0	.	0	0	0
<i>Bromus hordeaceus</i>	Poaceae**		0	0	0	0	0
<i>Festuca rubra/ovina*</i>	Poaceae**		0	0	0	0	0
<i>Lolium perenne*</i>	Poaceae**		0	.	0	0	0
<i>Molinia caerulea*</i>	Poaceae**		0	.	.	0	0
<i>Phleum pratense*</i>	Poaceae**		0	0.	0	0	.
<i>Poa pratensis*</i>	Poaceae**		0	0	0	0	0
<i>Poa trivialis*</i>	Poaceae**		0	0	0	0	0
<i>Holcus lanatus*</i>	Poaceae**		.	0	0	0	0
<i>Cynosurus cristatus*</i>	Poaceae**		.	.	0	0	0
<i>Dactylis glomerata*</i>	Poaceae**		.	.	0	0	0

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<i>Helictotrichon pratensis*</i>	Poaceae**	.	.	0	.	.
<i>Briza media*</i>	Poaceae**	.	.	.	0	.
<i>Bromus erectus</i>	Poaceae**	.	.	.	0	0
<i>Festuca pratensis*</i>	Poaceae**	.	.	.	0	0
<i>Holcus mollis*</i>	Poaceae**	.	.	.	0	.
<i>Alopecurus pratensis*</i>	Poaceae**	0
<i>Arrhenatherum elatius*</i>	Poaceae**	0
<i>Trisetum flavescens*</i>	Poaceae**	0
OTHER HERBS						
<i>Achillea millefolium</i>	Asteraceae (Asteroideae)**	0	.	0	0	0
<i>Cerastium holosteoides*</i>	Caryophyllaceae**	0	0	0	0	0
<i>Daucus carota</i>	Apiaceae**	0	0	0	0	0
<i>Heracleum sphondylium</i>	Apiaceae**	0	.	.	0	0
<i>Knautia arvensis</i>	Caprifoliaceae	0	.	0	0	0
<i>Leontodon cf. autumnalis*</i>	Asteraceae (Cichorioideae)**	0	.	.	0	0
<i>Leucanthemum vulgare*</i>	Asteraceae (Asteroideae)**	0	.	0	0	0
<i>Lychnis flos-cuculi*</i>	Caryophyllaceae**	0	0	0	0	0
<i>Pastinaca sativa*</i>	Apiaceae**	0	0	.	0	0
<i>Prunella vulgaris*</i>	Lamiaceae	0	0	0	0	0
<i>Ranunculus acris</i>	Ranunculaceae**	0	0	0	0	0
<i>Rumex cf. acetosa</i>	Polygonaceae	0	0	.	0	0
<i>Silaum silaus</i>	Apiaceae**	0	.	.	0	0
<i>Stellaria graminea</i>	Caryophyllaceae**	0	0	0	0	0
<i>Trifolium dubium*</i>	Fabaceae	0	.	0	0	.
<i>Trifolium repens</i>	Fabaceae	0	0	0	0	0
<i>Galium mollugo</i>	Rubiaceae	.	0	0	0	0

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<i>Lathyrus pratensis</i>	Fabaceae	.	0	.	.	.
<i>Linum catharticum</i>	Linaceae	.	0	0	0	0
<i>Medicago lupulina</i> *	Fabaceae	.	0	0	0	0
<i>Pimpinella saxifraga</i> (major)*	Apiaceae**	.	0	.	0	.
<i>Ranunculus bulbosus</i> (other)	Ranunculaceae**	.	0	.	0	0
<i>Scabiosa columbaria</i>	Caprifoliaceae	.	0	.	0	0
<i>Caltha palustris</i>	Ranunculaceae**	.	.	0	0	0
<i>Centaurea jacea</i> (other)	Asteraceae	.	.	0	0	.
<i>Hypochaeris radicata</i> *	Asteraceae (Cichorioideae)**	.	.	0	0	0
<i>Pimpinella major</i>	Apiaceae**	.	.	0	.	0
<i>Succisa pratensis</i>	Caprifoliaceae	.	.	0	.	.
<i>Trifolium campestre</i> (other)	Fabaceae	.	.	0	0	0
<i>Trifolium pratense</i>	Fabaceae	.	.	0	0	0
<i>Veronica chamaedrys</i> *	Plantaginaceae	.	.	0	0	.
<i>Anthriscus sylvestris</i>	Apiaceae**	.	.	.	0	0
<i>Carum carvi</i>	Apiaceae**	.	.	.	0	0
<i>Galium verum</i> *	Rubiaceae	.	.	.	0	0
<i>Salvia pratensis</i> *	Lamiaceae	.	.	.	0	.
<i>Senecio jacobaea</i>	Asteraceae (Asteroideae)**	.	.	.	0	0
<i>Tragopogon pratensis</i> *	Asteraceae (Cichorioideae)**	.	.	.	0	.
<i>Bellis perennis</i> *	Asteraceae (Asteroideae)**	0
ADVENTIVES						
<i>Ambrosia</i>	Asteraceae (Asteroideae)**					T
APOPHYTHES						
<i>Rumex obtusifolius</i>	Polygonaceae					H

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Melampyrum (pratense)	Orobanchaceae	T
<i>Pteridium aquilinum</i>	Dennstaedtiaceae	G
<i>Polypodium vulgare</i>	Polypodiaceae	Ch
<i>Calluna vulgaris</i>	Ericaceae	Ch
<i>Juniperus</i> -type	Cupressaceae	P

FAMILY (SUBFAMILY)

Poaceae**

Cyperaceae**

Caryophyllaceae**

Brassicaceae**

Ranunculaceae**

Apiaceae**

Chenopodiaceae / Amaranthaceae**

Campanulaceae**

H

Asteraceae (Asteroideae)**

Asteraceae (Cichorioideae)**

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Supplementary Information 2

ESM 2 Pollen taxonomy used in this study, based on the list of accepted pollen types (HL0) and the taxonomic harmonization in two hierarchical levels (HL1 and HL2) of the European Pollen Database (EPD; Giesecke et al. 2019). The first two columns refer to the names of the pollen types used in this study and include synonyms, but do not constitute the EPD accepted names. (*) pollen types that were not included as anthropogenic pollen indicators in the simulated datasets at that level. The indicative capacity categories were taken from (Chytrý et al. 2008; di Castri et al. 1990; Lang 1994; Söukand and Kalle 2015).

Indicative capacity in Var.	Var. (Pollen type synonyms)	HL0 (accepted EPD names)	HL1	HL2	Family
PI ¹ , Car	<i>Avena</i> -type	<i>Avena</i> -type (PI)	Cerealia-type (PI)	Poaceae (SI, APO)	Poaceae
PI ¹ , Car	Cerealia-type	Cerealia-type (PI)			
PI ¹ , Car	<i>Hordeum/Triticum</i>				
PI ¹ , Car	<i>Hordeum</i> -type	<i>Hordeum</i> -type (PI)			
	<i>Agropyron</i> -type*				
	<i>Glyceria</i> -type*				
PI ¹ , Car	<i>Secale cereale</i>	<i>Secale cereale</i> (PI)			
PI ¹ , Car	<i>Triticum</i> -type	<i>Triticum</i> -type (PI)			
PI ¹ , Car	<i>Zea mays</i>	<i>Zea mays</i> (PI)			
	<i>Lygeum spartum</i> *	<i>Lygeum spartum</i> *			
	Poaceae*	Poaceae	Poaceae (SI, APO)		
	<i>Hordelymus</i> *	(SI, APO)			
SI, Gr, ADV	<i>Bromus</i>				
	<i>Linum</i> *	<i>Linum</i> *	<i>Linum</i> *	<i>Linum</i> (SI, APO)	Linaceae
SI, APO, Hb	<i>Linum catharticum</i>	<i>Linum catharticum</i> (SI)	<i>Linum catharticum</i> -type (SI, APO)		
SI, APO, Hb	<i>Linum catharticum</i> -type	<i>Linum catharticum</i> -type (SI)			
	<i>Linum austriacum</i> -type*	<i>Linum austriacum</i> -type*			
	<i>Linum usitatissimum</i> /L. <i>bienne</i> *	<i>Linum usitatissimum</i> /L. <i>bienne</i> (PI)	<i>Linum usitatissimum</i> /L. <i>bienne</i> (PI)		
PI ¹ , Oil-f	<i>Linum usitatissimum</i> -type				
PI ¹ , Car	<i>Fagopyrum</i>	<i>Fagopyrum</i> (PI)	<i>Fagopyrum</i> (PI)	<i>Fagopyrum</i> (PI)	Polygonaceae
PI ¹ , Pro	<i>Vicia faba</i>	<i>Vicia faba</i> (PI)	<i>Vicia</i> -type (PI)		Fabaceae

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	<i>Vicia</i> -type*	<i>Vicia</i> -type		<i>Lathyrus</i> / <i>Vicia</i> -type (SI, APO)	
	<i>Vicia cracca</i> -type*				
PI ¹ , Pro	<i>Pisum sativum</i>	<i>Pisum sativum</i> (PI)			
	<i>Lathyrus/Vicia</i> -type*	<i>Lathyrus/Vicia</i> -type*	<i>Lathyrus/Vicia</i> -type*		
	<i>Humulus lupulus</i> *	<i>Humulus lupulus</i> *	<i>Cannabis/Humulus</i>	<i>Cannabis/Humulus</i> (SI, APO)	Cannabaceae
PI ¹ , Oil-f	<i>Cannabis sativa</i>	<i>Cannabis sativa</i> (PI)	(SI, APO)	(SI, APO)	
	<i>Cannabis/Humulus</i> *	<i>Cannabis/Humulus</i> *			
SI, ADV-An	<i>Centaurea cyanus</i> -type	<i>Centaurea cyanus</i> -type (SI, ADV)	<i>Centaurea cyanus</i> -type (SI, APO)	<i>Centaurea cyanus</i> -type (SI, APO)	Asteraceae
	<i>Centaurea montana</i> -type*	<i>Centaurea montana</i> -type*			
	<i>Polygonum</i> -type (tricolporate)*	<i>Polygonum</i> -type (tricolporate)*	<i>Polygonum</i> -type (tricolporate)*	<i>Polygonum</i> -type (tricolporate) (SI, APO)	Polygonaceae
	<i>Polygonum</i> -type*				
SI, ADV-An	<i>Polygonum aviculare</i> -type	<i>Polygonum aviculare</i> -type (SI, ADV)	<i>Polygonum aviculare</i> -type (SI, ADV)		
	<i>Bistorta officinalis</i> -type*	<i>Bistorta officinalis</i> -type*	<i>Bistorta officinalis</i> -type*		
	<i>Bistorta</i> -type*				
	<i>Bistorta vivipara</i> *	<i>Bistorta vivipara</i> *			
SI, ADV-An	<i>Fallopia</i>	<i>Fallopia</i> (SI, ADV)	<i>Fallopia</i> (SI, ADV)		
	Polygonaceae*	Polygonaceae*	Polygonaceae*	Polygonaceae*	
SI, NEO-An, ADV	<i>Spergula</i> -type*	<i>Spergula</i> -type (SI, ADV)	<i>Spergula</i> -type (SI, ADV)	<i>Spergula</i> -type (SI, ADV)	Caryophyllaceae
SI, NEO-An, ADV	<i>Spergula arvensis</i> -type				
	<i>Cerastium</i> -type*	<i>Cerastium</i> -type (SI, APO)	<i>Cerastium</i> -type (SI, APO)	Caryophyllaceae (periporate excl. Paronychioideae) (SI, APO)	
SI, APO-An	<i>Cerastium arvense</i> (SI, APO)				
	<i>Cerastium cerastioides</i> -type*				
	<i>Cerastium fontanum</i> *				

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	<i>Stellaria</i> cf. <i>S. holostea</i> *				
	Caryophyllaceae*	Caryophyllaceae (periporate excl. Paronychioideae)*	Caryophyllaceae (periporate excl. Paronychioideae)*		
	Caryophyllaceae (periporate excl. Paronychioideae)*				
	Caryophyllaceae undifferentiated*				
	Caryophyllaceae subfam. Silenoideae-type*				
	<i>Sagina</i> *	<i>Sagina</i> *	<i>Sagina</i> *		
SI, ADV	<i>Scleranthus</i> (SI, ADV)	<i>Scleranthus</i> (SI, ADV)	<i>Scleranthus</i> (SI, ADV)		
	<i>Silene dioica</i> -type*	<i>Silene dioica</i> -type*	<i>Silene</i> -type (SI, APO)		
	<i>Silene vulgaris</i> -type*	<i>Silene vulgaris</i> -type*			
	<i>Silene</i> -type*	<i>Silene</i> -type (SI, APO)			
	<i>Silene viscaria</i> -type*				
SI, ADV, NEO-An	<i>Arenaria</i> (SI, ADV)				
SI, APO, NEO-BiP,	<i>Saponaria</i> (SI, APO)	<i>Saponaria</i> (SI, APO)			
	<i>Stellaria holostea</i> *	<i>Stellaria holostea</i> *	<i>Stellaria holostea</i> *		
	<i>Gypsophila repens</i> -type*	<i>Gypsophila repens</i> -type*	<i>Gypsophila repens</i> -type*		
	<i>Gypsophila arrostii</i> *				
SI, ADV, NEO-An	<i>Agrostemma githago</i>	<i>Agrostemma githago</i> (SI, ADV)	<i>Agrostemma githago</i> (SI, ADV)		
	<i>Dianthus/ Petrorhaghia</i> *	<i>Dianthus/ Petrorhaghia</i> *	<i>Dianthus/ Petrorhaghia</i> *		
	<i>Dianthus</i> -type*				
	<i>Dianthus superbus</i> -type*				
	<i>Moehringia</i> -type*	<i>Moehringia</i> -type*	<i>Moehringia</i> -type*		

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	<i>Minuartia</i> -type*				
	<i>Corrigiola litoralis</i> *	<i>Corrigiola litoralis</i> *	<i>Corrigiola litoralis</i> *	<i>Corrigiola litoralis</i> *	
	<i>Herniaria</i> *	<i>Herniaria</i> *	<i>Herniaria</i> *	Caryophyllaceae subfam. Paronychioideae*	
	<i>Herniaria</i> -type*	<i>Herniaria</i> -type*			
	<i>Herniaria glabra</i> -type*	<i>Herniaria glabra</i> -type*			
	<i>Paronychia</i> *	<i>Paronychia</i> *	<i>Paronychia</i> *		
SI, APO, Hb	<i>Rumex acetosa</i> -type	<i>Rumex acetosa</i> -type	<i>Rumex acetosa</i> -type	Rumex/Oxyria (SI, APO)	Polygonaceae
SI, Hb, APO-BiP	<i>Rumex acetosa</i> / <i>R. acetosella</i> -type	(SI, APO)	(SI, APO)		
SI, APO- BiP	<i>Rumex acetosella</i> -type	<i>Rumex acetosella</i> -type (SI, APO)	<i>Rumex acetosella</i> -type (SI, APO)		
SI, APO- BiP	<i>Rumex acetosella</i>				
	<i>Rumex crispus</i> -type*	<i>Rumex obtusifolius</i> -type (SI, APO)	<i>Rumex obtusifolius</i> -type (SI, APO)		
SI, APO	<i>Rumex obtusifolius</i> -type				
	<i>Rumex/Oxyria</i> *	<i>Rumex/Oxyria</i> *	<i>Rumex/Oxyria</i> *		
	<i>Rumex</i> *				
	<i>Rumex scutatus</i> -type*				
	<i>Rumex alpinus</i> -type*	<i>Rumex alpinus</i> -type*	<i>Rumex alpinus</i> -type*		
	<i>Polygonum</i> (pericolpate/ periporate)*	<i>Polygonum</i> (pericolpate/ periporate)*	<i>Polygonum</i> (pericolpate/ periporate)*	<i>Polygonum</i> (pericolpate/ periporate) (SI, APO)	
SI, ADV-An	<i>Polygonum persicaria</i> -type	<i>Persicaria maculosa</i> -type (SI, ADV)	<i>Persicaria maculosa</i> -type (SI, ADV)		
SI, ADV-An	<i>Persicaria maculosa</i> -type				
	<i>Hornungia</i> -type*	<i>Hornungia</i> -type*	Brassicaceae (SI, APO)	Brassicaceae (SI, APO)	Brassicaceae
	<i>Matthiola</i> *	<i>Matthiola</i> *			
SI, APO	<i>Sinapis</i>	<i>Draba</i> -type			
	<i>Draba</i> -type*	(SI, APO)			
	<i>Cardamine</i> *				
	Brassicaceae*	Brassicaceae			
	Asteraceae subf. Asteroideae*	Asteraceae subf. Asteroideae*	Asteraceae subf. Asteroideae*	Asteraceae subf. Asteroideae	Asteraceae

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SI, ADV, NEO-An	<i>Matricaria</i> -type	<i>Matricaria</i> -type (SI, APO)	<i>Matricaria</i> -type (SI, APO)	(SI, APO)	
SI, APO, Gr	<i>Achillea</i> -type				
SI, APO	<i>Anthemis</i> -type				
	<i>Aster</i> -type*	<i>Aster</i> -type (SI, APO)	<i>Senecio</i> -type (SI, APO)		
	<i>Solidago</i> *				
SI, APO, Hb	<i>Bellis</i>				
	<i>Eupatorium</i> *				
SI, APO-An	<i>Bidens</i> -type	<i>Bidens</i> -type (SI, APO)			
	<i>Arnica montana</i> *				
SI, APO, Gr	<i>Senecio</i> -type	<i>Senecio</i> -type (SI, APO)			
	<i>Filago</i> -type*				
	<i>Gnaphalium</i> -type*				
SI, APO	<i>Erigeron</i>	<i>Gnaphalium</i> -type (SI, APO)			
	<i>Calendula</i> *				
	<i>Tussilago</i> -type*	<i>Calendula</i> *			
	<i>Petasites</i> *	<i>Tussilago</i> -type*			
	<i>Homogyne</i> -type*	<i>Petasites</i> *			
	<i>Ambrosia</i> / <i>Xanthium</i> *	<i>Ambrosia</i> / <i>Xanthium</i> *	<i>Ambrosia</i> / <i>Xanthium</i> (SI, APO)	<i>Ambrosia</i> / <i>Xanthium</i> (SI, APO)	
	<i>Xanthium</i> *				
	<i>Xanthium spinosum</i> -type*				
SI, APO	<i>Ambrosia</i>	<i>Ambrosia</i> (SI, APO)			
	Asteraceae subf. Cichorioideae*	Asteraceae subf. Cichorioideae*	Asteraceae subf. Cichorioideae (SI, APO)	Asteraceae subf. Cichorioideae (SI, APO)	
	<i>Scorzonera</i> -type*				
	<i>Scorzonera humilis</i> -type*	<i>Scorzonera humilis</i> -type*			
	<i>Trifolium</i> -type*	<i>Trifolium</i> -type*	<i>Trifolium</i> -type (SI, APO)	<i>Trifolium</i> -type (SI, APO)	Fabaceae
SI, APO, Hb	<i>Trifolium pratense</i> -type				
SI, APO, Hb	<i>Trifolium repens</i> -type				

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	<i>Trifolium alpestre</i> -type*	<i>Trifolium alpestre</i> -type*			
	<i>Trifolium badium</i> -type*	<i>Trifolium badium</i> -type*			
	<i>Trifolium alpinum</i> -type*	<i>Trifolium alpinum</i> -type*			
	Ranunculaceae *	Ranunculaceae *	Ranunculaceae *	Ranunculaceae *	Ranunculaceae
SI, APO, Hb	<i>Ranunculus acris</i> -type	<i>Ranunculus acris</i> -type (SI, APO)	<i>Ranunculus acris</i> -type (SI, APO)	Ranunculus-type (SI, APO)	
	<i>Ranunculus</i> -type*	<i>Ranunculus</i> -type*	<i>Ranunculus</i> -type*		
	<i>Anemone</i> / <i>Hepatica</i> *				
	<i>Anemone</i> / <i>Pulsatilla</i> *				
	<i>Clematis</i> *	<i>Clematis</i> *	<i>Clematis</i> *		
	<i>Ranunculus lingua</i> *	<i>Ranunculus lingua</i> *	<i>Ranunculus lingua</i> *		
	<i>Anemone nemorosa</i> -type*	<i>Anemone nemorosa</i> -type*	<i>Anemone nemorosa</i> -type*		
	<i>Anemone hortensis</i> -type*	<i>Anemone</i> -type*			
	<i>Ranunculus</i> sect. <i>Batrachium</i> *	<i>Ranunculus aquatilis</i> -type*	<i>Ranunculus aquatilis</i> -type*		
	<i>Aconitum</i> *	<i>Aconitum</i> *	<i>Aconitum</i> *		
SI, APO	<i>Adonis</i>	<i>Adonis</i> (SI, APO)	<i>Adonis</i> (SI, APO)	<i>Adonis</i> (SI, APO)	
SI, APO	<i>Caltha</i> -type	<i>Caltha</i> -type (SI, APO)	<i>Caltha</i> -type (SI, APO)	<i>Caltha</i> -type (SI, APO)	
SI, ADV, NEO-An	<i>Nigella</i>	<i>Nigella</i> (SI, ADV)	<i>Nigella</i> (SI, ADV)	<i>Nigella</i> (SI, ADV)	
	<i>Delphinium</i> -type*	<i>Consolida</i> -type*	<i>Consolida</i> -type*	<i>Consolida</i> -type*	
	<i>Consolida</i> -type*				
	<i>Helleborus viridis</i> -type*	<i>Helleborus viridis</i> -type*	<i>Helleborus viridis</i> -type*	<i>Helleborus viridis</i> -type*	
	<i>Thalictrum</i> *	<i>Thalictrum</i> *	<i>Thalictrum</i> *	<i>Thalictrum</i> *	
SI, APO	<i>Ranunculus arvensis</i> -type	<i>Ranunculus arvensis</i> -type (SI, APO)	<i>Ranunculus arvensis</i> -type (SI, APO)	<i>Ranunculus arvensis</i> -type (SI, APO)	
	<i>Trollius europaeus</i> *	<i>Trollius europaeus</i> *	<i>Trollius europaeus</i> *	<i>Trollius europaeus</i> *	

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	<i>Plantago</i> *	<i>Plantago</i> *	<i>Plantago</i> *	Plantago (SI, APO)	Plantaginaceae	
	<i>Plantago</i> undifferentiated*					
SI, ADV, PO-BiP	<i>Plantago lanceolata</i> -type	<i>Plantago lanceolata</i> -type (SI, ADV)	<i>Plantago lanceolata</i> -type (SI, ADV)			
SI, ADV- BiP	<i>Plantago major</i>	<i>Plantago major</i> (SI, ADV)	<i>Plantago major</i> - type (SI, ADV)			
SI, ADV- BiP	<i>Plantago major</i> - type	<i>Plantago major</i> - type (SI, ADV)				
SI, ADV- BiP	<i>Plantago major</i> / <i>P. media</i> -type					
SI, ADV- BiP	<i>Plantago media</i>	<i>Plantago media</i> (SI, ADV)				
SI, ADV- BiP	<i>Plantago media</i> - type					
	<i>Plantago maritima</i> -type*	<i>Plantago maritima</i> -type*	<i>Plantago maritima</i> -type*			
	<i>Plantago alpina</i> - type*					
	<i>Plantago tenuiflora</i> *	<i>Plantago tenuiflora</i> *	<i>Plantago tenuiflora</i> *			
	<i>Plantago montana</i> -type*	<i>Plantago atrata</i> - type*	<i>Plantago atrata</i> - type*			
	<i>Plantago atrata</i> - type*					
	<i>Plantago coronopus</i> -type*	<i>Plantago coronopus</i> -type*	<i>Plantago coronopus</i> -type*			
	<i>Cladium mariscus</i> *	<i>Cladium mariscus</i> *	Cyperaceae (SI, APO)	Cyperaceae (SI, APO)	Cyperaceae	
	Cyperaceae*	Cyperaceae*				
	<i>Cyperus</i> *	<i>Cyperus</i> *				
	<i>Rhynchospora</i> *	<i>Rhynchospora</i> *				
	<i>Rhynchospora alba</i> *					
	<i>Apium</i> *	<i>Apium</i> *	<i>Apium</i> *	Apiaceae (SI, APO)	Apiaceae	
	<i>Bupleurum</i> *	<i>Bupleurum</i> *				
SI, APO, Hb	<i>Heracleum</i>	<i>Heracleum</i> (SI, APO)				<i>Heracleum</i> (SI, APO)
SI, APO, Hb	<i>Pimpinella major</i> -type	<i>Pimpinella major</i> -type (SI, APO)				<i>Pimpinella major</i> -type (SI, APO)
	<i>Peucedanum</i> - type*	<i>Peucedanum</i> - type*				<i>Peucedanum</i> - typ

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SI, APO, Hb	<i>Anthriscus sylvestris</i> -type	<i>Anthriscus sylvestris</i> -type (SI, APO)	<i>Anthriscus sylvestris</i> -type (SI, APO)		
	<i>Sanicula europaea</i> *	<i>Sanicula europaea</i> *	<i>Astrantia</i> -type*		
	<i>Astrantia</i> -type*	<i>Astrantia</i> -type*			
	<i>Pleurospermum</i> -type*	<i>Pleurospermum</i> -type*	<i>Pleurospermum</i> -type*		
	<i>Cicuta virosa</i> *	<i>Cicuta virosa</i> *	<i>Cicuta virosa</i> *		
SI, APO, Hb	<i>Daucus</i>	<i>Daucus</i> (SI, APO)	<i>Daucus</i> (SI, APO)		
	<i>Oenanthe</i> *	<i>Oenanthe</i> *	<i>Oenanthe</i> *		
	<i>Eryngium</i> *	<i>Eryngium</i> *	<i>Eryngium</i> *		
	<i>Meum</i> -type*	<i>Meum</i> -type*	<i>Meum</i> -type*		
	<i>Chaerophyllum hirsutum</i> -type	<i>Chaerophyllum hirsutum</i> -type*	<i>Chaerophyllum hirsutum</i> -type*		
	<i>Bupleurum</i> -type*	Apiaceae (SI, APO)	Apiaceae (SI, APO)		
	<i>Daucus</i> -type*				
	<i>Heracleum</i> -type*				
	<i>Apium</i> -type*				
	<i>Chaerophyllum</i> *				
SI, APO, Hb	<i>Carum</i> -type				
	Apiaceae*				
	<i>Smyrniium</i> -type*				
	<i>Ammi</i> -type*				
SI, ADV, NEO-An	<i>Torilis japonica</i>	<i>Torilis japonica</i> (SI, ADV)	<i>Torilis japonica</i> (SI, ADV)		
	<i>Ligusticum mutellina</i> *	<i>Ligusticum mutellina</i> *	<i>Ligusticum mutellina</i> *		
	<i>Seseli</i> -type*	<i>Seseli</i> -type*	<i>Seseli</i> -type*		
	<i>Torilis arvensis</i> *	<i>Torilis arvensis</i> *	<i>Falcaria</i> -type*		
	<i>Torilis arvensis</i> -type*	<i>Falcaria</i> -type*			
	<i>Falcaria</i> -type*				
	<i>Turgenia latifolia</i> *	<i>Turgenia latifolia</i> *	<i>Turgenia latifolia</i> *		
SI, APO	<i>Orlaya</i>	<i>Orlaya</i> (SI, APO)	<i>Orlaya</i> (SI, APO)		
	<i>Sison amomum</i> *	<i>Sison amomum</i> *	<i>Sison amomum</i> *		
	Dipsacoideae*	Dipsacoideae*	Dipsacoideae		Caprifoliaceae

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SI, APO, NEO-BiP	<i>Dipsacus</i> -type	<i>Dipsacus</i> -type (SI, APO)	(SI, APO)	Dipsacoideae (SI, APO)	
SI, APO, Hb	<i>Knautia</i>	<i>Knautia</i> (SI, APO)	<i>Knautia</i> (SI, APO)		
	<i>Scabiosa</i> *	<i>Scabiosa</i> *	<i>Scabiosa</i>		
SI, APO, Hb	<i>Scabiosa columbaria</i> -type	<i>Scabiosa columbaria</i> -type (SI, APO)	(SI, APO)		
SI, APO, Hb	<i>Succisa</i> -type	<i>Succisa</i> -type (SI, APO)	<i>Succisa</i> -type (SI, APO)		
	Campanulaceae*	Campanulaceae*	Campanulaceae (SI, APO)	Campanulaceae (SI, APO)	Campanulaceae
SI, APO	<i>Jasione montana</i> -type	<i>Jasione montana</i> -type (SI, APO)			
	<i>Campanula/Phyteuma</i> *	<i>Campanula/Phyteuma</i> *	<i>Campanula/Phyteuma</i> *		
	<i>Phyteuma</i> -type*				
	<i>Campanula</i> -type*				
	<i>Arbutus</i> *	<i>Arbutus</i> *	<i>Arbutus</i> *	Ericales (tetrads) (SI, APO)	Ericaceae
SI, APO	<i>Calluna vulgaris</i>	<i>Calluna vulgaris</i> (SI, APO)	<i>Calluna vulgaris</i> (SI, APO)		
	Ericales (tetrads)*	Ericales (tetrads)*	Ericales (tetrads) (SI, APO)*		
	<i>Erica</i> *	<i>Erica</i> *			
	<i>Rhododendron</i> *	<i>Rhododendron</i> (SI, APO)*			
	<i>Vaccinium</i> *	<i>Vaccinium</i> *			
	<i>Vaccinium</i> -type*	<i>Vaccinium</i> -type*			
	<i>Erica arborea</i> -type*	<i>Erica arborea</i> -type*			
	<i>Empetrum/Ledum</i> *	<i>Empetrum/Ledum</i> *	<i>Empetrum/Ledum</i> *		
	<i>Juniperus</i> -type*	<i>Juniperus</i> -type*	<i>Juniperus</i> -type (SI, APO)	<i>Juniperus</i> -type (SI, APO)	Cupressaceae
SI, APO	<i>Juniperus communis</i> -type	<i>Juniperus communis</i> -type (SI, APO)			
SI, APO	<i>Melampyrum</i>	<i>Melampyrum</i> (SI, APO)	<i>Melampyrum</i> (SI, APO)	<i>Melampyrum</i> (SI, APO)	Orobanchaceae
SI, APO	<i>Pteridium aquilinum</i>	<i>Pteridium aquilinum</i> (SI, APO)	<i>Pteridium aquilinum</i> (SI, APO)	<i>Pteridium aquilinum</i> (SI, APO)	Dennstaedtiaceae
SI, APO	<i>Polypodium</i>	<i>Polypodium</i>	<i>Polypodium</i>	<i>Polypodium</i>	Polypodiaceae

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		(SI, APO)	(SI, APO)	(SI, APO)	
	<i>Atriplex*</i>	Amaranthaceae (SI, APO)	Amaranthaceae (SI, APO)	Amaranthaceae (SI, APO)	Amaranthaceae
	<i>Salsola-type*</i>				
	Amaranthaceae *				
SI, ADV, NEO	<i>Amaranthus-</i> type				
	<i>Parietaria*</i>	<i>Parietaria*</i>	<i>Parietaria*</i>	Urticaceae/ Moraceae (SI, APO)	Urticaceae/ Moraceae
SI, APO	<i>Urtica</i>	<i>Urtica</i>	<i>Urtica</i>		
SI, APO	<i>Urtica</i> <i>membranacea</i>	(SI, APO)	(SI, APO)		
SI, APO-BiP	<i>Urtica dioica-</i> type	<i>Urtica dioica-</i> type (SI, APO)			
	Urticaceae*	Urticaceae*	Urticaceae*		
	<i>Morus*</i>	<i>Morus*</i>	<i>Morus*</i>		
	<i>Morus alba*</i>	<i>Morus alba*</i>			
	<i>Urtica pilulifera*</i>	<i>Urtica pilulifera*</i>	<i>Urtica pilulifera*</i>		
	Urticaceae/ Moraceae*	Urticaceae/ Moraceae*	Urticaceae/ Moraceae*		
PI ² , Tr	<i>Ficus carica</i>	<i>Ficus carica</i> (PI)	<i>Ficus carica</i> (PI)	<i>Ficus carica</i> (PI)	Moraceae
SI, APO	<i>Artemisia</i>	<i>Artemisia</i> (SI, APO)	<i>Artemisia</i> (SI, APO)	<i>Artemisia</i> (SI, APO)	Asteraceae
	Oleaceae*	Oleaceae (PI)	Oleaceae (PI)	Oleaceae (PI)	Oleaceae
PI ² , NEO-TS	<i>Fraxinus/Phillyr</i> <i>ea</i>				
PI ² , Tr	<i>Olea europaea</i>	<i>Olea europaea</i> (PI)	<i>Olea europaea</i> (PI)	<i>Olea europaea</i> (PI)	
	<i>Juglans*</i>	<i>Juglans</i> (PI)	<i>Juglans</i> (PI)	<i>Juglans</i> (PI)	Juglandaceae
PI ² , Tr	<i>Juglans regia</i>	<i>Juglans regia</i> (PI)			
PI ² , Tr	<i>Castanea sativa</i>	<i>Castanea sativa</i> (PI)	<i>Castanea sativa</i> (PI)	<i>Castanea sativa</i> (PI)	Fagaceae
PI ² , Tr	<i>Vitis</i>	<i>Vitis</i> (PI)	<i>Vitis</i> (PI)	<i>Vitis</i> (PI)	Vitaceae
PI ¹ , NEO-TS	<i>Eucalyptus</i>	<i>Eucalyptus</i> (PI)	Myrtaceae (PI)	Myrtaceae (PI)	Myrtaceae
	Myrtaceae	Myrtaceae*			
	<i>Myrtus</i> <i>communis*</i>				
PI ² , Tr	<i>Pistacia</i>	<i>Pistacia</i> (PI)	<i>Pistacia</i> (PI)	<i>Pistacia</i> (PI)	Anacardiaceae

PI¹ =primary indicators (crops) non-native to Europe; PI² =primary indicators native to Europe. Car = carbohydrate plants; Pro= protein plants; Oil-f= oil and fiber plants; Tr= fruit trees and nuts. SI= secondary indicators (weeds): ADV= adventives; APO= apophytes; NEO= neophytes; BiP= biennials and perennials; An=annuals. Grassland species: Gr=grasses; Hb=other herbs. NEO-TS= cultivated neophytes (trees and shrubs)

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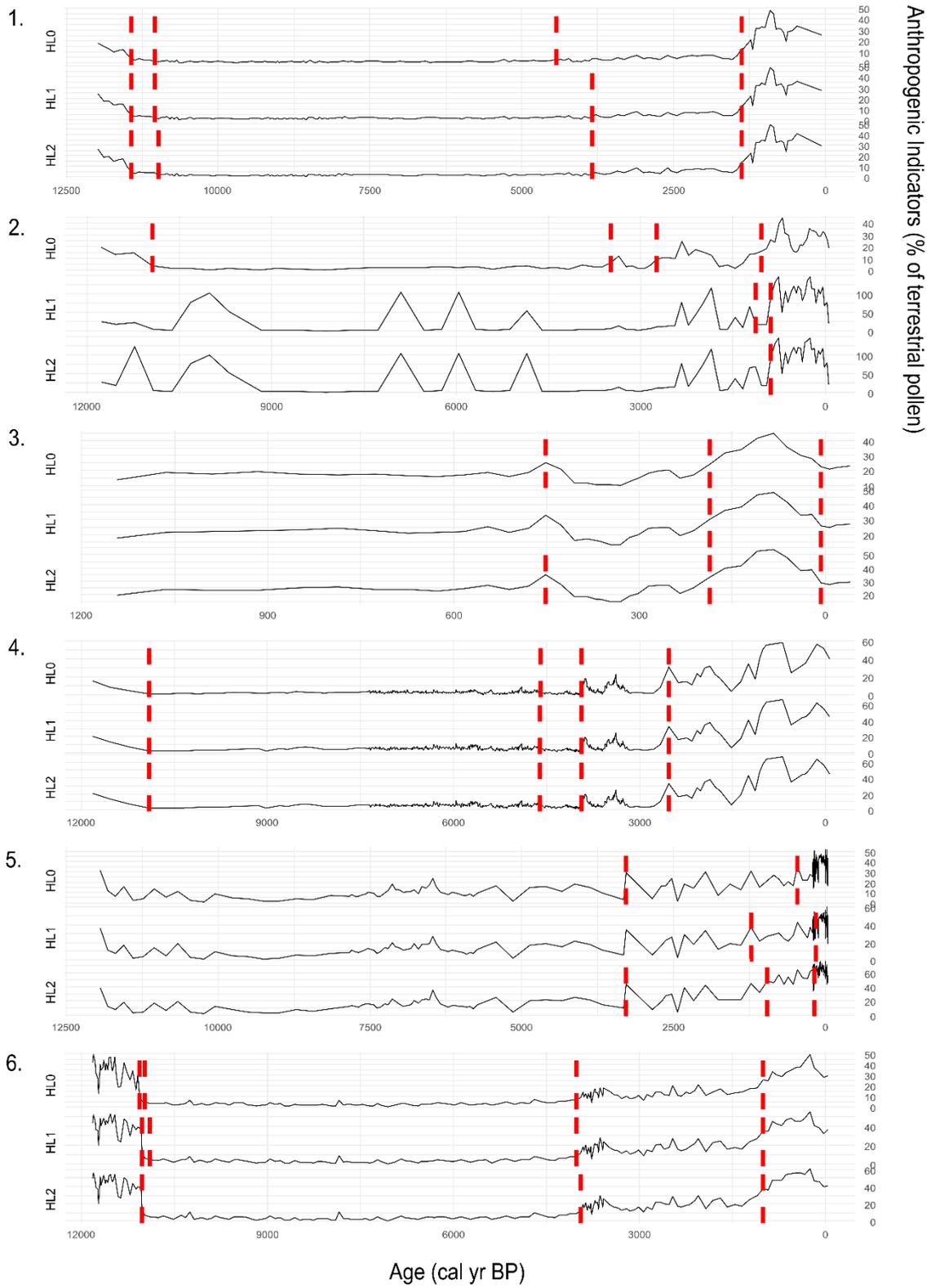
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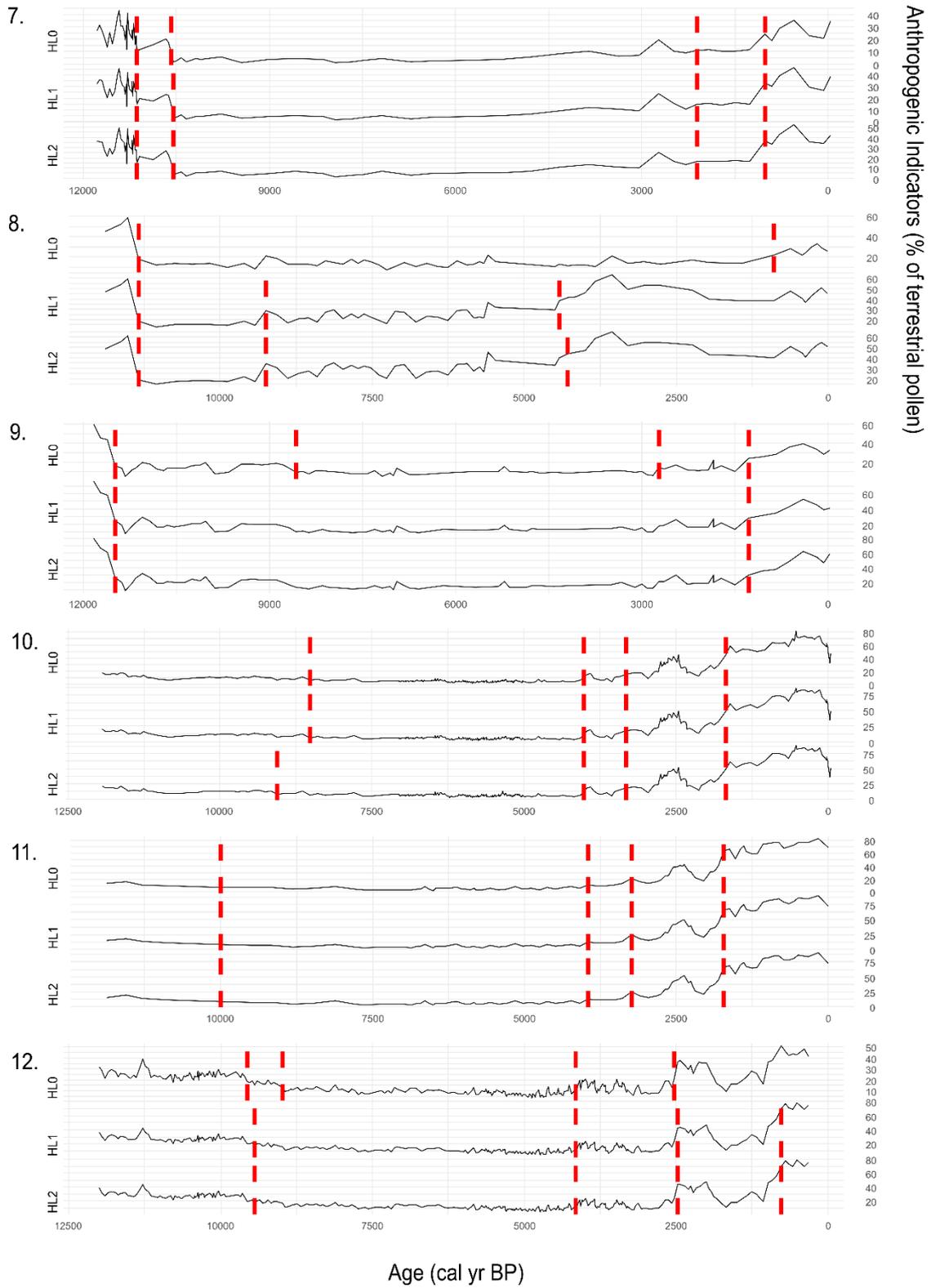
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Supplementary Information 3

ESM 3 Change point analysis of the pollen percentage of human indicators at HL0, HL1 and HL2 for each study site using the binary segmentation approach. 1= Egelsee (Menzingen), 2= Burgäschisee, 3= Soppensee, 4= Moossee, 5= Bachalpsee; 6= Lej da San Murezzan, 7= Lej da Champfèr, 8= Lengi Egga, 9= Gouillé Rion, 10= Lago di Origgio, 11= Lago di Muzzano, 12= Lago Piccolo di Avigliana, 13= Pavullo nel Frignano, 14= Lago del Greppo, 15=Lago dell'Accesa, 16=Gorgo Basso. Black solid lines represent pollen percentages, red dashed lines represent detected change points (constrained to a maximum of 4 for each sequence). Note that y-axes (pollen percentage) have different scales

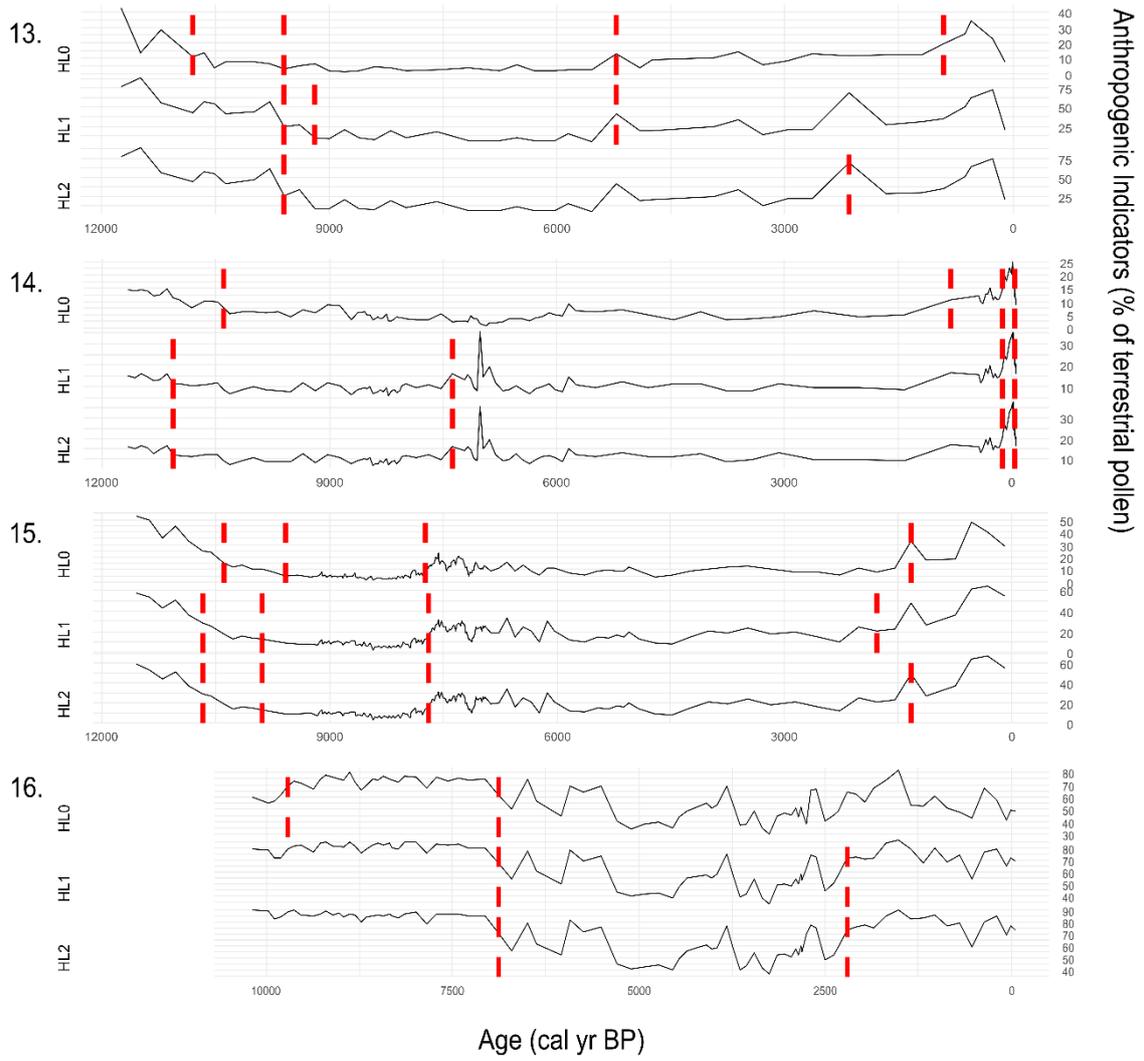
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A new indicator approach to reconstruct agricultural land use from sedimentary pollen assemblages

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Keywords Cultural indicator pollen types, human impact, palynology, palaeoecology, archaeobotany, archaeology, Europe

Abstract

The reconstruction of human impact is pivotal in palaeoecological studies, as humans are among the most important drivers of Holocene vegetation and ecosystem change. Nevertheless, separating the anthropogenic footprint on vegetation dynamics from the impact of climate and other environmental factors (disturbances such as fire, erosion, floods, landslides, avalanches, volcanic eruptions) is a challenging and still largely open issue. For this purpose, palynologists mostly rely on cultural indicator pollen types and related indices that consist of sums or ratios of these pollen types. However, the high environmental and biogeographical specificity of cultural indicator plants hinders the application of the currently available indices to wide geographical settings. Furthermore, the achievable taxonomic resolution of cultural indicator pollen types may hamper their indicative capacity. In this study, we propose the agricultural land use probability (LUP) index, a novel approach to quantify human impact intensity on European ecosystems based on cultural indicator pollen types. From the ‘classic’ cultural indicators, we construct the LUP index by selecting those with the best indicator capacity based on bioindication criteria. We first train the LUP index using twenty palynological sequences along a broad environmental gradient, spanning from treeless alpine to subtropical mediterranean evergreen plant communities. We then validate the LUP index using independent pollen datasets and archaeological proxies. Finally, we discuss the suitability of the selected pollen types and the potential of the LUP index for quantifying Holocene human impact in Europe, concluding that careful application of the LUP index may significantly contribute to refine pollen-based land-use reconstructions.

Keywords Cultural indicator pollen types, human impact, palynology, palaeoecology, archaeobotany, archaeology, Europe

1. Introduction

Human transformation of European terrestrial ecosystems accelerated with the emergence of agriculture (Stephens et al., 2019), when agrarian societies opened the woodlands to gain land for arable and pastoral farming. Over the millennia, environmentally transformative human use of land (e.g., land clearance by burning for arable farming) has resulted in the widespread occurrence of ‘anthromes’ (i.e., anthropogenic biomes) over most of Europe and elsewhere (Ellis, 2011; Ellis and Ramankutty, 2008), that are characterised by varying intensities of human impacts. The assessment of long-term human impacts on the landscape often relies on the use of plants as bioindicators (Burger, 2006), whereby the occurrence or absence of indicator species provides quantitative estimates of the intensity of human disturbance (Diekmann, 2003; Zinnen et al., 2021). Such bioindicator-based methodologies are widely used in plant ecology and rely on the sensitivity of organisms to their environment (Diekmann, 2003; Gerhardt, 2002).

The bioindicator approach can be extended to the past through the analysis of microfossils preserved in lake sediments, peat sequences or other natural archives. For instance, analysing the abundance of crop and weed pollen in fossil assemblages allows reconstructing anthropogenic impacts on ecosystems over long timescales. The most widely used approach in Europe is calculating the abundance of a set of cultural indicator pollen types with demonstrated associations with human activities, especially agriculture (Behre, 1981, 1990). The ground-breaking work by Behre (1981) to select cultural indicator pollen types complies to some extent with the bioindicator methodology, although their final definition does not explicitly and fully meet standard bioindication criteria (Gerhardt, 2002). Moreover, human impact indices including the relative abundances of various cultural indicator pollen types have been developed for European pollen assemblages, therefore providing summary evidence for different types of farming (Lang, 1994; Tinner et al., 2003; Mercuri et al., 2013a, b; Kouli, 2015; Roberts et al., 2019; for a summary see Table 1 in Deza-Araujo, 2020). Similarly, palynological human-impact ratios such as the ‘arable/pastoral index’, which considers the proportion of *Plantago* pollen with respect to other cultural indicator pollen types (Turner, 1964), the arboreal pollen to non-arboreal pollen (‘AP/NAP’) ratio, which aims at reconstructing landscape openness (Berglund et al., 1991), and the ‘Cerealia-t. (t. = pollen type) to *Plantago lanceolata*-t.’ index (C/PL index), are used as proxies for the changing relationship of cultivated to fallow land through time (Tserendorj et al., 2021).

Such indices drawing upon cultural indicator pollen types are presently widely used because of their potential to provide a readily interpretable quantification of past human impacts. However, available indices were originally

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conceived to be used in geographically restricted areas (e.g., Brun, 2011; Mercuri, et al., 2013b) or to reconstruct specific land-use practices (e.g., Kouli, 2015), which suggests caution in their widespread application in Europe because of potential shifts in the response of indicator plants along climatic and geographical gradients (Diekmann, 2003). In particular, the selection of cultural indicator pollen types should vary regionally to account for important aspects like the native distribution range and timing of introduction of the concerned species (Deza-Araujo et al., 2020). Moreover, the taxonomic resolution of pollen types (Deza-Araujo et al., 2022) and their relative contribution to the pollen assemblage need to be considered to avoid false attributions and to account for the overrepresentation of certain pollen types (Brun, 2011; Deza-Araujo et al., 2020). In fact, an important issue concerning existing indicator approaches is that they often combine abundant (e.g., high pollen-producer *Olea*) with rare (e.g., low pollen-producer *Vitis*) pollen types without any correction factor (Deza-Araujo et al., 2020). Such biases are typically due to the overrepresentation of wind-pollinated taxa producing large loads of well-dispersed pollen and wetland taxa growing locally (Birks et al., 2016), which may result in misleading estimates and distorted indicator values (Diekmann, 2003; Urban et al., 2012).

In this study, we propose a new agricultural land use probability (LUP) index that aims to assess Holocene human-impact intensity in pollen diagrams in a rigorous and widely applicable manner that makes pollen-inferred reconstructions of past agricultural land use accessible to non-specialists. Our probabilistic approach first identifies a list of cultural indicator pollen types that is suitable for a specific location, and then adjusts their importance as predictors of impact intensity using anthropogenic indicator values (AIV; modified with respect to Birks et al., 1988) that account for the native distribution range, time of introduction and pollen representation. Thus, the LUP index consists of the sum of the weighted pollen abundances of cultural indicator taxa. By incorporating the AIV concept, the LUP index becomes adaptable over wide geographical gradients. Specifically, our probabilistic index emphasises the co-occurrence of indicator taxa in a pollen assemblage and the abundances of taxa with a high AIV. By doing so, we assume that pollen samples featuring more pollen types of cultural indicator taxa with higher AIV are more likely to express agricultural land use, as quantified by the LUP value.

To implement the LUP we use a set of twenty palynological sequences from lakes located along a large environmental gradient spanning from the treeless alpine belt of the Swiss Alps to the subtropical thermomediterranean belt in coastal Sicily (southern Italy). The lakes are comparable in terms of size (small to medium), and their sediment records mostly consist of autochthonous organic sediment (i.e., gyttja and silty gyttja).

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We pay attention to general bioindication criteria (Diekmann, 2003; Gerhardt, 2002) like the achieved taxonomic resolution (Deza-Araujo et al., 2022) and the historical biogeography of the taxa (e.g., adventive vs. apophyte; Deza-Araujo et al., 2020; Figure S1). We perform two external validations, using on the one hand an independent set of pollen sequences and on the other hand a set of archaeological radiocarbon dates as an independent proxy for human activity. We finally suggest possible implications of the LUP index as a proxy for human impact quantification.

2. Sites and methods

Study sites and pollen data

For the assemblage and calibration of the LUP index, we selected 20 well-dated lake pollen records in a latitudinal transect encompassing Switzerland and Italy (Figures 1a, 2; Table 1). We selected these sites because (i) they were analysed in the same laboratory (Institute of Plant Sciences, University of Bern, Switzerland) and the pollen taxonomic resolution is therefore comparable, and (ii) they are located along an environmental gradient which covers all major vegetation types of Europe. The study sites are located in five vegetation belts (Lang, 1994): 1) the cold subalpine/alpine belt with treeless meadows and scrubland above the tree line, conifer-dominated forests (mostly evergreen but sometimes deciduous or mixed when *Larix decidua* is present) and the transitional tree line ecotone (high elevation areas in the Alps). 2) The cool-temperate colline/montane belt with mostly broadleaved deciduous forests of the northern Alpine forelands (e.g. *Quercus robur*, *Quercus petraea* or *Fagus sylvatica*). 3) The warm-temperate and rather humid submediterranean belt in the low and mid elevation sites of the southern Alps and the northern Apennines with mixed broadleaved deciduous forests characteristic for southern Europe (e.g., *Castanea sativa*, *Ostrya carpinifolia*, *Quercus pubescens*, *Quercus cerris*, *Fraxinus ornus*). 4) The warm and summer-dry mesomediterranean belt with evergreen and deciduous oak forests in lowland central Italy (e.g. with *Quercus ilex* and *Quercus pubescens*). 5) The very warm and summer-dry thermomediterranean belt with evergreen forests, woodlands and maquis in coastal areas of Sardinia and Sicily (e.g. *Quercus ilex*, *Quercus coccifera*, *Olea europaea*, *Chamaerops humilis*, *Ceratonia siliqua*; Figures 1a, 2). These vegetation belts correspond to different climatic conditions, and these are relevant to farming activities (e.g., crop selection for securing and maximising harvest success).

The pollen datasets were retrieved from the Alpine Palaeoecological Database (ALPADABA) via Neotoma (Williams et al., 2018). The chronologies in ALPADABA correspond to those produced by the authors in the original

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publications (see Table 1). For each study site, we calculated the percentages of the most frequently used cultural indicator pollen types according to Behre (1981, 1990), Mercuri et al. (2013a) and Deza-Araujo et al. (2021). Pollen percentages were calculated with respect to the terrestrial pollen sum (trees, shrubs and upland herbs), excluding *Cannabis-t.*, which is often overrepresented in lake sediments due to retting. We plotted every potential cultural indicator using ‘*tidyverse*’ version 1.3.0 (Wickham et al., 2019) running in the R environment (R Core Team, 2020).

Selection of cultural indicator pollen types

We identified five criteria out of the full list considered by the bioindicator approach as the most relevant to pollen analysis after Gerhardt (2002). The criteria used to select and rank the considered pollen types on a four-point scale (i.e., excellent, good, fair and poor) according to their cultural indicative capacity (Tables 2, S1) are as follows:

- i. ‘*Adventive/apophyte status*’ (Lang, 1994; Deza-Araujo et al., 2020). Pollen from adventive plants (non-native, introduced with agriculture) has higher indicative value than those from apophytes (native, favoured by human disturbances) because their introduction resulted from human agency and their habitats are mostly restricted to places disturbed by farming activities. The most reliable human indicators will be adventive primary agricultural indicators (i.e., crops non-native to the study area).
- ii. ‘*Taxonomic resolution*’ (Deza-Araujo et al., 2022). Precise pollen identification is key to the interpretation of pollen data in terms of agricultural land use. The closer the taxonomic correspondence between pollen types and their potential source plants, the more accurate the reconstruction of the anthropogenic environments around the study site. In this regard, easiness of the determination of the pollen grains to high taxonomic resolution fosters the indicative power of cultural indicator pollen types. Complete ecological knowledge of the indicator plant species is a needed prerequisite.
- iii. ‘*Pollen production/dispersal/robustness*’. Anemophilous taxa are better represented in pollen spectra than zoophilous species (Regal, 1982). For this reason, certain indicators such as the autogamous cereals (e.g., *Hordeum vulgare*), which are dispersed on shorter distances than wind-pollinated species such as *Secale cereale* (Josefsson et al., 2014), are considered less consistent cultural indicators. Likewise, pollen of plants usually grown in extensive monocultures will be better represented in pollen assemblages –and will therefore be more consistent cultural indicators than taxa only found in small amounts in family gardens or orchards-.

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Thus, ‘ubiquity’ and abundance in pollen records is a desirable feature that reinforces indicative power.

Additionally, selecting pollen types not particularly prone to degradation is important to avoid differential preservation issues that might bias land-use reconstructions based on pollen data. For example, the great indicative capacity of *Cerealia-t.* as an indicator of agricultural activities is somewhat hampered because its large pollen grains (>37 µm; Beug, 2004) may be more prone to chemical and mechanical damage, resulting in broken or crumpled grains (Delcourt and Delcourt, 1980) that do not allow more precise identification.

- iv. ‘*Exponential increase in the pollen diagram*’. This feature is assumed to reflect the sensitivity and responsivity of the plant taxon to human-induced disturbance or its deliberate cultivation. Although exponential growth of plant populations can also occur independently of human action (Magri, 1989), here we consider only the exponential growth of taxa unambiguously related to human activities (Deza-Araujo et al., 2020).
- v. ‘*Representation in pollen assemblages*’. Good correspondence between plant and pollen abundances is important. Cultural indicator pollen types should increase monotonically alongside the rising dominance of the corresponding crop or weed.

We assessed each cultural indicator in our calibration datasets by conducting a literature review on their pollen characteristics and visually inspecting the pollen curves to identify the temporal distribution of their relative abundances and to ascertain whether their curves behaved as expected (overall exponential increase in the pollen diagram). To keep the LUP index as parsimonious as possible, only taxa with the highest overall indicative capacity were retained (Figure 1b), irrespective of their presence in all calibration pollen datasets (Table S2).

Assemblage and calibration of the LUP index

The LUP index of a given pollen assemblage is calculated as follows:

$$LUP_i = \sum_{j=1}^n x_{ji} AIV_j$$

where LUP_i is the value of the LUP index for the pollen sample i ; x_{ji} is the relative abundance of the pollen type j (one of the n selected cultural indicator pollen types present in the pollen sequence) in the pollen sample i , expressed as a

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percentage of the terrestrial pollen sum; and AIV_j is the anthropogenic indicator value assigned to the pollen type j at the study site, according to the vegetation belt where this is located because this is relevant to the adventive/apophyte status and the agricultural systems used (Figures 1, 2). Thus, the AIVs modulate the LUP index to account for the adventive/apophyte status of the selected cultural indicators in the different vegetation belts.

Selected pollen indicators differ in their relative abundances in the calibration pollen datasets. To standardise their percentages around similar values and thus correct over- and underrepresentation in pollen diagrams, we used AIVs as weighting coefficients. AIVs for a given pollen type can differ among vegetation belts, which allows accounting for different crops and historical biogeographical aspects specific to each location. As a result, AIV values for the selected cultural indicators vary among pollen types and the five vegetation belts considered.

We assigned an AIV of 10 to most cultural indicator pollen types in all vegetation belts (Figure 1b) with the following aims: (i) to increase the weights of cultural indicator pollen types because these are often rare or underrepresented, particularly during the initial stages of farming development, and (ii) to enhance visualisation. In contrast, we downweighted and assigned lower AIVs to pollen types which tend to be overrepresented or to accounting for the native status of the plants producing such pollen types (Figure 1b). This correction was sometimes applied to specific vegetation belts (Figure 1b). For example, *Cannabis sativa* received an AIV of 0.25 to counterbalance its large overrepresentation in lake pollen assemblages due to retting. Likewise, fruit trees with moderate to large pollen production and good dispersal such as *Olea europaea*, *Castanea sativa* and *Juglans regia* received AIVs lower than 10 in areas where they have been widely cultivated and/or are considered native (i.e., in submediterranean and thermomediterranean settings; Figure 1b).

The LUP index values were then plotted for the 20 pollen records of the training dataset to check if the LUP curves showed long-term increasing trends as expected from the archaeologically and historically inferred developments in population density and technology (Deza-Araujo et al., 2020 and references therein). AIVs < 10 were assigned to apophytes and overrepresented taxa following an iterative process aimed at meeting the two following requirements: (i) LUP maximum values on a given pollen diagram are close to 100 to allow comparisons among sites and vegetation belts, and (ii) LUP curves follow a monotonically increasing trend towards present (with generally rising human impact; Figure S1). We grouped the results of the LUP index by archaeologically inferred levels of human impact intensity, from very low to very high (Palaeolithic to Modern Era; Deza-Araujo et al., 2020), and plotted them as

boxplots to assess whether the LUP values followed the desirable monotonic increasing trend across the gradient in land-use intensity (Figure 3).

Validation of the LUP index

The validation of the LUP index was two-fold. First, we evaluated the performance of the LUP index in predicting agricultural land use by applying it to an independent dataset consisting of eleven lake pollen records from the five investigated vegetation belts (Table 3), and checking if the trends of LUP were comparable to those observed at the sites used for its development. These pollen records were obtained from ALPADABA and the European Pollen Database (EPD), and we used the chronologies produced by the authors for the ALPADABA records and the MADCAP ones for the EPD sites (Giesecke et al., 2014). Then, LUP values of both the 20 calibration and 11 validation datasets were compared to the density of archaeological radiocarbon dates around the sites (Rykiel, 1996; Figures 2, 5, 6). This comparison is intended as an independent validation. We assume that the more sites per time interval and area are recorded through radiocarbon dates, the higher the archaeological site density known for that time, and therefore the larger the overall past human activity and/or population density (Shennan et al., 2013). This approach is one of the few archaeological options to develop continuous records of human activity (Hinz, 2020) that can be used for comparison with the selected pollen datasets. We used the radiocarbon dates available within a 50-km radius around most palynological sites. However, for thermomediterranean sites this radius was increased to 100 km because these sites are located on the coast where there is less adjacent land area and in turn lower amounts of radiometric data. The dates for the cumulative radiocarbon proxy curves come primarily from the database XRONOS, but the set was enlarged using data from Laabs (2019) for Switzerland, Martínez-Grau et al. (2021) for Switzerland and northern Italy, Palmisano et al. (2018) for Italy, and Lugliè (2018) for Corsica and Sardinia (a complete list of the archaeological dates can be found in Table S3). The summed probability distributions (SPD) were calculated using the R package 'Rcarbon' (Crema and Bevan, 2021). We used the unnormalised approach and binned the dates according to site. No temporal binning was accomplished to avoid artificial separation of connected use phases. The cumulative radiocarbon proxy curves were then grouped into the five vegetation belts considered in this study (Figures 4, 5, S2). Because of this grouping (method category 1 in Crema et al., 2017), our approach is not spatially explicit, and corrections for potential spatial-temporal autocorrelation of the sites are therefore not necessary. We used a smoothing window of 50 years.

3. Results and interpretation

Cultural indicator pollen types included in AIV

Non-native primary indicators (PII)

We selected the following pollen types that can be unambiguously identified at the highest taxonomic resolution attainable and are directly associated with agriculture (food and fibre crops): *Avena-t.*, *Fagopyrum*, *Hordeum-t.*, *Linum usitatissimum-t.*, *Pisum sativum-lath.*, *Secale cereale*, *Triticum-t.*, *Vicia faba-t.* and *Zea mays* (Figures 1b, 3). *Hordeum-t.* may include pollen of some wild grasses in certain sites (Beug, 2004), which could be corrected readily by reducing its AIV. These taxa are mostly self- and insect-pollinated, resulting in low pollen production and relatively poor pollen dispersal, except for wind-pollinated *Secale cereale* (Trondman et al., 2015). These crop species are non-native to Europe and are therefore almost unequivocal indicators of farming, particularly north of the Alps (Behre, 1981; Zohary et al., 2012). Although some close relatives of these crops (sometimes within the same genus) are native to Europe, we assume that the contribution of such native taxa to these pollen types is very low (Beug, 2004). These pollen types were included in the LUP index for all vegetation belts. However, at some sites several pollen types are grouped as *Cerealia-t.*, which includes *Avena-t.*, *Hordeum-t.* and *Triticum-t.*, but not *Zea mays* or *Secale cereale*. Furthermore, pollen of non-cultivated Mediterranean grasses, such as *Bromus-t.* may be classified as *Cerealia-t.* (Tweddle et al., 2005). Cereal pollen is usually very rare in fossil pollen assemblages (Lechterbeck et al., 2014) and regular occurrences of *Cerealia-t.* pollen are mostly recorded in close proximity to cultivated fields (Niebieszczański et al., 2019). Further, pollen deposition of autogamous cereals (e.g., *Triticum*, *Hordeum*) increases notably during harvesting and threshing and cereal pollen is consequently rather abundant in pollen sites near Neolithic lakeshore dwellings (Behre, 1981). Consequently, *Cerealia-t.* pollen is an overall very good indicator of agricultural land use.

Another pollen indicator with high cultural value is *Cannabis-t.* (Figures 1b, 3). The exponential growth of the *Cannabis-t.* curve at most sites largely coincides with the intensification of human activities during the last centuries. Prominent peaks of this indicator in the Middle Ages and Modern Era, particularly in temperate settings such as the colline/montane and submediterranean belts (e.g., Egelsee, Burgäschisee, Soppensee, Origlio, Muzzano, and

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Avigliana; Figure 1a), are related to water retting for fibre extraction (Bradshaw et al., 1981), which justifies a lower AIV of 0.25 (Figure 1b). Until ca. 100-200 years ago, *Cannabis sativa*, which is not native to Europe (McPartland et al., 2019), was widely planted for medicinal, food and fibre uses (Plants for a future, 2018; Russo, 2007).

Native primary indicators (PI2)

Although several more fruit trees and vines of cultural importance are native to Europe (e.g., *Corylus avellana*, *Vitis*, *Pistacia*), we selected *Castanea sativa*, *Olea europaea* and *Juglans regia* for the LUP index because these trees are usually rare in the natural forests or woodlands. *Castanea sativa* is currently dominant in submediterranean woodlands and forests but palaeoecological evidence has proven that humans extended its range and increased its abundances through Roman Times and the Middle Ages until the Modern Period (e.g., Morales-Molino et al., 2015). This is the underlying reason why we have included *Castanea* in the LUP formula assigning to it a lower AIV in this environmental context (Figure 1b). Similarly, *Olea europaea* is a relevant component of thermomediterranean woodlands, but its importance declines sharply outside of this southern vegetation type. For instance, in the mesomediterranean vegetation type, other species like *Quercus ilex* are more competitive under natural conditions (Costa et al., 2005). The abundance of *Olea europaea* pollen in thermomediterranean records under natural conditions (e.g., Gorgo Basso; Tinner et al., 2009) led us to remove it from this vegetation belt. *Castanea sativa*, *Olea europaea* and *Juglans regia* are routinely found in Holocene pollen assemblages from Europe because they are (partly) anemophilous. However, *Juglans* and *Castanea* pollen percentages are sometimes low, even in the presence of crops, except when they are very close to the pollen site (di Pasquale et al., 2010) or dominating in the forest vegetation (Tinner et al. 1999). Therefore, occasionally the finding of few pollen grains might be considered indicative of their cultivation (Russo Ermolli et al., 2018).

Non-native and native secondary indicators

Plantago lanceolata-t. pollen has been conventionally regarded as an excellent cultural indicator (Iversen, 1941) because in temperate and boreal Europe it is considered to mostly derive from *Plantago lanceolata*, which is an adventive species that is favoured by farming practices. The pollen type is absent or only very rarely found in non-Mediterranean pollen assemblages before the onset of agricultural activities. *Plantago lanceolata* features a

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remarkable adaptation capacity to environmental variation (Bischoff et al., 2006), plays a significant role in the recolonisation of abandoned cultivated land (Behre, 1981), and is a ruderal and trampling indicator. However, *Plantago lanceolata*-t. pollen is quite abundant in thermomediterranean pollen sequences during the Early Holocene (e.g., Gorgo Basso; Tinner et al., 2009), perhaps because of the presence of other *Plantago* species producing the same pollen type, so we excluded it as a cultural indicator in that setting.

Urtica dioica-t. pollen is mostly produced by the homonymous plant species (Lang 1994), which is an apophyte in Europe, typical of ruderal communities. In pollen diagrams, it usually presents a regular, increasing curve, particularly marked in the subalpine vegetation belt (e.g., Bachalpsee, Gouillé Rion). *Urtica dioica* has long been consumed as food (leaves and oil) and has medicinal properties (Plants for a future, 2018). It is among the commonest food plant found in Neolithic Linear Pottery culture (LPC) sites (Colledge and Conolly, 2014). Additionally, its fibres were used for fabric weaving as early as the Bronze Age, representing a valuable resource traded over long distances in Europe (Bergfjord et al., 2012). *Urtica membranacea*, which has less specific ecological requirements, is often combined with *Urtica dioica* as *Urtica*-t. in thermomediterranean settings. Therefore, we did not include *Urtica*-t. as a cultural indicator in the thermomediterranean belt.

Finally, *Mercurialis annua* consists of a complex of closely related wind-pollinated annual plant taxa native to central and western Europe, the Mediterranean region and western Asia that grow mainly in ruderal places (e.g., fallow land, vineyards, or vegetable gardens) and roadsides on nutrient-rich, loamy and relatively dry to moderately moist soils (Güemes, 1997; Pignatti, 2005; Lauber et al., 2018). Because of these ecological requirements, *Mercurialis annua* has been used as an indicator of early human habitation in the Mediterranean (e.g., Bottema and Sarpaki, 2003). This pollen type was not found in all the training sites, although it had a good representation at the thermomediterranean sites. Due to its often-low taxonomic identification as *Mercurialis*-t., we could not use *Mercurialis annua* at every site, as the related pollen type, *Mercurialis perennis*, grows in woodlands.

Evaluation and validation of the LUP index

The LUP index values show a general exponential growth throughout the Holocene, with first non-zero values occurring in the study area around the early Neolithic (8000-6000 cal. BP) and remarkable increases usually during the early Bronze Age at ca. 4200 cal. BP or at the latest at the onset of the Iron Age at ca. 2800 cal. BP (Figures 3, 4).

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Whereas this general trend is observed in all vegetation types (Figures 3, 4) increases in LUP are punctuated by several transient troughs corresponding to times of land abandonment and population decline such as the “Late Bronze Age collapse” at ca. 3200 cal. BP (Figures 4, S2). The boxplots show a significant variability in LUP values for the ‘high’ and ‘very high’ categories of human impact intensity, which correspond to the Iron Age to Early Middle Ages and High Middle Ages to present respectively, as shown by the large interquartile ranges (Figure 3).

Maximum LUP values are reached at the colline/montane and submediterranean sites where high peaks of *Cannabis-t.* occur (Figures 3, 4). In contrast, LUP values from the cold subalpine/alpine vegetation belt are rather low (Figures 3, 4). Similarly, LUP values are generally low in the four thermomediterranean sites where LUP curves do not show marked oscillations (Figures 3, 4).

The application of the LUP index to the eleven independent palynological records (Table 3) produced land-use patterns similar to those observed in the pollen datasets used for the LUP development (Figures 4, 5, S2). Although the mesomediterranean validation site of Lago di Martignano shows similar patterns, the range of LUP values is notably wider than in the calibration datasets and the rest of validation sites due to the high pollen percentages of *Olea europaea*. Taken together, LUP patterns suggest that agricultural land use increased towards the present but fluctuated considerably, likely in association with episodes of ‘*landnám*’ and land abandonment (Figures 4, 5, S2). Lower LUP values in the cold subalpine/alpine vegetation belt may reflect less intensive agricultural land use due to the harsh environmental conditions. In contrast, lower LUP in the thermomediterranean (Figure 5) are most likely a calculation artefact due to the exclusion of major food sources such as *Olea*, if compared to the other vegetation types. Finally, the archaeological radiocarbon proxy (Figures 4, 5, S2) for anthropogenic activity closely resembles the overall increasing trends observed in the LUP curves, some of their wiggles, as well as events of rapid decline of human population (dependent and independent data) for the prehistorical periods. This finding suggests that the LUP index generally produces realistic agricultural land use trends (Figures 4, 5, S2). Discrepancies between the two proxies might derive from uncertainties inherent to both approaches.

4. Discussion

What is new in the LUP approach?

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In this study, we used bioindication criteria to select the best suited cultural indicator pollen types for reconstructing past agrarian land use. Compared to Behre's (1981) list of 38 cultural indicator pollen types, in this study we have considered 17 cultural indicators, a figure that can be reduced depending on the vegetation and climate setting (Figure 1). Such a procedure allows the identification and straightforward interpretation of a limited number of pollen indicators for land-use reconstruction purposes in very different ecosystems, from the alpine/subalpine belt to the thermomediterranean vegetation types (i.e., most major land-use conditions in Europe). We acknowledge that focusing on a limited number of pollen types may mean a loss of information. Earlier studies aimed at land-use reconstruction also focused on a reduced number of cultural indicator pollen types to stay as parsimonious as possible, often considering just two to four diagnostic pollen types out of several hundred (e.g., Tinner et al., 2003; Mercuri et al., 2013a, b). In comparison, our new approach is more integrative because it considers up to 17 cultural indicators. Moreover, to some extent, the LUP index overcomes misleading interpretations of anthropogenic impact related to the imprecise assignment of pollen types to the crop and adventive categories (Deza-Araujo et al., 2022).

Further, the geographical scope of the LUP index may be expanded to other regions because most of the selected cultural indicators correspond to plants widely distributed, in contrast to other previously proposed methodologies for land-use reconstruction in Europe (Mercuri et al., 2013b; Kouli, 2015). Additionally, the LUP index has the capacity to detect human impact coming from various land-use systems, as it considers cultural indicator pollen types specifically used as proxies for agricultural (*Cerealia-t.*, *Plantago lanceolata-t.*), pastoral (*Urtica dioica-t.*), and agroforestry or arboriculture systems (*Olea europaea*, *Castanea sativa*, *Juglans regia*). These cultural indicator pollen types have been widely used separately as part of indices previously proposed for local human-impact reconstructions (Tinner et al., 2003; Mercuri et al., 2013b; Kouli, 2015).

The LUP-based quantification of human impact was possible thanks to the use of region-specific weighting coefficients (AIV) to adjust the relative abundances of cultural indicators. These region-specific AIVs aim to boost the relative abundances of often scarce but very important primary pollen indicators. This adjustment also downweights spikes deriving from overrepresented indicators such as *Cannabis sativa*-type that may inflate the estimation of human impacts. As a result, the abundances of all the selected indicators should be comparable. The use of AIV also allows accounting for the native status of a given taxon to certain geographic areas, thus disentangling the land-use impact from the possible natural occurrence of the indicator (e.g., *Olea europaea* at thermomediterranean sites). Considering these factors, i.e., pollen representation and nativeness, AIVs could be assigned to the selected cultural indicators in

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other geographical settings enabling the use of the LUP index. One of the most important criteria when selecting the pollen indicators used in the LUP index was that their relative pollen abundances in the calibration datasets showed steady increases in response to changes in land-use intensity (Behre, 1981). AIVs are intended to be a first step to refine such approximation, but there is room for further developments of the weighting procedure.

Overall performance of the LUP index

At the sites used to develop the LUP index, the curves follow the expected increasing trend in human impact intensity during the Holocene (Figure 3; Deza-Araujo et al., 2020; Mottl et al., 2021), with major rises usually occurring in periods when European civilizations became more complex (i.e., Iron Age, Roman Times, Middle Ages and Modern Period; Moore and Armada, 2012). The overall good match between the curve of the LUP index and the radiocarbon proxy for anthropogenic activity suggests a good performance of the LUP index in quantifying Holocene human impact (Figure 4). We acknowledge that both, LUP and the radiocarbon time series, have their own data-inherent limitations as proxies of past human impact (see e.g. discussion in Freeman et al. 2018), however given the good match in the general trends across many sites, we assume that both proxies are primarily related to the intensity of past anthropogenic activities, e.g. via number of dated remains of material culture (radiocarbon proxy) or number of flowering crops and weeds (LUP). Often, changes in some cultural indicators like *Cerealia-t.* can be closely related to demographic trends because they directly determine the carrying capacity (Izdebski et al., 2016; Tinner et al., 2003). This relationship is not always straightforward but may be particularly explicit during early agriculture phases, when worn-out fields were abandoned as fallow land, and later subjected to colonization by native pioneer vegetation. This was often the case between the Neolithic and the Early Bronze Age (Montgomery, 2007), as observable in the pollen records of Lago di Origlio and Lago Piccolo di Avigliana (Figure SI). During these prehistoric periods, human population dynamics and land-cover change appear intimately linked, as shown by the overall close correspondence between cultural indicator pollen types and archaeological radiocarbon date density (Lechterbeck et al., 2014). This relationship is also marked during times of rapid land abandonment at the end of the farming cycles of the Neolithic, Bronze Age, Iron Age and Roman societies, and the Medieval and Modern periods (Montgomery, 2007). Such oscillations may correspond to major breaks like the “Neolithic decline” in northern and western Europe (~3000 BC, ~4950 cal. BP; Kristiansen, 2015), the probable “Late Bronze Age collapse” in the Mediterranean (~1200 BC, ~3150

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cal. BP; Knapp and Manning, 2016), the fall of the Western Roman Empire at AD 476 (1474 cal. BP), the AD 1315-1317 European famine (635-633 cal. BP), or the AD 1348 (602 cal. BP) Black Death (Figure 4). Moreover, high-resolution studies on varved sediments in Central Europe with an extremely high chronological precision suggest several synchronous agrarian land-use oscillations over the Neolithic, probably in response to changing environmental conditions (Rey et al., 2019a, b). However, synchronous long-term oscillations of agrarian land-use activities over wide areas were reconstructed for the Bronze Age and the subsequent periods, including the Little Ice Age (Maise, 1998; Tinner et al., 2003, 2009).

High LUP values may be associated to environments with a high degree of vulnerability to human impact, as in the colline/montane and submediterranean belts. For instance, the Neolithic agriculture expansion from the valley bottoms up to treeline and higher up (Hafner and Schwörer, 2018) may have increased erosion on formerly forested steep slopes (Montgomery, 2007). Human transformation of forest into arable fields may have triggered soil degradation and/or eutrophication and favoured the extensive spread of taxa such as *Plantago lanceolata* and *Urtica dioica* (higher LUP values at the submediterranean and colline/montane sites, Figures 4, 5, S2). Moreover, evergreen mediterranean woodlands are among the most sensitive ecosystems to human activities such as grazing or agriculture, because they are subjected to soil-water deficit during summer and usually grow on steep and unstable slopes (Burri et al., 1999).

In the LUP formula, we combine woody and herbaceous taxa to accomplish a more nuanced understanding of changing impacts, as we acknowledge the relevance of using short-living taxa such as *Cerealia-t.* together with other non-native primary indicators and adventive herbs. This combination is because wind-pollinated fruit trees are better represented in pollen records and thus among the most widely used cultural indicator pollen types (Mercuri et al., 2013b) compared to annual and biannual herbaceous plants with annual or biannual life cycle and low pollen taxonomic resolution (Deza-Araujo et al., 2022). However, fruit trees such as *Castanea* and *Olea*, may persist longer during land abandonment phases (Morales-Molino et al., 2015) and are therefore unsuitable to track decadal-scale events.

Evolution of LUP values in the different vegetation types of the study region

The sites located in the cool-temperate colline/montane vegetation belt north of the Alps (Figure 1) do not show continuous signs of human impact before ca. 6000 cal. BP (Figures 4, S2). In the original pollen diagrams, these sites

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include late Mesolithic occurrences (after ca. 8700 cal. BP) of *Cerealia-t.* and *Plantago lanceolata-t.* pollen (Lotter, 1999). Later, more detailed palynological analyses showed that among them are more diagnostic cereal taxa such as *Triticum-t.* and *Avena-t.* (Tinner et al., 2007), which suggests that agricultural activities may have initiated long before signs of human impact became continuous (i.e., 6750 vs. 4050 BC, 8700 vs. 6000 cal BP). During the Neolithic (ca. 5500-2200 BC, 7450–4150 cal. BP), pollen of cereals and weeds such as *Plantago lanceolata* occurs regularly and this translates into very low (< 20) but continuous LUP curves. In prehistoric times, the introduction or expansion of cultivated plants (*Cerealia-t.*) and weeds (*Plantago lanceolata-t.*) is linked directly with phases of increased human impact in the form of forest clearances at ca. 3700, 2700, 1900, 1550 BC (5650, 4650, 3850, 3500 cal. BP) and after 650 BC (2600 cal. BP; Rey et al., 2019a). Similarly, from the Bronze Age to the Middle Ages, episodes of forest clearance in the study region were connected to agricultural land use intensification at ca. 2100-1900 BC (4050-3850 cal. BP), 1750-1650 BC (3700-3600 cal. BP), 1450-1250 BC (3400-3200 cal. BP), 800 BC (2750 cal. BP), 650-450 BC (2600-2400 cal. BP), 50 BC-AD 100 (2000-1850 cal. BP) and ca. AD 700 (1250 cal. BP; Tinner et al., 2003). Concerning the general long-term trends, pollen of crops and weeds increased during the Bronze Age, suggesting an expansion of permanent settlements and agricultural activities, including intensified transhumance (Wehrli et al., 2007). Human impact increased further during the Iron Age and the Roman period (ca. 2800–1600 cal. BP), as indicated by the appearance of new crops such as *Juglans regia* and *Castanea sativa* (e.g., Rey et al., 2020). Dominant species such as beech were able to recover even after the periods of greatest anthropogenic impact and forest clearance (e.g., Iron Age, Roman Period) as soon as agricultural land use decreased (e.g., Migration Period at ca. 1600-1400 cal. BP; Rey et al., 2020). Agricultural land use increased during the Early Middle Ages and later, causing widespread forest opening (Rey et al., 2017). Whereas major episodes of forest clearance and establishment of permanent fields and pastures occurred during the Iron Age near environmentally favoured population centres, they occurred only during the late Middle Ages in cool and/or humid marginal areas (Lotter, 1999; Tinner et al., 2005). The widespread cultivation of *Cannabis sativa* during the Middle Ages is reflected in pollen values of up to 70% during the past millennium (Rey et al., 2017; Wehrli et al., 2007). After low LUP values related to the European famine of 1315-17 AD (~ 635 cal. BP) and the Black Death of 1348 AD (~ 602 cal. BP, Figures 4, S2), LUP reaches particularly high values during the past ca. 600 years. This period experienced a marked vegetational change with the expansion of *Plantago lanceolata-t.*, Poaceae and other herbaceous pollen types and the decline of tree taxa such as *Abies alba* and *Fagus sylvatica* (e.g., Wehrli et al., 2007).

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At the cold subalpine/alpine sites in the Alps (Figure 1), LUP and archaeological radiocarbon density curves show similar trends to those at the cool-temperate colline/montane sites north of the Alps (Figures 4, S2). However, the magnitude of LUP is lower at the subalpine/alpine sites, which suggests lower land-use activities at the cold sites. Here, the archaeological radiocarbon density curves may overestimate human activities, given that the large radius (50 km) considered may include warmer and more fertile valley bottoms and lowlands, which are more attractive for human settlers. The catchments of the subalpine/alpine sites have been used as summer pasturelands at the latest since the Bronze Age (Gobet et al., 2003; Hafner and Schwörer, 2018). From 3000 cal. BP onwards, human-induced deforestation was the main driver of timberline lowering, which reached its most intense pulses since the Middle Ages (Gobet et al., 2003). The agricultural intensification phases recorded regionally during the Bronze Age, the Iron Age and the Roman period at the colline/montane sites (Tinner et al., 2003) are also documented in the subalpine sites (4050-3850, 3700-3600, 3400-3200, and 2000-1850 cal. BP; 2100–1900 BC, 1750–1650 BC, 1450–1250 BC, 50 BC–AD 100; Gobet et al., 2003, 2005; Tinner et al., 1996). The palynological results suggest for this vegetation belt continuous human influence and the absence of trees near the lakes up to the present (e.g., Lotter et al., 2006), with progressively lower human impact in the last 200 years (Figures 4, S2).

At the submediterranean sites south of the Alps (Figure 1), the LUP values become continuous at ca. 6000-5000 BC (7950-6950 cal. BP, Figures 4, S2), which corresponds to the onset of the Neolithic in this region. This pattern is mirrored in the archaeological radiocarbon density curve (Figures 4, S2). Marked vegetation changes occurred during the late Neolithic and Bronze Age, when archaeological findings suggest increased human impact and pollen shows clearly marked land-use phases (Finsinger and Tinner, 2006; Vescovi, et al., 2010b). Both the LUP index and the archaeological radiocarbon density curve feature very low values at the submediterranean sites simultaneously at ca. 1200 BC (3150 cal. BP, “Late Bronze Age collapse”; Knapp and Manning, 2016; Cardarelli, 2009). During the Middle Bronze Age (1650-1350 BC, 3600–3300 cal. BP), human activities increased steadily, as indicated by the significant rise of *Plantago lanceolata*-t. pollen around 1550 BC (3500 cal. BP) at Pavullo nel Frignano (Vescovi, et al., 2010b). Forest clearance further peaked during the Iron Age at ca. 650–450 BC (2600-2400 cal BP, Tinner et al., 2003; Finsinger and Tinner, 2006). Subsequently, trees associated with Roman agricultural activities such as *Olea*, *Castanea* and *Juglans* were commoner in Insubria in the southern Pre-Alps than in the Northern Apennines (Watson 1996; Morales-Molino et al. 2021). LUP suggests that human activities were not substantially more intense during Roman and early Middle Ages than during the Iron Age, but this may relate to *Castanea* pollen being downgraded in

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the LUP formula, and not to a decline in agriculture (Figures 4, 5, S2). Agricultural intensification continued towards the present, suggesting that agricultural land use further intensified during the past millennium (Finsinger et al., 2006; Finsinger and Tinner, 2006; Vescovi et al., 2007, 2010a).

In the mesomediterranean sites of central Italy (Figure 1), LUP values become continuous at the beginning of the Neolithic (ca. 6000 BC, 7950 cal. BP) at most sites (Figures 4, S2). For instance, the decline of *Quercus ilex* around 6000-5700 BC (7950–7650 cal. BP) at Lago dell'Accesa was associated with an increase of deciduous oak and plants indicating disturbance and/or human activities (e.g. *Pteridium*, *Poaceae*, *Plantago lanceolata*-t. at 7900–7700 cal. BP, see Colombaroli et al., 2008). In contrast to other European regions where the “Neolithic decline” was quite conspicuous, the archaeological radiocarbon density curve denotes population growth during the late Neolithic around the Italian mediterranean sites, as also found in previous studies (Palmisano et al., 2017). In general, the LUP values for the Bronze Age at the mesomediterranean sites are comparable to those of the submediterranean sites south of the Alps and to those of the colline/montane sites north of the Alps. This suggests increasing agricultural activities during the Bronze age, in agreement with estimates of human population growth during the Bronze Age in the Mediterranean region (Vannièrè et al., 2008). However, after having remained rather stable during the Iron Age, the LUP index shows further increases ca. 2000 years ago at the mesomediterranean sites perhaps related to the Roman Empire. The match with the strongly oscillating archaeological radiocarbon density curve (and with fewer dates) is generally poor for this vegetation belt, but increases towards the end of the Roman Times, after a very acute depopulation period at the fall of the Western Roman Empire (around 476 AD, Figures 4, S2). Prehistoric and historical agricultural land use changed dramatically vegetation structure and composition at the mesomediterranean sites (Colombaroli et al., 2007, 2008; Drescher-Schneider et al., 2007). For instance, land use gradually converted natural mixed *Quercus ilex-Abies alba* forests into coastal maquis and garrigue (evergreen scrub communities that replace lowland Mediterranean woodlands following disturbances) during the middle and late Holocene (Colombaroli et al., 2007). The vegetational degradation to maquis and garrigue increased during the past 700 years and was strongly related to an intensification of agriculture (Colombaroli et al., 2007).

At the thermomediterranean sites in Sardinia and Sicily (Italy), the Neolithic land use dynamics is well documented by the LUP values (Figures 4, S2). Neolithic farming started at ca. 6000 BC (7950 cal BP) in Sicily, where the first unambiguous pollen imprint has been dated to around 5500 BC (7450 cal BP) at Gorgo Basso as indicated by *Cerealia*-t. increases, together with *Ficus* (Tinner et al. 2009). Similarly, in Sardinia, the first archaeological evidence

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of Neolithic farming dates to 6000-5700 BC (7950–7650 cal. BP, Pedrotta et al., 2021), although pollen (e.g., *Cerealia-t.*, *Plantago lanceolata-t.*) and macrofossil evidence suggests only marginal farming activities until 5300 BC (7250 cal. BP), when a first prominent peak of arable farming occurred (Pedrotta et al. 2021). Increases in pastoral farming indicators such as *Urtica*, *Rumex acetosa-t.*, *Rumex acetosella-t.* and Poaceae suggest an intensification of agricultural land use at 6500-6100 cal. BP (Pedrotta et al., 2021). Interestingly and in agreement with very low radiocarbon date density, LUP values seem to document the “Neolithic decline” around 3000 BC (4950 cal. BP) in the thermomediterranean belt of Sicily and Sardinia around 3000 BC (4950 cal. BP; Figures 4, S2). During this period, a gradual but marked vegetation shift from evergreen oak woodland to maquis occurred at Biviere di Gela in Sicily in association with increased fire activity (Noti et al., 2009), while forests remained dense at Gorgo Basso, the other Sicilian coastal site (Tinner et al., 2009). In Sardinia, evergreen oak forests expanded massively into *Erica* woodlands (Beffa et al., 2016; Pedrotta et al., 2021) at ca. 3000 BC (4950 cal BP), when farming activities were low. Pollen evidence from Sicily and Sardinia points to an intensification of agricultural activities during the Bronze Age at ca. 2000-1000 BC (3950-2950 cal BP), which continued until 800 BC (2750 cal. BP, Noti et al., 2009; Tinner et al., 2009; Beffa et al., 2016), when agricultural activities peaked at most thermomediterranean sites during the Iron Age (with the exception of San Rafael in south-eastern Spain; Figures 4, 5, S2). At AD 450-1750 (1500-200 cal. BP), a further pronounced intensification of land use resulted in the current (mostly) open landscape of coastal Sicily and Sardinia (Noti et al., 2009; Tinner et al., 2009, Beffa et al., 2016; Pedrotta et al., 2021). As in other vegetation belts, depopulation following the Great European Famine of 1315-17 AD (~ 635 cal. BP) and the Black Death of 1347 AD (~ 603 cal. BP), also occurred in the thermomediterranean area (Figures 4, S2). Sa Curcurica and to a lesser extend Gorgo Basso might be an exception for the Great European Famine, as it is not reflected in LUP data (sites 18 and 19 in Figures 4, S2). This finding is in agreement with historical evidence pointing to southern Italy as one of the regions that exported food during the climatically-driven Great European Famine (Baek et al., 2020).

5. Conclusions

In this study, we developed and tested a new agricultural land use probability (LUP) index based on selected and weighted anthropogenic indicator values (AIV). Because the AIV values account for regional differences in plant distributions, abundances, and agricultural practices, the new LUP index is in its nature probabilistic and region-

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specific. The LUP index represents a general procedure with a high indicative power for most major biomes of Europe that, with due caution, is easy to apply for pollen-inferred land-use reconstructions. When the boundary conditions and premises for its applicability are met (e.g., sufficient taxonomic resolution), our index faithfully reflects the trajectory of human impacts as inferred from the original pollen profiles. The LUP index is parsimonious and makes comparisons across sites within similar vegetation types possible (e.g., subalpine/alpine, colline/montane, submediterranean, mesomediterranean and thermomediterranean). The crops and weeds native to the Mediterranean deserve special attention and are in our case probably leading to an underestimation of human activity in the warmest thermomediterranean belt.

The determination of the most useful quantitative pollen indicators for a given area needs a thorough validation with independent evidence, for instance from archaeology and archaeobotany. So far, numerical archaeological evidence readily comparable to stratigraphic land-use evidence like that coming from palynology is very scarce. Our tentative validation with independent pollen sequences and compiled radiocarbon dates from archaeological contexts suggests that the LUP index procedure may be applied outside the regions used for its development, as long as new cultural indicator pollen types can be incorporated to adjust the AIVs. Further developments in this field include the use of new technologies (e.g., sedimentary ancient DNA, molecular biomarkers) for refining the taxonomic resolution of the pollen indicators and the biogeography studies that attribute categories of adventive or apophyte, according to geographic location.

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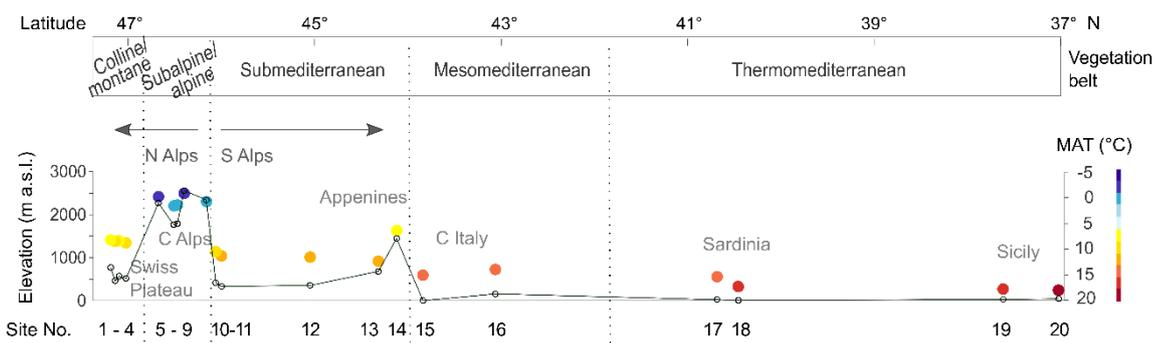
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(a) Environmental gradients of calibration sites



(b) Anthropogenic Indicative Value (AIV) for the selected pollen indicators included in the LUP index

AIV (to be multiply by pollen %)	10	10	10	10	10	PI1 others (§)	PI1	
	10	10	10	10	10	Cerealia-type		
	0.25	0.25	0.25	0.25	0.25	<i>Cannabis sativa</i> *		
	10	10	0.25	10	10	<i>Castanea sativa</i> *		
	10	10	2.5	10	10	<i>Juglans regia</i> *		PI2
	10	10	10	10	0	<i>Olea europaea</i> *		
	10	10	10	10	0	<i>Plantago lanceolata</i> -type*		ADV
	10	10	10	10	10	<i>Mercurialis annua</i>		APO
	10	10	10	10	0	<i>Urtica dioica</i> -type*		

Figure 1. (a) Environmental gradients of the pollen sites considered in this study: Elevation (m a.s.l.), mean annual temperature (MAT; °C), latitude (°N), geographical region and vegetation belts. (b) Selected pollen indicators and their corresponding anthropogenic indicative values (AIV) in the land use probability (LUP) index. PI1 others (§): *Avena*-t., *Hordeum*-t., *Triticum*-t., *Secale*-t., *Zea mays*, *Pisum sativum*, *Vicia faba*-t., *Fagopyrum*, *Linum usitatissimum*-t. * denotes pollen indicators with reduced or not AIV in at least one vegetation belt. The LUP index does not consider the use of *Olea europaea*, *Plantago lanceolata*-t. and *Urtica dioica*-t. in the thermomediterranean vegetation belts. *Juglans regia* is seldom recorded in the thermomediterranean study sites. Site No.: 1= Egelsee (Menzingen), 2= Burgäschisee, 3= Soppensee, 4= Moossee, 5= Bachalpsee; 6= Lej da San Murezzan, 7= Lej da Champfèr, 8= Lengi Egga, 9= Gouillé Rion, 10= Lago di Origlio, 11= Lago di Muzzano, 12= Lago Piccolo di Avigliana, 13= Pavullo nel Frignano, 14= Lago del Greppo, 15=Lago di Massaciucoli, 16=Lago dell'Accesa, 17=Lago di Baratz, 18=Sa Curcurica, 19=Gorgo Basso, 20=Biviere di Gela.

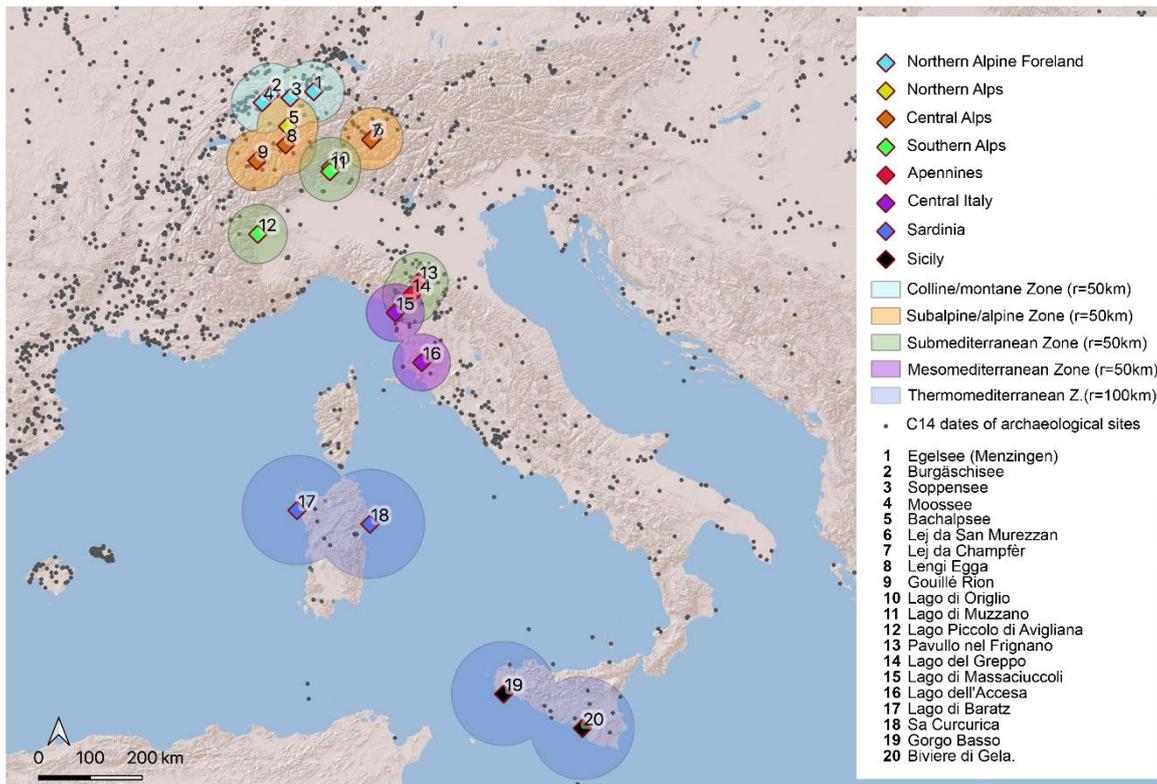


Figure 2. Calibration sites and buffer areas used to select the radiocarbon data. The radius around the sites is 50 km for all sites with exception of the thermomediterranean areas in Sardinia and Sicily, due to the reduced number of available radiocarbon dates due to coastal location.

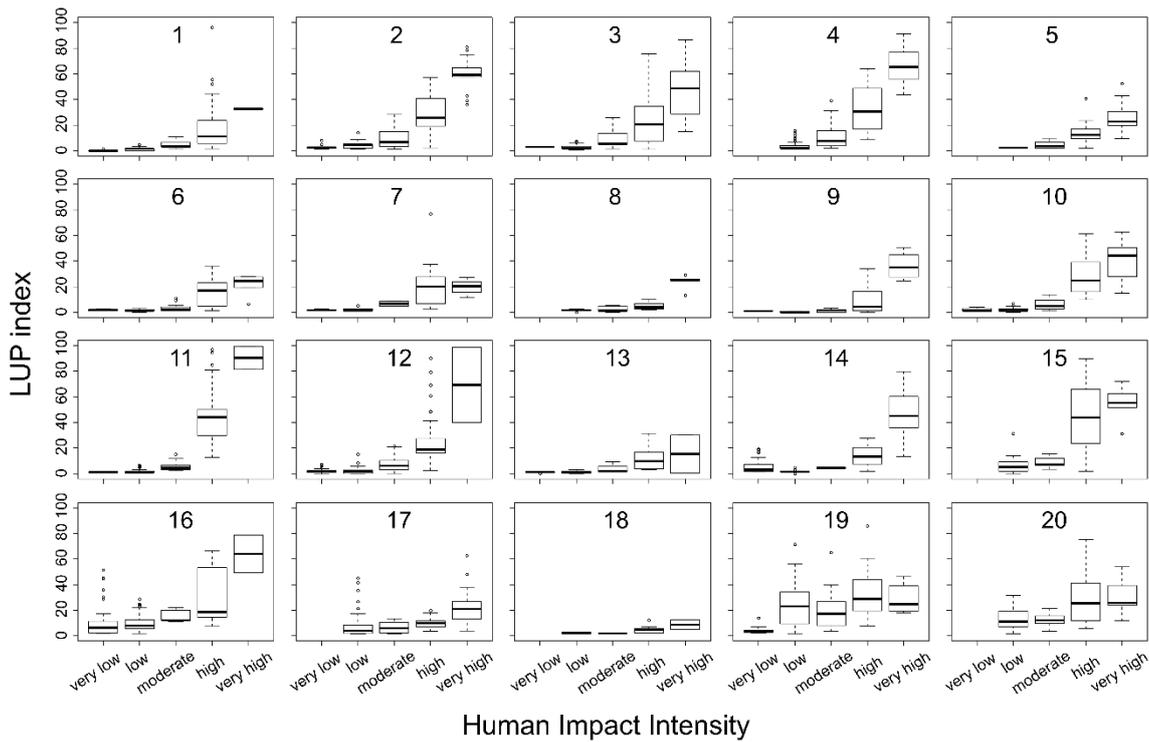


Figure 3. Boxplots of the land use probability (LUP) index response to degrees of human impact intensity (Deza-Araujo et al., 2020) in the calibration sites: 1= Egelsee (Menzingen), 2= Burgäschisee, 3= Soppensee, 4= Moossee, 5= Bachalpsee; 6= Lej da San Murezzan, 7= Lej da Champfèr, 8= Lengi Egga, 9= Gouillé Rion, 10= Lago di Origlio, 11= Lago di Muzzano, 12= Lago Piccolo di Avigliana, 13= Pavullo nel Frignano, 14= Lago del Greppo, 15=Lago di Massaciucoli, 16=Lago dell'Accesa, 17=Lago di Baratz, 18=Sa Curcurica, 19=Gorgo Basso, 20=Biviere di Gela. The degrees of Human Impact Intensity correspond with the following archaeological and historical periods: very low= Palaeolithic and Mesolithic; low= Neolithic; moderate= Bronze Age; high= Iron Age, Roman Imperial Period, Early Middle Ages; and very high= High Middle Ages, Modern Era.

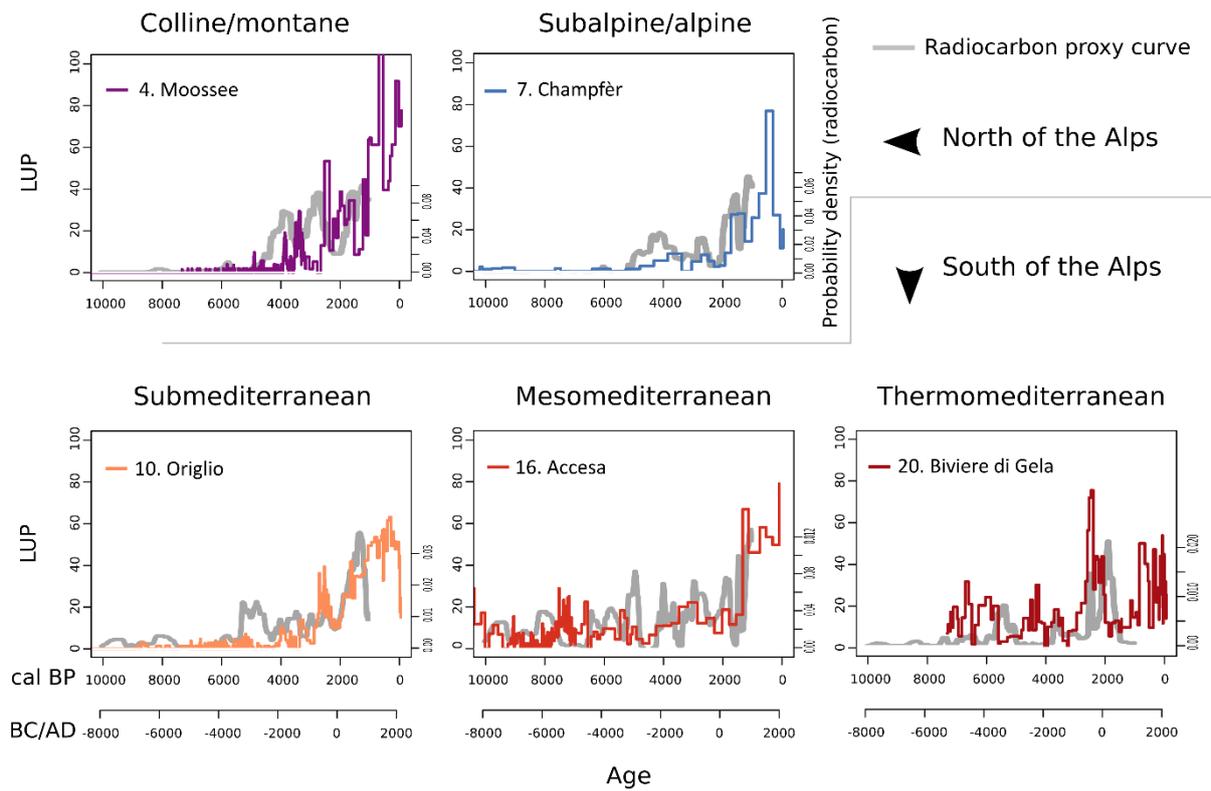


Figure 4. Land use probability (LUP) index at some of the sites included in the calibration dataset. Only one site per vegetation belt is shown (see Figure S2 for the curves of all the sites of the calibration dataset). Y-axis “LUP” is limited to a maximum of 100. In grey, the curve of radiocarbon proxy calculated from sites within a 50-km radius buffers around the sites combined into one curve per vegetation type (subalpine/alpine to thermomediterranean, see Fig. 2) used for archaeological validation, except at the thermomediterranean sites, where the buffers had 100-km radius.

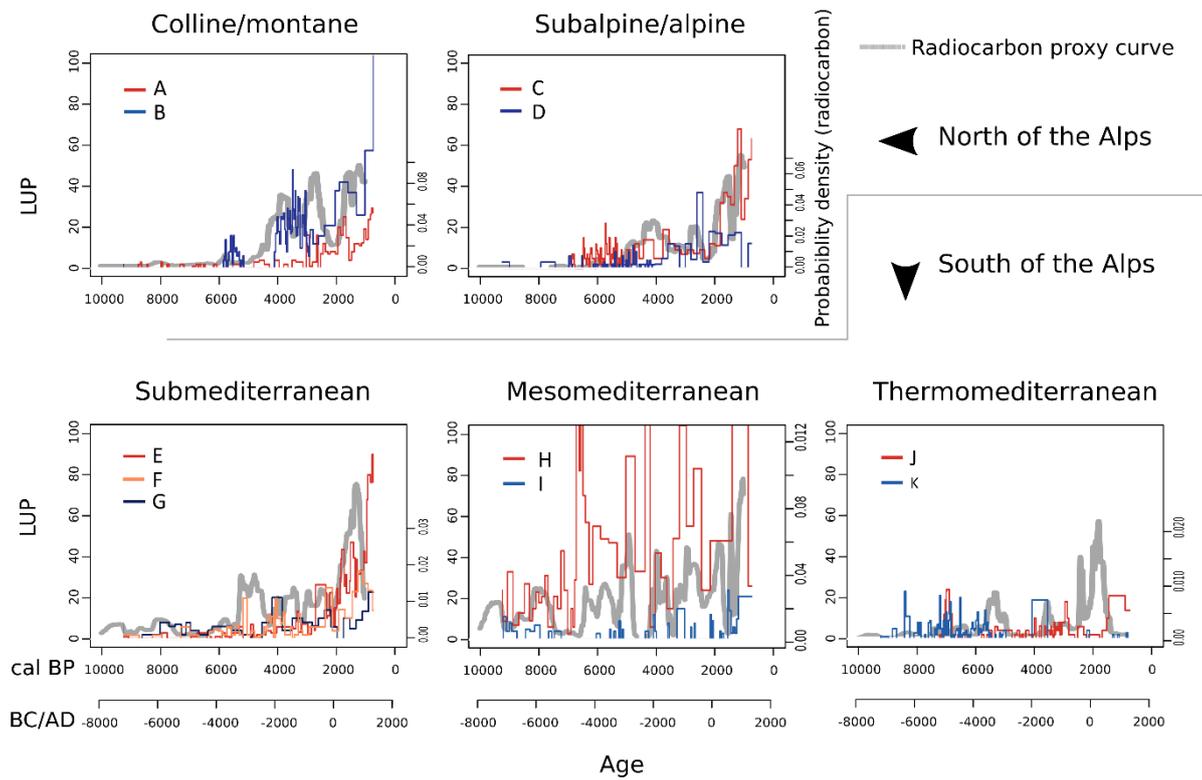


Figure 5. Validation of the land use probability (LUP) index with independent sites: A= Etang de la Gruère, B= Launensee, C= Iffigsee, D= Hopschensee, E= Lago del Segrino, F= Lago Verdarolo, G= Limni Zazari, H= Lago di Martignano, I= Ojos de Villaverde, J= Stagno di Chia, K=San Rafael.

Y-axis “LUP” is limited to a maximum of 100. In gray, the curve of radiocarbon proxy calculated from sites within a 50-km radius buffers around the sites combined into one curve per vegetation type (subalpine/alpine to thermomediterranean, see Fig. 2) used for archaeological validation, except at the thermomediterranean sites, where the buffers had 100-km radius. For the individual site plots, see Figure S3.

Table 1. Main features of the palynological records considered in the calibration of the land use probability (LUP) index.

<i>Vegetation belt</i>	<i>Site</i>	<i>Lat (°N), Long (°E)</i>	<i>Elevation (m a.s.l.)</i>	<i>Area (ha)</i>	<i>Age range (cal. yr BP)</i>	<i>MAT (°C) (Fick and Hijmans, 2017)</i>	<i>Reference</i>
Colline/montane	1. Egelsee (Menzingen)	47.183480, 8.582379	770	1.2	50 – 16200	8.7	Wehrli et al., 2007
	2. Burgäschisee	47.148056, 7.658333	465	21	-50 – 18700	8.9	Rey et al., 2017; Rey et al., 2019b; Rey et al., 2019a
	3. Soppensee	47.090421, 8.080115	596	22.7	-50 – 14200	8.6	Lotter, 1999
	4. Moossee	47.021944, 7.480278	521	31	3850 – 7100	9	Rey et al., 2020; Rey et al., 2019b; Rey et al., 2019a
Subalpine/alpine	5. Bachalpsee	46.670356, 8.023247	2265	8	-50 – 12900	0.2	Lotter et al., 2006
	6. Lej da San Murezzan	46.495168, 9.845067	1768	78	-50 – 11900	1.9	Gobet et al., 2003, 2005
	7. Lej da Champfèr	46.471268, 9.807297	1791	50	-50 – 11850	1.8	Gobet et al., 2003, 2005
	8. Lengi Egga	46.396840, 7.980020	2557	2.89	10 – 12600	-0.6	Tinner and Theurillat, 2003
	9. Gouillé Rion	46.157222, 7.362778	2343	0.16	-50 – 11950	1.0	Tinner et al., 1996
Submediterranean	10. Lago di Origlio	46.060435, 8.942306	416	8	-50 – 18900	10.6	Tinner et al., 1999
	11. Lago di Muzzano	45.996621, 8.928177	337	22	-50 – 15150	11.5	Tinner et al., 1999; Gobet et al., 2000
	12. Lago Piccolo di Avigliana	45.05000, 7.383334	356	60	320 – 19350	11.8	Finsinger et al., 2006; Finsinger and Tinner, 2006; Vescovi et al., 2007
	13. Pavullo nel Frignano	44.318335, 10.837500	675	ca. 20	100 – 16300	12.6	Vescovi et al., 2010a
	14. Lago del Greppo	44.119722, 10.683055	1442	0.018	-50 – 14950	6.7	Vescovi et al., 2010b
Mesomediterranean	15. Lago di Massaciuccoli	43.83784, 10.3308	0	700	0-7000	15	Colombaroli et al., 2007
	16. Lago dell'Accesa	43.059388, 10.898260	157	16	50 – 11600	14.2	Colombaroli et al., 2008, 2009; Vannièrè et al., 2008
Thermomediterranean	17. Lago di Baratz	40.68089, 8.22551	27	60	-20-8000	15.8	Pedrotta et al., 2021
	18. Sa Curcurica	40.45547, 9.78752	0	38	-50-8100	17.3	Beffa et al., 2016
	19. Gorgo Basso	37.609174, 12.654939	6	3	-50– 10200	18.1	Tinner et al., 2009
	20. Biviere di Gela	37.01879, 14.34455	7	120	-50– 7350	18.5	Noti et al., 2009

Excellent indicator ●●●●	Good indicator ●●●○	Fair indicator ●●○○	Poor indicator ●○○○
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Human Pollen indicators	Overall indicative capacity	Adventive-ness	Taxonomic resolution	Pollen production/deposition	Exponential increase in the pollen diagram	Over-representation in the pollen diagram
	Excellent indicator	Adventive= Excellent	High= Excellent	High= Excellent	Always= Excellent	Almost Never True = Excellent
	Poor indicator	Apophyte= Poor	Low= Poor	Low= Poor	Rarely = Poor	Almost Always True = Poor
<i>Included in the LUP index</i>						
PI1						
<i>Avena</i> -type	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Fagopyrum</i>	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Hordeum</i> -type	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Triticum</i> -type	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Zea mays</i>	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Pisum sativum</i>	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Secale cereale</i>	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Vicia faba</i> -type	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Linum usitatissimum</i> -type	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
PI1 - other						
<i>Cannabis sativa</i> -type	●●●●	●●●●	●●●●	●○○○	●●●●	●○○○
Cerealia-type*	●●●●	●●●●	●●●○	●●●●	●●●●	●●●●
PI2						
<i>Castanea sativa</i> §	●●●●	●●○○	●●●●	●●●○	●●●●	●●●●
<i>Juglans regia</i> §	●●●●	●●○○	●●●●	●●●○	●●●●	●●●●
<i>Olea europaea</i> §	●●●●	●●○○	●●●●	●○○○	●●●●	●○○○
ADV						
<i>Plantago lanceolata</i> -type	●●●●	●●●●	●●●●	●●●○	●●●●	●●●●
APO						
<i>Mercurialis annua</i>	●●●●	●●○○	●●●●	●●●○	●●●●	●●●●
<i>Urtica dioica</i> -type	●●●●	●●○○	●●●●	●●●○	●●●●	●●●●

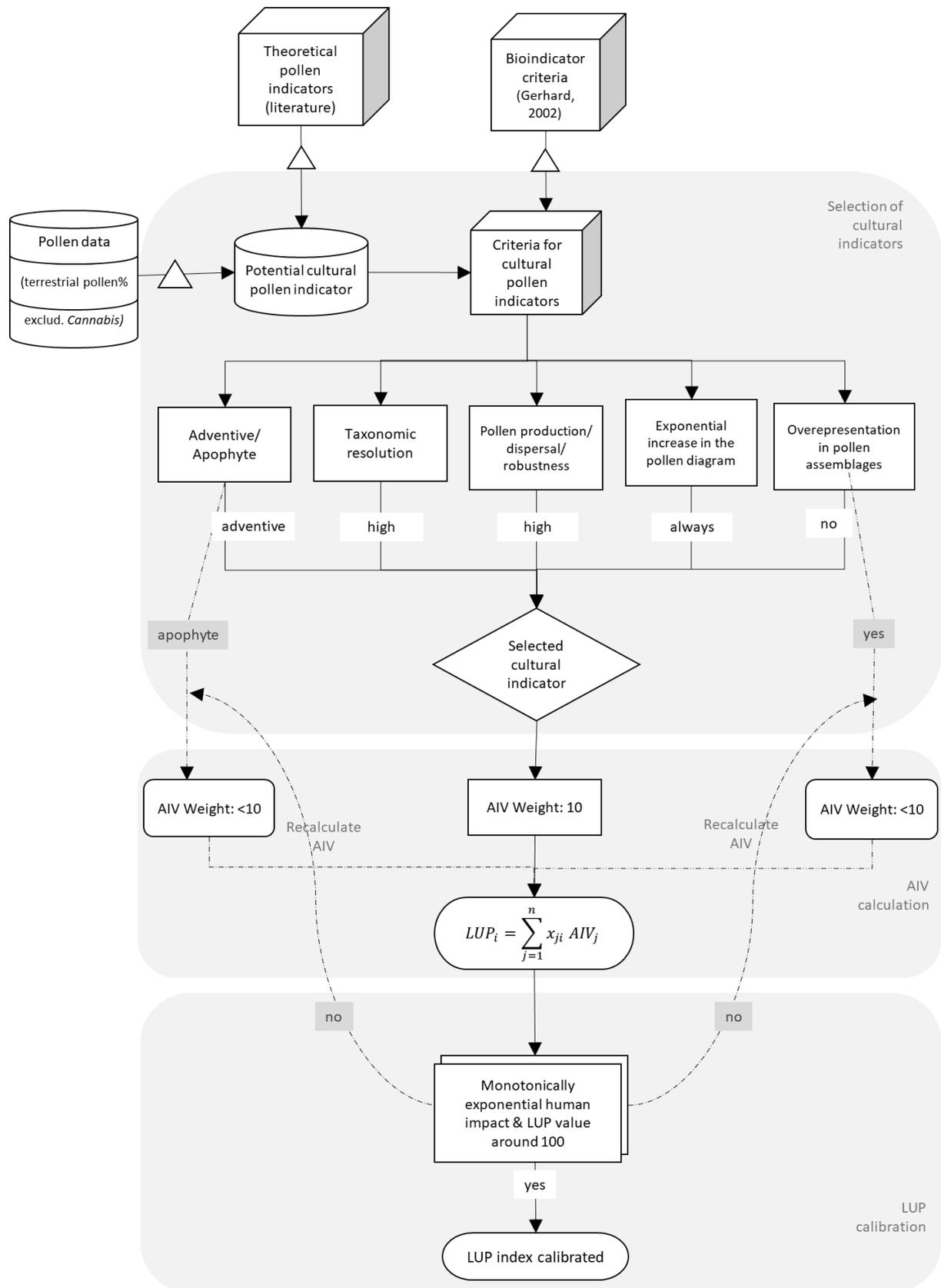
Table 2. Pollen indicators included in the land use probability (LUP) index and results of the four-point scale analysis to measure empirical relationships between various aspects of the indicators and their importance to record land use in pollen diagrams (Bradshaw et al., 1981; Broström et al., 2005; Deza-Araujo et al., 2020, 2021; Lang, 1994; Molina et al., 1996; Prentice and Webb, 1986). See also Table S1 for a complete list of the cultural indicator pollen types considered in the analysis but eventually not included in LUP. *Cerealia-t. refers to the same Cerealia taxa indicated in PI1, but at lower taxonomic resolution.

PI1 =primary indicators (crops) non-native to Europe; PI2 =primary indicators native to Europe. SI= secondary indicators (weeds); ADV= adventives (non-native); APO= apophytes (native). (§) adventive in the colline/montane and subalpine vegetation belts

Table 3. Main features of the palynological records considered in the external validation of the land use probability (LUP) index.

<i>Vegetation belt</i>	<i>Site</i>	<i>Lat (°N), Long (°E)</i>	<i>Elevation (m a.s.l.)</i>	<i>Area (ha)</i>	<i>Age range (cal. yr BP)</i>	<i>MAT (°C)</i>	<i>Reference</i>
Colline/ montane	A) Etang de la Gruère	47.240556, 7.050000	1005	22.5	800 – 11900	5.5	Roos-Barraclough et al., 2004
	B) Launensee	46.39684, 7.331430	1381	8.78	-50 – 14200	4.9	Rey et al., 2013
Subalpine/ alpine	C) Iffigsee	46.38679, 7.405890	2065	10	-50 – 11250	6.5	Schwörer et al., 2014, 2015
	D) Hopschensee	46.25250, 8.023056	2026	1	100 – 13600	7	Curdy et al., 2020
Submedi- terranean	E) Lago del Segrino	45.82802, 9.26482	374	38	-50 – 14350	12	Gobet et al., 2000
	F) Lago Verdarolo	44.359222, - 10.123111	1390	1	-50 – 14450	6	Morales-Molino et al., 2021
	G) Limni Zazari	40.625277, - 21.547222	606	200	-50 – 22300	12.3	Gassner et al., 2020
Mesomedi- terranean	H) Lago di Martignano	42.11227, 12.31566	204	244	0-11700	17	Kelly and Huntley, 1991
	I) Ojos de Villaverde	38.79895, - 2.36032	870	0	-50 – 9700	13-14	Carrión et al., 2001
Thermome- diterranean	J) Stagno di Chia	38.896512, 8.874978	0	16	-50 – 7850	19	Unpublished data
	K) San Rafael	36.773611, - 2.601389	0	ex- marsh	0 – 20580	18-21	Pantaléon-Cano et al., 2003

Figure S1. Methodology workflow for the land use probability (LUP) index.



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Table S1. Complete list of pollen indicators present in our study areas and the results of the four-point scale analysis to measure empirical relationships between various aspects of the indicators and their importance to register human land use in pollen diagrams.

		Excellent indicator ●●●●	Good indicator ●●●○	Fair indicator ●●○○	Poor indicator ●○○○	
Human Pollen indicators	Overall indicative capacity	<i>Adventive-ness</i>	<i>Taxonomic resolution</i>	<i>Pollen production/deposition</i>	<i>Exponential increase in the pollen diagram</i>	<i>Over-representation in the pollen diagram</i>
	Excellent indicator	<i>Adventive=Excellent</i>	<i>High=Excellent</i>	<i>High=Excellent</i>	<i>Always=Excellent</i>	<i>Almost never true = excellent</i>
	Poor indicator	<i>Apophyte= Poor</i>	<i>Low= Poor</i>	<i>Low= Poor</i>	<i>Rarely = Poor</i>	<i>Almost always true = poor</i>
<i>Included in the LUP index</i>						
PI1						
<i>Avena</i> -type	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Fagopyrum</i>	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Hordeum</i> -type	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Triticum</i> -type	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Zea mays</i>	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Pisum sativum</i>	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Secale cereale</i>	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Vicia faba</i> -type	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
<i>Linum usitatissimum</i> -type	●●●●	●●●●	●●●●	●●●●	●●●○	●●●●
PI1 - other						
<i>Cannabis sativa</i> -type	●●●●	●●●●	●●●●	●○○○	●●●●	●○○○
Cerealia-type*	●●●●	●●●●	●●●○	●●●●	●●●●	●●●●
PI2						
<i>Castanea sativa</i> §	●●●●	●●○○	●●●●	●●●○	●●●●	●●●●
<i>Juglans regia</i> §	●●●●	●●○○	●●●●	●●●○	●●●●	●●●●
<i>Olea europaea</i> §	●●●●	●●○○	●●●●	●○○○	●●●●	●○○○
ADV						
<i>Plantago lanceolata</i> -type	●●●●	●●●●	●●●●	●●●○	●●●●	●●●●
APO						
<i>Mercurialis annua</i>	●●●●	●●○○	●●●●	●●●○	●●●●	●●●●
<i>Urtica dioica</i> -type	●●●●	●●○○	●●●●	●●●○	●●●●	●●●●
<i>NOT Included in the LUP index</i>						
PI2						
<i>Ficus carica</i>	●●●○	●●●○	●●●●	●●●●	●○○○	●●●●
<i>Vitis</i>	●●●○	●○○○	●●●●	●●●○	●○○○	●○○○
ADV						
<i>Agrostemma githago</i>	●●●○	●●●○	●●●●	●●●○	●○○○	●●●●
<i>Arenaria</i>	●●●○	●●●○	●●●●	●●●○	●○○○	●●●●
<i>Bromus</i>	●●●○	●●●○	●●●●	●●●○	●○○○	●●●●
<i>Centaurea cyanus</i> -type	●●●○	●●●○	●●●●	●●●○	●○○○	●●●●
<i>Nigella</i>	●●●○	●●●○	●●●●	●●●○	●○○○	●●●●

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<i>Persicaria maculosa</i> -type	●●●○	●●●○	●●●●	●●○○	●○○○	●●●●
<i>Plantago major</i>	●●●○	●●●○	●●●●	●●○○	●○○○	●●●●
<i>Plantago media</i>	●●●○	●●●○	●●●●	●●○○	●○○○	●●●●
<i>Plantago major/P. media</i> -type	●●●○	●●●○	●●●●	●●○○	●○○○	●●●●
<i>Polygonum aviculare</i> -type	●●●○	●●●○	●●●●	●●○○	●○○○	●○○○
<i>Scleranthus</i>	●●●○	●●●○	●●●●	●●○○	●○○○	●○○○
<i>Spergula</i> -type	●●●○	●●●○	●●●●	●●○○	●○○○	●○○○
<i>Torilis japonica</i>	●●●○	●●●○	●●●●	●●○○	●○○○	●●●●
APO						
<i>Achillea</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Adonis</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
Amaranthaceae	●●○○	●○○○	●○○○	●○○○	●○○○	●○○○
<i>Ambrosia</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Anthemis</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Anthriscus sylvestris</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Artemisia</i>	●●○○	●○○○	●●●○	●○○○	●○○○	●●●●
Asteraceae subf. Asteroideae**	●●●○	●○○○	●●●○	●○○○	●●●●	●●●●
Apiaceae	●●○○	●○○○	●○○○	●●○○	●○○○	●○○○
Asteraceae subf. Cichorioideae	●●●○	●○○○	●●○○	●○○○	●○○○	●●●●
<i>Bellis</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Bidens</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
Brassicaceae	●●○○	●○○○	●○○○	●○○○	●○○○	●○○○
<i>Caltha</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Calluna vulgaris</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
Campanulaceae	●●○○	●○○○	●●○○	●●○○	●○○○	●●●●
Cannabaceae	●●○○	●○○○	●●○○	●○○○	●○○○	●●●●
Caprifoliaceae subf. Dipsacoideae	●●○○	●○○○	●○○○	●●○○	●○○○	●●●●
<i>Carum carvi</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Carum</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
Caryophyllaceae	●○○○	●○○○	●○○○	●●●○	●○○○	●●●●
<i>Cerastium arvense</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
Cyperaceae	●○○○	●○○○	●○○○	●●○○	●●●●	●○○○
<i>Daucus</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Daucus carota</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Dipsacus</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Draba</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Erigeron</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Gnaphalium</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Heracleum</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Humulus</i> -type	●●○○	●○○○	●●●○	●○○○	●○○○	●●●●
<i>Jasione</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Juniperus</i> -type	●○○○	●○○○	●●●○	●○○○	●○○○	●●●●
<i>Knautia</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●

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<i>Knautia arvensis</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Linum</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Linum catharticum</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Linum catharticum</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Melampyrum</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Orlaya</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Orlaya grandiflora</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Pimpinella major</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Pistacia</i>	●●○○	●○○○	●●●●	●●○○	●○○○	●●●●
<i>Plantago</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
Poaceae	●●●○	●○○○	●○○○	●●●●	●○○○	●○○○
<i>Polygonum</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●○○○
Ranunculaceae	●○○○	●○○○	●○○○	●●○○	●○○○	●○○○
<i>Ranunculus acris</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Ranunculus arvensis</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Ranunculus</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Rumex acetosa</i> -type	●●●○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Rumex acetosa</i> / <i>R. acetosella</i> -type	●●●○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Rumex acetosella</i> -type	●●●○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Rumex obtusifolius</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Saponaria</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Senecio</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Scabiosa</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Scabiosa columbaria</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Silene</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Sinapis</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Succisa</i>	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Succisa pratensis</i> -type	●●○○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Trifolium pratense</i> -type	●●●○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Trifolium repens</i> -type	●●●○	●○○○	●●●○	●●○○	●○○○	●●●●
<i>Trifolium</i> -type	●●●○	●○○○	●●○○	●●○○	●○○○	●●●●
<i>Urtica</i>	●●○○	●○○○	●○○○	●●○○	●●●●	●●●●
<i>Urtica membranacea</i>	●●○○	●○○○	●●●○	●●○○	●●●○	●●●●
<i>Vicia/Lathyrus</i> -type	●●○○	●○○○	●●○○	●●○○	●○○○	●●●●

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Table S2. Selected cultural indicator pollen types of the land use probability (LUP) index, showing their presence (x) or absence (-) in each calibration site: Site No.: 1= Egelsee (Menzingen), 2= Burgäschisee, 3= Soppensee, 4= Moossee, 5= Bachalpsee; 6= Lej da San Murezzan, 7= Lej da Champfèr, 8= Lengi Egga, 9= Gouillé Rion, 10= Lago di Origlio, 11= Lago di Muzzano, 12= Lago Piccolo di Avigliana, 13= Pavullo nel Frignano, 14= Lago del Greppo, 15=Lago di Massaciuccoli, 16=Lago dell'Accesa, 17=Lago di Baratz, 18=Sa Curcurica, 19=Gorgo Basso, 20=Biviere di Gela.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Avena</i> -type	x	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Fagopyrum</i>	-	-	-	-	-	-	-	x	-	x	x	-	-	-	-	-	-	-	-	-
<i>Hordeum</i> -type	x	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Triticum</i> -type	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Zea mays</i>	-	-	x	x	x	x	-	x	-	x	-	-	-	-	x	-	-	-	-	x
<i>Pisum sativum</i>	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
<i>Secale cereale</i>	x	x	x	x	x	x	x	x	x	x	x	x	-	x	x	-	-	-	-	x
<i>Vicia faba</i> -type	-	-	-	-	x	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-
<i>Linum usitatissimum</i> -type	x	x	-	-	x	x	-	-	-	x	-	-	-	-	-	-	-	-	x	-
PI1 - other																				
<i>Cannabis sativa</i> -type	x	x	-	-	x	x	x	x	-	x	x	-	-	x	x	x	x	x	x	x
Cerealia-type	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
PI2																				
<i>Castanea sativa</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Juglans regia</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-	x
<i>Olea europaea</i>	-	x	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
ADV																				
<i>Plantago lanceolata</i> -type	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
APO																				
<i>Mercurialis annua</i>	x	x	-	x	x	-	-	-	-	-	-	-	-	x	-	x	x	-	x	x
<i>Urtica dioica</i> -type	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	x	x

Table S3. Archaeological data used to calculate radiocarbon date frequency distributions.

Vegetation belt	Site Name	Longitude	Latitude	No dates
Colline/montane	Abri Bergilbalm	8.75	46.97	5
Colline/montane	Abri de la Souche	7.12	46.75	1
Colline/montane	Abri des Gripons	7.15	47.37	1
Colline/montane	Abri St Joseph	7.38	47.47	8
Colline/montane	Aesch/Clus/Tschäpperli	7.57	47.47	6
Colline/montane	Affoltern, Zwillikon-Weid	8.43	47.29	2
Colline/montane	Arlesheim, Birseck-Ermitage	7.63	47.5	7
Colline/montane	Auvernier, La Saunerie	6.88	46.98	19
Colline/montane	Baar - Früebergstrasse	8.52	47.2	2
Colline/montane	Baar ZG, Martinspark	8.52	47.19	5
Colline/montane	Baar - Früebergstrasse	8.52	47.2	3
Colline/montane	Baie d'Auvernier	6.88	46.97	1
Colline/montane	Basel BS, Neuhausstrasse 31	7.6	47.58	1
Colline/montane	Birch, Düdingen	7.19	46.86	1
Colline/montane	Birmensdorf-Rameren	8.45	47.36	14
Colline/montane	Birmensdorf-Wannenboden	8.46	47.34	3
Colline/montane	Birsmatten, Basisgrotte	7.55	47.45	8
Colline/montane	Boswil AG, Eibolde	8.32	47.29	2
Colline/montane	Burgäschisee-Süd	7.67	47.15	2
Colline/montane	Cham - Erlen	8.46	47.18	6
Colline/montane	Cham - St. Andreas, Strandbad	8.47	47.18	1
Colline/montane	Cham-Oberwil	8.46	47.21	13
Colline/montane	Champreyres	6.97	47.02	1
Colline/montane	Courgevaux FR, Le Marais 1	7.1	46.91	2
Colline/montane	Courgevaux-En Triva	7.11	46.91	1
Colline/montane	Dachlissen, Wandacher	8.44	47.26	2
Colline/montane	Delley-Portalban	6.96	46.91	13
Colline/montane	Delley-Portalban II	6.96	46.91	1
Colline/montane	Derrière la Croix	6.98	46.88	1
Colline/montane	Dolmen of Oberbipp	7.67	47.27	68

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Colline/montane	Dornach - Landskronstrasse	7.61	47.48	2
Colline/montane	Egolzwil 3	8	47.18	13
Colline/montane	Egolzwil 4	8.01	47.18	9
Colline/montane	Egolzwil 5	8.01	47.19	3
Colline/montane	En Chaplix	7.05	46.89	2
Colline/montane	Erlach-Heidenweg	7.12	47.06	2
Colline/montane	Eschenbach	8.92	47.24	1
Colline/montane	Eschenbach SG, Balmenrain	8.93	47.23	1
Colline/montane	Eschenbach SG, Neuhaus, Bärstli, Balmenrainstrasse	8.94	47.24	2
Colline/montane	Faug VD-Derrière-le- Chaney	7.08	46.9	4
Colline/montane	Feldbach	8.79	47.24	2
Colline/montane	Feldmeilen-Vorderfeld	8.62	47.28	9
Colline/montane	Freienbach	8.76	47.21	2
Colline/montane	Freienbach SZ-Hurden Rosshorn	8.81	47.22	81
Colline/montane	Frick AG, Königsweg	8.03	47.5	2
Colline/montane	Fällanden	8.64	47.37	1
Colline/montane	Fällanden-Fröschbach	8.64	47.37	6
Colline/montane	Greifensee-Storen	8.63	47.28	2
Colline/montane	Grundrebenstrasse	8.46	47.25	1
Colline/montane	Herblingen	8.19	47.13	1
Colline/montane	Hergiswil-Renggpas	8.29	46.98	1
Colline/montane	Herzogenbuchsee, Badwald	7.73	47.21	1
Colline/montane	Hochdorf-Baldeg	8.28	47.18	6
Colline/montane	Hof, Cham	8.46	47.22	3
Colline/montane	Hofacher, Ebmatingen	8.64	47.35	5
Colline/montane	Horn	7.96	47.48	1
Colline/montane	Hegenheim	7.53	47.56	1
Colline/montane	Hüneberg - Chämleten	8.45	47.18	11
Colline/montane	Hünenberg-Chämleten, Strandbad	8.43	47.18	29
Colline/montane	Inkwil BE/Bolken SO, Inkwilersee	7.66	47.2	1

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Colline/montane	Ipsach-Räberain	7.23	47.11	1
Colline/montane	Jona SG, Wagen-Erlen	8.88	47.23	2
Colline/montane	Jona SG, Wagen-Geretswis	8.89	47.23	2
Colline/montane	Kernenried, Holzmühle	7.54	47.06	1
Colline/montane	Klausenpasshöhe	8.85	46.87	1
Colline/montane	Kleiner Hafner	8.55	47.37	1
Colline/montane	Koppigen, Usserfeld	7.59	47.14	1
Colline/montane	Köniz-Niederwangen, Stegenweg	7.37	46.93	6
Colline/montane	Lenzburg - Goffersberg	8.18	47.39	3
Colline/montane	Les Fiefs	8.23	46.8	14
Colline/montane	Les Picettes	7.02	47.02	4
Colline/montane	Loppburg	8.33	46.98	5
Colline/montane	Mannlefelden	7.24	47.46	4
Colline/montane	Marin NE-Le Chalvaire	7.01	47.01	5
Colline/montane	Maur	8.66	47.34	1
Colline/montane	Meikirch, Magazingebäude	7.36	47.01	1
Colline/montane	Meilen-Feldmeilen, Vorderfeld	8.62	47.28	1
Colline/montane	Meilen-Obermeilen	8.66	47.29	4
Colline/montane	Meinisberg, Scheidwege	7.36	47.17	4
Colline/montane	Montbec	6.97	46.93	2
Colline/montane	Moos	7.42	46.92	2
Colline/montane	Muntelier	7.14	46.94	1
Colline/montane	Murten - Vorder Prehl 3	7.13	46.93	1
Colline/montane	Murten-Löwenberg	7.14	46.94	8
Colline/montane	Männedorf	8.7	47.26	1
Colline/montane	Münchenwiler-Im Loch 1	7.12	46.92	3
Colline/montane	Münchenwiler-Im Loch 3	7.12	46.92	2
Colline/montane	Mänchringen, Mooswald	7.53	47.04	1
Colline/montane	Neftenbach I (Steinmüri)	8.67	47.53	3
Colline/montane	Neftenbach II (Zürichstrasse 55)	8.66	47.53	4
Colline/montane	Niederwil	8.9	47.57	10
Colline/montane	Niederwil - Egelsee	8.86	47.55	1

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Colline/montane	Oberlarg, Abri du Mannlefelsen	7.23	47.45	1
Colline/montane	Ostermundigen, Dennikofe	7.49	46.94	5
Colline/montane	Payerne VD, route de Bussy	6.91	46.83	1
Colline/montane	Payerne VD-Neyremont	6.92	46.82	1
Colline/montane	Pfäffikon, Feld/Kempttalstrasse	8.77	47.38	1
Colline/montane	Pieterlen, Under-Siedebrunne 3	7.36	47.17	5
Colline/montane	Pieterlen, Vorem Holz 1	7.35	47.17	1
Colline/montane	Pleigne, Löwenburg	7.32	47.44	4
Colline/montane	Pont de Thielle	7.04	47.02	2
Colline/montane	Rapperswil - Kempraten	8.82	47.22	2
Colline/montane	Rhinsberg	8.54	47.55	4
Colline/montane	Ried-Hölle	7.2	46.95	1
Colline/montane	Risch	8.47	47.14	3
Colline/montane	Russikon, Furtbäel	8.77	47.41	2
Colline/montane	Saint-Ursanne	7.15	47.36	2
Colline/montane	Schenkon	8.13	47.18	2
Colline/montane	Seeberg, Burgäschisee-Süd	7.67	47.16	12
Colline/montane	Seeberg-Burgaeschisee-Sued	7.67	47.17	2
Colline/montane	Silenen-Amsteg, Flüeli	8.67	46.79	2
Colline/montane	Spiez-Einigen, Holleeweg 3	7.64	46.71	12
Colline/montane	Spreitenbach	8.36	47.43	5
Colline/montane	Spreitenbach AG, Willenacher IKEA	8.38	47.42	2
Colline/montane	Station	7.98	47.17	20
Colline/montane	Steinhausen	8.48	47.2	3
Colline/montane	Steinhausen - Sennweid	8.49	47.19	23
Colline/montane	Studen, Studenwald/Waldhaus	7.29	47.11	1
Colline/montane	Thielle-Mottaz (Neuchatel)	7.03	47.01	1
Colline/montane	Thunstetten, Bifang	7.75	47.21	1

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Colline/montane	Thunstetten, Längmatt	7.76	47.21	1
Colline/montane	Twann	7.16	47.09	19
Colline/montane	Twann-Bahnhof	7.16	47.09	1
Colline/montane	Uetikon	8.68	47.26	1
Colline/montane	Vinelz	7.12	47.03	2
Colline/montane	Vorderfeld	8.63	47.27	1
Colline/montane	Wauwilermoos	8.02	47.18	2
Colline/montane	Widen, Höckleri	8.36	47.37	6
Colline/montane	Winterthur, Oberwinterthur, Römerstrasse 229	8.76	47.51	8
Colline/montane	Wädenswil	8.67	47.23	7
Colline/montane	Zug - Schützenmatt	8.51	47.17	5
Colline/montane	Zug, Lorzeninsel	8.5	47.17	3
Colline/montane	Zürich - AKAD/Pressehaus	8.55	47.36	2
Colline/montane	Zürich - Grosser Hafner	8.54	47.36	3
Colline/montane	Zürich - Mozartstrasse (Off-Site)	8.54	47.37	5
Colline/montane	Zürich, Dufourstrasse	8.55	47.36	3
Colline/montane	Zürich, Kleine Hafner	8.54	47.37	19
Colline/montane	Zürich, Mozartstrasse	8.55	47.36	8
Colline/montane	Zürich, Utoquai	8.55	47.37	1
Colline/montane	Zürich, Wallisellen- Langachermoos	8.6	47.42	30
Colline/montane	Zürich, Wollishofen	8.53	47.34	2
Colline/montane	Zürich-Bauschanze	8.54	47.37	2
Colline/montane	Posieux, La Pila	7.11	46.72	2
Colline/montane	Seengen, Primarschule	8.2	47.33	1
Colline/montane	Spiez, Einigen Holeeweg	7.64	46.71	3
Colline/montane	Spreitenbach, Moosweg	8.39	47.42	7
Colline/montane	Stansstad, Kehrsiten	8.36	47	2
Colline/montane	Stüsslingen, Hauptstarsse 52	7.97	47.39	4
Colline/montane	Thielle-Warve, La Mottaz	7.03	47.01	1
Colline/montane	Thielle-Warve, Pont de Thielle	7.03	47.02	2
Colline/montane	Thun, Wilerhölzli	7.6	46.74	1

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Colline/montane	Thun, Schloss	7.63	46.76	1
Colline/montane	Vallon, Sur Dompierre	6.96	46.88	2
Colline/montane	Münchenwiler, Im Loch 1	7.13	46.92	1
Colline/montane	Aarwangen, Eymatte	7.77	47.25	1
Colline/montane	Pieterlen, Under Siedebrunne 1/2	7.35	47.17	1
Colline/montane	Bussy, Prés de Fond	6.9	46.83	2
Colline/montane	Wangen bei Olten, Dorfstrasse 255	7.88	47.35	6
Colline/montane	Hilterfingen, Im Äbnit / Tannenbühlstrasse 38	7.67	46.74	1
Colline/montane	Hilterfingen, Schlosspark Hünegg	7.65	46.74	1
Colline/montane	Illens, Le Château, Abri du Chamois	7.11	46.74	1
Colline/montane	Düdingen, Birch	7.19	46.86	1
Colline/montane	Allmendingen, Kienermätteli	7.52	46.91	2
Colline/montane	Rechterswil, Grod; Jäggenenwald	7.62	47.16	3
Colline/montane	Arconciel, Pré de l'Arche	7.12	46.75	1
Colline/montane	Arconciel, Sous les Châteux; abris 1 et 2	7.11	46.74	4
Colline/montane	Courgevaux, Le Marais 2	7.1	46.91	1
Colline/montane	Courgevaux, Le Marais 1	7.09	46.9	3
Colline/montane	Delley-Portalban, Portalban II	6.95	46.92	4
Colline/montane	Delley-Portalban, Portalban II / Route due Port 57	6.95	46.92	1
Colline/montane	Burgäschi, Burgäschisee-Ost	7.67	47.17	1
Colline/montane	Forel, En Chéseau	6.89	46.88	1
Colline/montane	Haut-Vully, Fischillien 1 et 2	7.08	46.95	1
Colline/montane	Hersiwil, Rainacker	7.63	47.16	2
Colline/montane	Herznach, Unterdorf	8.05	47.48	1
Colline/montane	Hochdorf, Baldegg	8.28	47.18	2
Colline/montane	Kehrsatz, Breitenacher	7.47	46.92	1
Colline/montane	Avenches, En Chaplix	7.05	46.9	2

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Colline/montane	Lenzburg, Goffersberg	8.19	47.39	6
Colline/montane	Marin, Le Chalvaire	7.01	47.01	3
Colline/montane	Baden, Kappelerhof	8.29	47.48	1
Colline/montane	Moosseedorf, Strandbad/Moossee-Ost	7.49	47.02	1
Colline/montane	Morat/Murten, Ober Prehl 2	7.13	46.92	6
Colline/montane	Morat/Murten, Vorder Prehl 2-3	7.13	46.93	4
Colline/montane	Morat/Murten, Löwenberg	7.15	46.94	1
Colline/montane	Bas-Vully, Le Cugnet I	7.09	46.98	1
Colline/montane	Mumpf, Kapf	7.92	47.54	4
Colline/montane	Münchenwiler, Craux Wald	7.13	46.92	2
Colline/montane	Muntelier, Dorf (Fischergässli - Strandweg)	7.12	46.94	1
Colline/montane	Mur, Chenevières de Guévaux II	7.05	46.93	2
Colline/montane	Morat/Murten, Pantschau	7.12	46.93	2
Colline/montane	Payerne, Route de Bussy	6.92	46.83	1
Subalpine/ alpine	Alp Hermettji	7.7	45.97	9
Subalpine/alpine	Alpe Veglia 1	8.14	46.27	2
Subalpine/alpine	Altersheim	7.99	46.33	1
Subalpine/alpine	Aoste	7.31	45.73	1
Subalpine/alpine	Avagna, Colm da Boys, Tinzener	9.68	46.56	1
Subalpine/alpine	Ayent VS-le Château	7.41	46.27	1
Subalpine/alpine	Bagnes-Villette - Les Dzardis	7.21	46.08	3
Subalpine/alpine	Barmaz	6.95	46.27	1
Subalpine/alpine	Biel Valley	10.12	46.9	1
Subalpine/alpine	Bieler Höhe	10.08	46.9	3
Subalpine/alpine	Bivio GR, Stalveder, nördlich Guet da Beiva	9.64	46.49	1
Subalpine/alpine	Carrières MTA	7.42	46.25	10
Subalpine/alpine	Cazis - Petrushügel	9.41	46.74	3
Subalpine/alpine	Cazis-Cresta	9.43	46.71	7

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Subalpine/alpine	Chateau-d'Oex VD	7.13	46.47	1
Subalpine/alpine	Chateau de la Soie	7.33	46.25	4
Subalpine/alpine	Collombey-Muraz - Barmaz I	6.95	46.27	18
Subalpine/alpine	Cretazz-Polet	7.14	46.08	1
Subalpine/alpine	Davos, Tigignas	9.84	46.78	1
Subalpine/alpine	Es-cha Dadour	9.93	46.59	1
Subalpine/alpine	Evolène VS-Barme Bertol	7.5	46.12	1
Subalpine/alpine	Evolène-Arolla - Ouarts- les-Jouttes	7.48	46.03	1
Subalpine/alpine	Grandvillard FR, Fin de la Porta	7.09	46.54	1
Subalpine/alpine	Hergiswil-Renggpas	8.29	46.98	1
Subalpine/alpine	Hohen Rätien	9.44	46.69	2
Subalpine/alpine	Klosmattenstrasse	7.99	46.32	1
Subalpine/alpine	La Baume	6.92	46.4	2
Subalpine/alpine	La Grande Charnie	6.94	46.22	2
Subalpine/alpine	Les Fiefs	8.23	46.8	14
Subalpine/alpine	Loppburg	8.33	46.98	5
Subalpine/alpine	Lötschenpass	7.72	46.42	3
Subalpine/alpine	Massaboden	8	46.33	8
Subalpine/alpine	Mesocco - Tec Nev	9.23	46.39	1
Subalpine/alpine	Mottata			
Subalpine/alpine	Padnal	9.61	46.59	33
Subalpine/alpine	Padnal de Savognin	9.61	46.59	5
Subalpine/alpine	Petit-Chasseur III	7.35	46.23	2
Subalpine/alpine	Piz Böhel	9.26	46.63	1
Subalpine/alpine	Pranoé	7.41	46.23	4
Subalpine/alpine	Pranoé-Villa Chamartin	7.41	46.23	3
Subalpine/alpine	Riparo Pian	8.15	46.27	1
Subalpine/alpine	Rudnal	9.61	46.59	1
Subalpine/alpine	S. Martin de Corléans	7.3	45.73	30
Subalpine/alpine	Saint-Léonard - Les Bâtiments	7.42	46.25	1
Subalpine/alpine	Saint-Martin-de-Corléans	7.3	45.74	3

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Subalpine/alpine	Savièse - Château de la Soie	7.33	46.24	4
Subalpine/alpine	Savièse VS-la Soie	7.33	46.25	1
Subalpine/alpine	Sembrancher - Crettaz Polet	7.15	46.08	1
Subalpine/alpine	Sion	7.36	46.23	1
Subalpine/alpine	Sion - Chemin des Collines	7.35	46.23	12
Subalpine/alpine	Sion - La Gillière 1	7.3	46.2	39
Subalpine/alpine	Sion Petit-Chasseur I	7.35	46.23	22
Subalpine/alpine	Sion, Planta	7.36	46.23	28
Subalpine/alpine	Sion, Tourbillon (VS)	7.36	46.23	4
Subalpine/alpine	Sion-Avenue Ritz	7.36	46.24	10
Subalpine/alpine	Sion-Planta	7.36	46.23	1
Subalpine/alpine	Spiez-Einigen, Holleeweg 3	7.64	46.71	12
Subalpine/alpine	St. Léonard	7.43	46.25	1
Subalpine/alpine	Tanatzalp-Surette	9.33	46.51	1
Subalpine/alpine	Tec Nev	9.22	46.38	1
Subalpine/alpine	Tiragn	9.53	46.66	3
Subalpine/alpine	Val Bavona, Val Calneggia	8.53	46.36	1
Subalpine/alpine	Val Tuoi	10.16	46.78	1
Subalpine/alpine	Val Urschai	10.38	46.62	14
Subalpine/alpine	Valle Bavona, Corte Randinascia	8.5	46.44	1
Subalpine/alpine	Vex - Le Château	7.41	46.21	1
Subalpine/alpine	Viège VS-grotte In Albon	7.87	46.3	1
Subalpine/alpine	Vollein	7.45	45.75	1
Subalpine/alpine	Zermatt - Alp Hermettji	7.75	46.02	2
Subalpine/alpine	avenue Ritz	7.37	46.23	58
Subalpine/alpine	Spiez, Einigen Holeeweg	7.64	46.71	3
Subalpine/alpine	Stansstad, Kehrsiten	8.36	47	2
Subalpine/alpine	Thun, Wilerhölzli	7.6	46.74	1
Subalpine/alpine	Thun, Schloss	7.63	46.76	1
Subalpine/alpine	Bex, Les Mûriers	7.01	46.24	1
Subalpine/alpine	Hilterfingen, Im Äbnit / Tannenbühlstrasse 38	7.67	46.74	1

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Subalpine/alpine	Hilterfingen, Schlosspark Hünegg	7.65	46.74	1
Subalpine/alpine	Charmey, Les Arolles	7.22	46.56	2
Subalpine/alpine	Charmey, Petit Mont Points 2 et 2A	7.23	46.56	1
Subalpine/alpine	Allmendingen, Kienermätteli	7.52	46.91	2
Subalpine/alpine	Grandvillard, Fin de la Porta	7.09	46.54	1
Subalpine/alpine	Lenk, Schnidejoch	7.39	46.37	12
Subalpine/alpine	Ollon, St-Triphon; En la Porte	6.97	46.29	1
Submediterranean	Anzola	11.19	44.55	3
Submediterranean	Baggiovara	10.86	44.61	2
Submediterranean	Barberino del Mugello	11.25	44.01	2
Submediterranean	Bellinzona, Castel Grande	9.02	46.19	1
Submediterranean	Bilancino, Firenze	11.26	43.98	2
Submediterranean	Buca della Sabbia	9.34	45.83	1
Submediterranean	Cantone di Magreta	10.8	44.6	2
Submediterranean	Casalecchio di Reno	11.35	44.51	4
Submediterranean	Casinalbo	10.85	44.59	10
Submediterranean	Castaneda - Pian del Remit	9.14	46.26	1
Submediterranean	Castelfranco di Sotto	10.75	43.7	1
Submediterranean	Castelgrande, Bellinzona	9.02	46.19	9
Submediterranean	Cava Due Madonne	11.24	44.31	1
Submediterranean	Café Manzini	10.52	44.66	1
Submediterranean	Chiozza di Scandiano	10.71	44.6	1
Submediterranean	Fiorano Modenese	10.82	44.54	3
Submediterranean	Gaggio	11.05	44.6	1
Submediterranean	Grotta Calindri	11.39	44.44	2
Submediterranean	Grotta all'Onda, Camaiore	10.33	43.96	2
Submediterranean	Grotta del Farneto	11.38	44.43	1
Submediterranean	Isola Santa, Careggina	10.31	44.06	1
Submediterranean	Isola Santa, Careggine	10.31	44.06	13
Submediterranean	Isolino Virginia	8.72	45.82	20

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Submediterranean	LE CHATEAU	6.99	45.32	9
Submediterranean	La Greppia II, San Romano in Garfagnana	10.33	44.19	2
Submediterranean	Lagozza	8.8	45.7	5
Submediterranean	Lagozza di Besnate	8.77	45.7	3
Submediterranean	Lagozzetta	8.77	45.7	1
Submediterranean	Marina di Torre del Lago	10.27	43.82	1
Submediterranean	Mesocco - Tec Nev	9.23	46.39	1
Submediterranean	Montale	10.9	44.58	13
Submediterranean	Monte Santa Giulia	10.67	44.39	1
Submediterranean	Montecavolo	10.54	44.63	5
Submediterranean	Muraccio, Pieve Fosciana	10.42	44.13	4
Submediterranean	Paradiso di Laorca	9.4	45.88	1
Submediterranean	Passo Comunella, Basilicata	10.33	44.15	1
Submediterranean	Piana degli Ossi	11.42	44.21	4
Submediterranean	Piastricoli	10.35	44.08	1
Submediterranean	Piazza del Duomo, Pisa	10.4	43.72	2
Submediterranean	Piazzana, Coreglia	10.56	44.11	8
Submediterranean	Pizzo di Bodio	8.75	45.79	4
Submediterranean	Poggiaccio	11.37	44.16	1
Submediterranean	Poggio Castelluccio	11.39	44.11	5
Submediterranean	Poggio di Mezzo	10.47	43.74	2
Submediterranean	Riparo Fredian	10.35	44.08	4
Submediterranean	Riparo Grande	10.33	43.94	1
Submediterranean	Riparo del Lauro	10.24	43.91	2
Submediterranean	Riparo delle Felci di Candalla	10.32	43.96	1
Submediterranean	Roc del Col	6.98	45.05	1
Submediterranean	Romita di Asciano (Riparo La Romita)	10.46	43.75	1
Submediterranean	Rubiera	10.78	44.65	1
Submediterranean	S. Michele di Valestra	10.56	44.45	2
Submediterranean	San Rocchino	10.33	43.86	9
Submediterranean	Savignano	11.03	44.48	1
Submediterranean	Spilamberto	11.02	44.53	3

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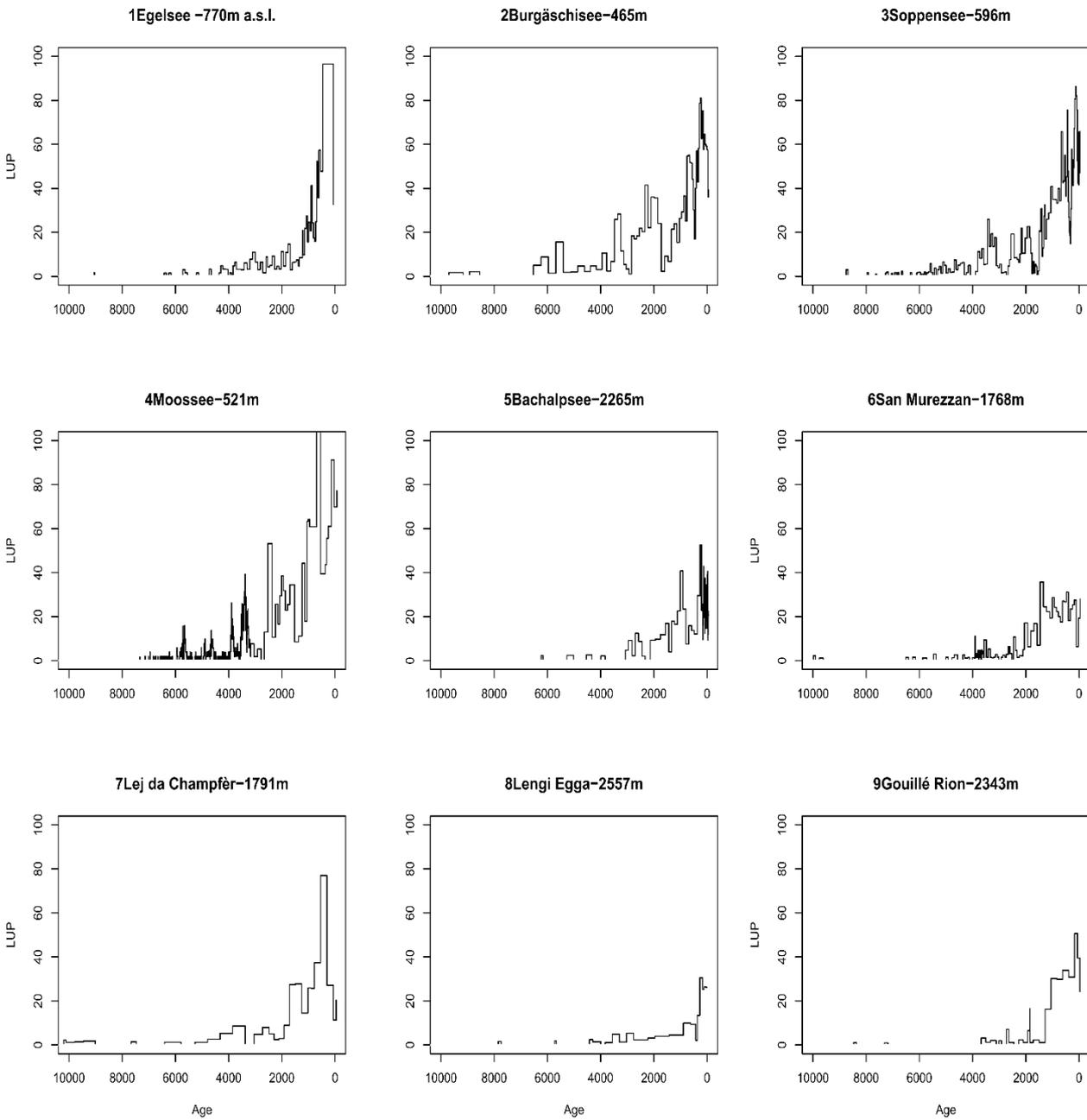
Submediterranean	Tec Nev	9.22	46.38	1
Submediterranean	Vado All'Arancio, Massa Marittima	10.89	43.98	2
Submediterranean	Val Bavona, Val Calneggia	8.53	46.36	1
Mesomediterranean	Casa Querciolaia	10.36	43.56	1
Mesomediterranean	Castelfranco di Sotto	10.75	43.7	1
Mesomediterranean	Grotta all'Onda, Camaione	10.33	43.96	2
Mesomediterranean	Grotta del Chiostraccio	11.19	43.37	3
Mesomediterranean	Grotta del Fontino	11.09	42.88	1
Mesomediterranean	Grotta della Spinosa, Massa Marittima	10.89	43.05	4
Mesomediterranean	Isola Santa, Careggina	10.31	44.06	1
Mesomediterranean	Isola Santa, Careggine	10.31	44.06	13
Mesomediterranean	La Greppia II, San Romano in Garfagnana	10.33	44.19	2
Mesomediterranean	Lavandone	10.63	43.62	1
Mesomediterranean	Livorno-Stagno	10.36	43.59	4
Mesomediterranean	Marina di Torre del Lago	10.27	43.82	1
Mesomediterranean	Muraccio, Pieve Fosciana	10.42	44.13	4
Mesomediterranean	Passo Comunella, Basilicata	10.33	44.15	1
Mesomediterranean	Petriolo III South	11.13	43.1	2
Mesomediterranean	Piastricoli	10.35	44.08	1
Mesomediterranean	Piazza del Duomo, Pisa	10.4	43.72	2
Mesomediterranean	Piazzana, Coreglia	10.56	44.11	8
Mesomediterranean	Poggio di Mezzo	10.47	43.74	2
Mesomediterranean	Pontedera	10.63	43.66	1
Mesomediterranean	Populonia	10.49	42.99	1
Mesomediterranean	Populonia-Baratti	10.5	42.99	2
Mesomediterranean	Riparo Fredian	10.35	44.08	4
Mesomediterranean	Riparo Grande	10.33	43.94	1
Mesomediterranean	Riparo del Lauro	10.24	43.91	2
Mesomediterranean	Riparo delle Felci di Candalla	10.32	43.96	1
Mesomediterranean	Romita di Asciano (Riparo La Romita)	10.46	43.75	1

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Mesomediterranean	San Rocchino	10.33	43.86	9
Mesomediterranean	Tombolo	10.33	43.67	1
Mesomediterranean	Vado All'Arancio, Massa Marittima	10.89	43.98	2
Thermomediterranean	Aci Trezza	15.16	37.56	2
Thermomediterranean	Case Bastione	14.46	37.67	12
Thermomediterranean	Castelluccio	14.93	36.95	4
Thermomediterranean	Corbeddu	9.45	40.29	1
Thermomediterranean	Duos Nuraghes	8.81	40.22	1
Thermomediterranean	Filiestru	8.66	40.5	12
Thermomediterranean	Grotta Corbeddu	9.49	40.26	1
Thermomediterranean	Grotta Palombara	13.53	37.4	1
Thermomediterranean	Grotta Rifugio	9.48	40.3	3
Thermomediterranean	Grotta Su Coloru	8.82	40.84	7
Thermomediterranean	Grotta del Guano, Oliena	9.51	40.29	4
Thermomediterranean	Grotta dell'Uzzo	12.79	38.11	8
Thermomediterranean	Monte d'Accoddi	8.45	40.79	6
Thermomediterranean	Montegrande	13.68	37.2	2
Thermomediterranean	Morgantina	14.5	37.44	1
Thermomediterranean	Muculufa	14.18	37.19	5
Thermomediterranean	Nuraghes	8.93	40.11	2
Thermomediterranean	Sa Turricula	8.61	40.7	1
Thermomediterranean	Valsavoia	15	37.28	2

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Figure S2. Land use probability index (LUP) at the sites included in the calibration dataset. Y-axis “LUP” is limited to a maximum of 100.



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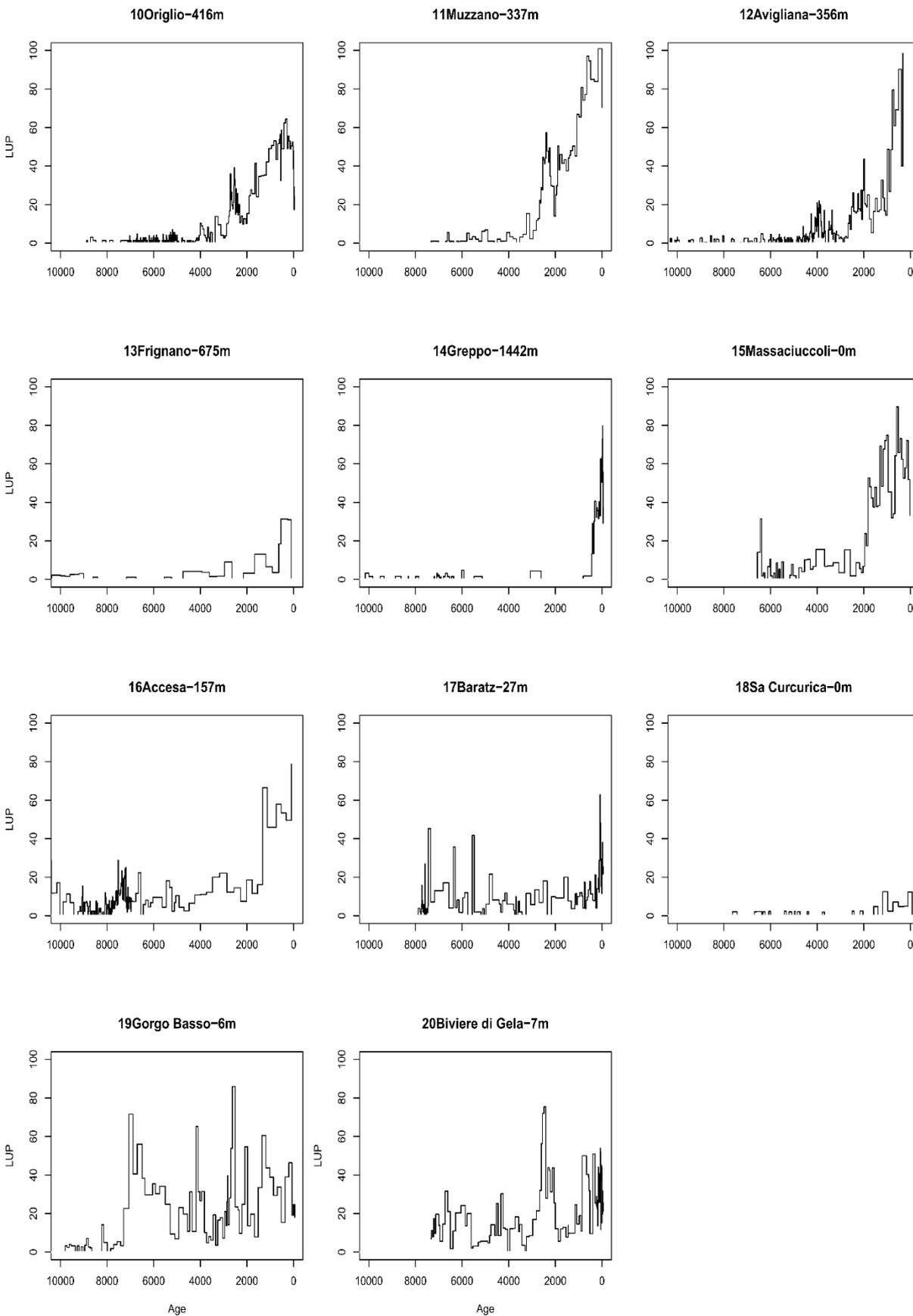
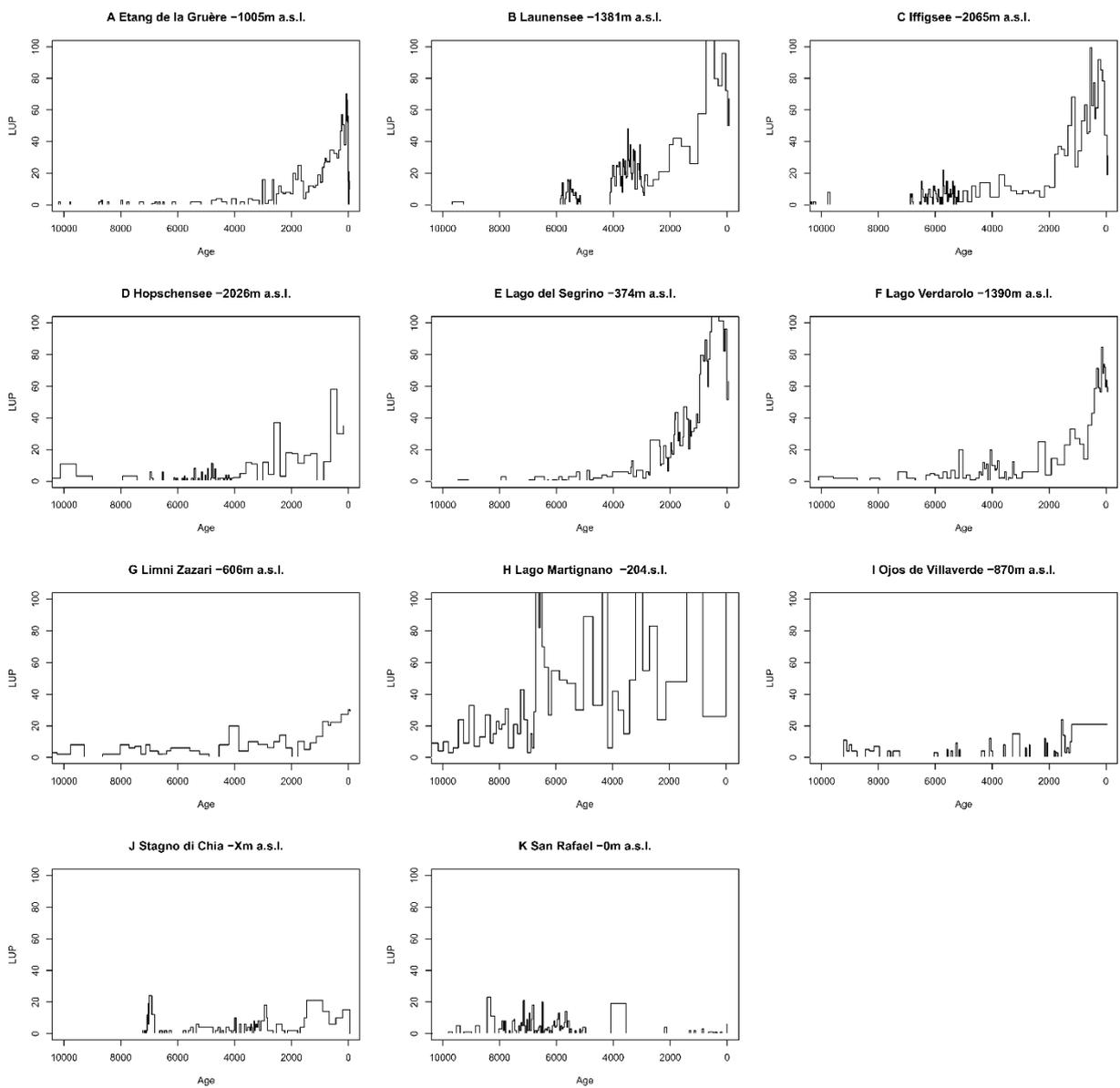


Figure S3. Land use probability index (LUP) at the sites included in the validation dataset. Y-axis “LUP” is limited to a maximum of 100.

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Summary

Main outcomes and summary

Cultural pollen indicators in pollen records are an established tool to reconstruct the history of human impact on vegetation and landscape, particularly useful to disentangle the influence of human activities and climatic variability on ecosystems. To infer human impact from pollen diagrams, Behre (1981) established a list of cultural pollen indicators that represent plant taxa that benefit from human activities directly (crops) or indirectly (weeds). The pollen indicators methodology remains the prevalent approach when assessing land-use and its related anthropogenic impact in pollen diagrams. For this purpose, the list of cultural indicators developed by Behre (1981) and elaborated by following research has been widely used and adapted in very different geographical, cultural and vegetational contexts. More recently, index-like approaches, based on the cultural pollen indicators, aim to adapt the method for numerous geographical locations and land use types. In **Manuscript 1**, we review the most common European approaches to assess their performance at six sites spanning a continental gradient over the boreal, temperate and Mediterranean biomes. We present new insights on how these methodologies can assist in the interpretation of pollen records and on how a careful selection of pollen types and/or indexes according to the specific geographical scope of each study is key to get meaningful reconstructions of human activity through time. We emphasise how important it is to determine if an indicator is adventive (exotic) or apophyte (native) within a study area. Although we can identify approaches or indexes that perform much better than others, we conclude that alongside the increasing wealth of pollen datasets there is a need for developing novel tools that may assist for numeric human-impact reconstructions.

Another factor that affects the indicative capacity of cultural pollen indicators is the taxonomic resolution in which they are identified. This is because different levels of taxonomic resolution are reached in palynology, depending on several factors such as the analyst's expertise, the palynological school, the aim of the study, the preservation of the pollen grains, the reference collections, the available determination keys and the microscope facilities. In **Manuscript 2**, we assess the impact of taxonomic resolution on the indicative capacity of cultural pollen types. To achieve this, we attribute the pollen types of sixteen sedimentary records, located along a latitudinal gradient spanning from Switzerland to Italy, to three levels of taxonomic resolution previously proposed at the European scale (Giesecke et al., 2019). Our results show that higher taxonomic resolution improves the identification

Summary

of human impact by enhancing the indicative power of important pollen indicators widely used in the research field.

On this basis, we identify highly resolved sensitive pollen types, especially some most commonly used such as *Plantago lanceolata*-type, *Centaurea cyanus*, and *Cannabis sativa*-type. Our results may contribute to the improvement of palynological reconstructions of land use by identifying key pollen types with important detail of identification. We conclude that it is essential to aim at highest taxonomic resolutions for reconstructing past human impact, even if in specific geographical contexts (e.g., the Mediterranean) this might not be sufficient to fully discriminate human impact from natural processes.

Taken together with these first two studies, we aim to contribute to the improvement of palynological reconstructions of land use and human impact by identifying key pollen types whose microscopic identification and origin and timing of introduction requires particular attention. In order to have a semi quantitative methodology and to further contribute to human pollen reconstructions, we propose a new methodology based on cultural pollen indicators, the agricultural LUP (Land Use Probability Index), in **Manuscript 3**. We train the novel index by using the most suitable cultural indicators found in twenty Holocene pollen sequences along a latitudinal transect encompassing cool temperate colline/montane, cool to cold subalpine/alpine, warm temperate submediterranean, warm mesomediterranean, and subtropical thermomediterranean vegetation conditions, in Switzerland and Italy. We validate the LUP index by (1) applying the generated LUPs to independent pollen records and (2) with a proxy curve for past human activity generated using radiocarbon data from the archaeological context. We discuss the potential of our method to be applied along Europe, which may significantly contribute to refine pollen-based land-use reconstructions in Europe.

To conclude, the cultural pollen indicators methodology (Behre, 1981) was and still is the most important tool that palynologists have to infer human impact from pollen diagrams. In this thesis, we aim to call attention to how the methodology is used, especially when adapting it to areas outside its original calibration realm. We recommend that when identifying human pollen indicators, the highest possible taxonomic precision should be aimed. Also, it is important to define if a human indicator is an adventive or an apophyte within a study area. This very much depends on the vegetational context in the different biomes of Europe. In future, novel methodologies as aDNA or eDNA approaches may additionally inform palaeoecologists and archaeologists to gain better reconstructions of past human activities.

Summary

References

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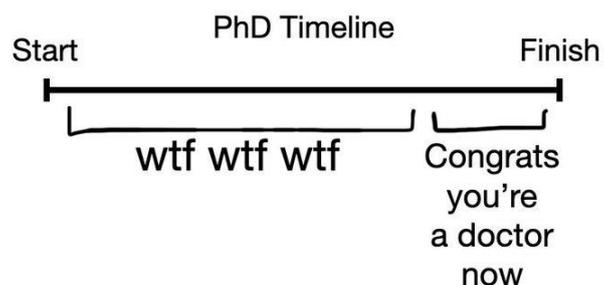


Fig 2. Representation of the Dunning–Kruger effect undergoing a PhD program (@mightdaaropout, 2021).

Declaration of consent

on the basis of Article 18 of the PromR Phil.-nat. 19

Name/First Name: Renn, Mara Muriel

Registration Number: 17-144-031

Study program:

Bachelor

Master

Dissertation

Title of the thesis: Quantifying human impacts to tease apart cultural and climatic drivers of Holocene vegetation change

Supervisor: Prof. Dr. Willy Tinner,
Institute of Plant Sciences and Oeschger Centre for Climate Change Research
University of Bern

I declare herewith that this thesis is my own work and that I have not used any sources other than those stated. I have indicated the adoption of quotations as well as thoughts taken from other authors as such in the thesis. I am aware that the Senate pursuant to Article 36 paragraph 1 litera r of the University Act of September 5th, 1996 and Article 69 of the University Statute of June 7th, 2011 is authorized to revoke the doctoral degree awarded on the basis of this thesis.

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