

Anthropogenic indicators in pollen diagrams in eastern France: a critical review

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Abstract The focus of palaeoenvironmental sciences on past human activities and their impact on the environment necessitates a precise understanding of the history and functioning of past and present anthropogenic ecosystems. A process is outlined which uses palaeoenvironmental and historical documentation as well as present-day observations of vegetational changes from two different plant communities, which are characterised by a very specific anthropogenic flora: arable weeds and ruderals. This study is coupled with modern pollen deposition data to deduce a set of pollen types characteristic of the range of human activities practised in eastern France, a region rich in pollen data. First, phytogeographical analysis of the evolution of these plant communities since the Neolithic enables the comparison to be validated. By distinguishing between native plants and aliens introduced long ago (archaeophytes), or more recently (neophytes), and by refining their ecological characteristics, the method also enables identification of species that are strong indicators of human activities. Next, local pollen deposition in these vegetation types is examined with a number of statistical analyses (PCIA, Davis indices), confirming the relationships between a given vegetation community, its theoretical pollen rain and its actual pollen rain, thus distinguishing

local and regional pollen indicators. Lastly, comparison of the results obtained by these two approaches leads to a critical synthesis of the traditional anthropogenic pollen indicators (Behre's "indicator species") in the study area and to the establishment of more specific local pollen indicators.

Keywords Modern pollen · Arable weed flora · Ruderal flora · Pollen–vegetation relationships · Anthropogenic indicators · France

Introduction

Palaeoenvironmental analyses, pollen, charcoal (anthracology) and macrofossils are an indispensable complement to the study of archaeological remains in the understanding of past societies, their changes in agricultural practices and their impacts on the environment.

Palynology attempts to identify anthropogenic dynamics such as presence and development of human activities, phases of abandonment etc. from fossil pollen spectra.

The perception of human impact on vegetation is based primarily on the use of anthropogenic indicators in pollen diagrams, that is, pollen types associated with human activities. Some are well known since the early 1980s, especially in central Europe, thanks to classifications proposed by Behre (1981, 1988).

The method proposed by Behre (1981) relies on recognition by their pollen of plant taxa directly associated with human activities, like crop plants such as cereals, their associated floras of arable weeds, the ruderal floras etc. This identification of various categories among non-arboREAL taxa is based on the ecological requirements of species and relies on phytosociological references. Behre uses the

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distribution of species in modern plant communities and takes into account their traditional distributions before the introduction of modern farming methods, according to Oberdorfer (1970), Ellenberg (1979) and others. Furthermore, to consider the changes in these communities since prehistoric times, he uses the “empirical knowledge” acquired from large numbers of pollen analyses and studies of macro-remains. Behre (1981) thus offers a list of “the principal anthropogenic indicators in pollen diagrams and their occurrence in various farming contexts within that part of Europe north of the Alps”.

These indicators have been widely used and adapted in northern European regions, for example Berglund and Ralska-Jasiewiczowa (1986) for Sweden, Vorren (1986) for Norway, Hicks (1988) for Finland, as well as in France (Jalut 1991; Marguerie 1992; Galop 1998; Gauthier 2004).

But beyond the general reconstruction of vegetation dynamics, current research aspires to identify at a fine scale each type of human activity, where it took place, and for how long. In the context of lively discussion of early traces of agriculture (Behre 2007, 2008; Tinner et al. 2007, 2008), an improvement of our perception through palynology of vegetation influenced by human activity could help resolve this difficult question.

This aspiration for precise reconstruction requires sound knowledge of the ecosystems associated with human activities such as hay meadows, lowland or mountain grazing land, cultivated and ruderal environments, and of the plant communities in them. It also implies studying the relations between current anthropogenic habitats and their pollen rain (Gaillard et al. 1992, 1994; Broström et al. 1998; Hjelle 1999; Broström et al. 2008). Furthermore, these researchers all agree on the importance of the historical and floristic characteristics of each study area, and this has led to more of this type of analysis being done at a local scale (Galop et al. 2003; Mazier et al. 2006).

In this context, there has still been little work in France on different vegetation types created by human activity (Court-Picon et al. 2006; Mazier et al. 2006; Brun et al. 2007). So far there are no studies combining archaeobotanical, historical, phytogeographical and current approaches to the floras of arable fields and ruderal environments.

In order to improve interpretation of the fossil pollen assemblages and to refine the definition of the anthropogenic pollen indicators proposed by Behre (1981, 1988), two human-influenced vegetation types, arable weed and ruderal vegetation, were studied in the Jura mountains and the adjacent plains of Franche-Comté, eastern France, a region rich in peat bogs and pollen investigations .

This study examined:

- Change in the biodiversity of these anthropogenic floras, using an interdisciplinary method combining

ecology, phytogeography and palaeoenvironmental sciences;

- local pollen deposition in these human-influenced vegetation types, in order to establish the relationship between the vegetation and the pollen evidence.

As the results of these two approaches have already been published (Brun et al. 2007, 2008; Brun 2009), the aims of the present article are:

- (1) to present briefly the methods and the principal results of these two approaches;
- (2) to identify specific modern pollen indicators for cultivated fields and ruderal habitats and establish whether they add to or differ from those already defined in central Europe, for the study area in eastern France;
- (3) to establish whether these approaches could lead to a critical review of the traditional anthropogenic pollen indicators.

Materials and methods

Identification of natives, archaeophytes and neophytes as a means of exploring the history of the introduction of plants

Through historical study of anthropogenic vegetation at a regional level, from the Neolithic to the present day, it is possible to distinguish native and alien plants present in floras and to understand the development of their populations through time. Depending on their residence time, alien plants can be classified as archaeophytes, plants introduced into a study area before A.D. 1500, and neophytes, plants which became established after A.D. 1500 (Pyšek et al. 2004; Brun 2009). Although this classification of aliens has traditionally been used in central European countries (Holub and Jirásek 1967), there is no a detailed list of alien plants for France.

This distinction between natives, archaeophytes and neophytes is sometimes a difficult one to make, and relies on a combination of evidence from archaeobotanical data from pollen and seed analyses, archaeology, history from botanical records in ancient floras, phytogeographical data on origin and distribution, and ecology (preferential habitats, life-history traits) (Preston et al. 2004; Pyšek et al. 2002).

Moreover, in order to infer the evolution of human induced plant colonisation during the last 7,500 years, from 5500 B.C. to A.D. 2000, the date of the first fossil or historical record of each alien species was determined by combining these data; for more details about the data used and compiled for this work in eastern France, see Brun (2009).

Study of pollen–vegetation relationships and identification of local and regional pollen indicators

The data set of this survey includes 141 modern vegetation relevés (samples) made in cultivated fields and ruderal environments throughout the entire region in 2003 and 2004. In order to estimate the pollen rain, moss polsters were collected in some relevés of each floristic group defined by statistical analyses, 52 samples in all, details of which are given in Brun et al. (2007, 2008). When it was possible, extensive counts of pollen grains were done with the aim of detecting rare indicator taxa. A minimum of 500 pollen grains were counted on each slide and attempting to determine a minimum of 400 NAP grains, an average of 798 grains was counted per sample, see Brun et al. (2007, 2008). Pollen analysis was made using the modern reference collection of the laboratory of Chrono-Environnement, Besançon, France, the pollen atlas of Reille (1992, 1995, 1998) and the identification key of Beug (2004).

Fieldwork consisting of vegetation surveys, pollen collection and identification was undertaken in order to analyse the relationships between a given vegetation community, with the vegetation data expressed at a species taxonomic level, its theoretical pollen rain, with the vegetation data expressed as pollen types, and its actual pollen rain, with the pollen data expressed as pollen types.

- First, to test the relationship between the three data-sets, two by two, we used procrustean co-inertia analysis (PCIA, Dray et al. 2003). This enabled us (1) to assess whether or not the taxonomic level of identification influences the structure of the vegetation data-sets and (2) to establish whether the vegetation and pollen data-sets are similar in structure.
- Next, for pollen types which are present in both vegetation and pollen rain, calculation of the three indices of Davis (1984) provided some information on the qualitative relationships between pollen and vegetation. They revealed a good association (A) between the presence of a taxon in pollen rain and vegetation on the same site, or its under- or over-representation (U or O) in pollen rain compared to vegetation.

In order to take into consideration some of the factors which influenced the pollen representativity and to interpret these results, each taxon was related to the mean size of its pollen grain, using data of Beug (2004) and to its mode of pollination, using the data of Proctor et al. (1996), Hjelle (1997) and Julve (1998).

Lastly, the combination of the results obtained by these two approaches led to a critical examination of the traditional anthropogenic pollen indicators (“indicator species”, Behre 1981) in the study area.

Results

Strong pollen indicators of human activities

Among the 494 species that potentially grow in anthropogenic habitats, 183 grow in cultivated fields, 267 in ruderal environments and 43 in both habitats. More than half of these, 250, are aliens, among which 60.8% are archaeophytes, 25.2% are neophytes and 14% are of undetermined status. The largest number of aliens is found on arable land with almost two-thirds of the 225 species, while less than half of the 310 ruderal species are aliens. Furthermore, archaeophytes are over-represented on arable land where almost half of the arable weeds are archaeophytes, but in contrast, neophytes are twice as common in ruderal habitats (Brun 2009).

The history of introduction of plants allows us to reconstruct an approximate pattern of the constant enrichment of the flora by aliens. It is possible to distinguish two main periods: the first began at the end of the Neolithic and reached a peak in the late Bronze Age, when the majority of the archaeophytes came from the Mediterranean area and grew on arable land. Later, the beginning of the modern period after about A.D. 1500 was also characterised by another peak in immigration of aliens, in our study area as well as in the rest of Europe. However, these neophytes had more diverse geographic origins than the archaeophytes and were more frequently associated with annual ruderal vegetation types (for details, see Brun 2009).

By distinguishing between earlier and more recent introductions (archaeophytes and neophytes) and by refining their phytogeographical and ecological characteristics, the results show that in vegetation communities created by human activity, the plants are found in a varied range of habitats. Some of them occur only in specific habitats, such as arable fields or various ruderal situations, while others are opportunists which may grow on disturbed ground in both arable and ruderal sites but also in pasture or grassland, for example.

The study of the biological and ecological attributes of the plants, such as life form, flowering time, pollination and dispersal mode etc., and current habitats, enables us to demonstrate that aliens are more specialized plants than natives and tend to occur in only a few habitats. Moreover, among the aliens, archaeophytes are more often confined to specific habitats than neophytes and are therefore even more closely associated with human activities (Brun 2009).

Consequently, these taxa should be considered as strong indicators of human activities. Their identification in a fossil record indicates, without any doubt, human presence and sometimes they can even inform us about a specific habitat or human practices.

The grouping of taxa in higher taxonomic ranks, corresponding to the level of pollen determination such as pollen types, allows us to estimate the possibility of detecting these strong indicator taxa in the pollen record. Moreover the study of the history of the introduction of alien plants permits us to suggest a possible period of introduction for each strong indicator taxon. These assessments are based on macro-remains, pollen and historical records for each species which comprises these pollen types and they are presented in Table 1 and Appendix A (Supplementary material).

Relationships between modern pollen and vegetation assemblages

Correlation between the vegetation, theoretical pollen rain and actual pollen rain

The results of the Procrustean Co-Inertia Analyses (PCIA) show that it seems possible to characterize general crop vegetation (Brun et al. 2007) and ruderal vegetation (Brun et al. 2008) based on their pollen spectra.

First, the difference of taxonomic level of determination between the flora and the theoretical pollen rain (species vs pollen types) is a negligible factor in the perception of plant communities of cultivated fields and ruderal habitats. This fact is now generally accepted.

Next, the actual pollen rain of these communities satisfactorily reflects the vegetation. This is particularly true for those of ruderal habitats where, despite a lack of

taxonomic precision, we can differentiate each group of ruderal vegetation, such as in trampled places etc. at the floral and pollen level. However, the results obtained in fields are less clear-cut as we were unable to differentiate each group from its pollen assemblage, such as arable weed floras of acidic from those of basic soil.

The major part of the high residuals found in the PCIA is due to the lack of taxonomic precision in pollen identification even if all the dominant taxa in the vegetation assemblages are found in the pollen spectra. Moreover, variation in pollen production and dispersal between plant species and differential preservation of pollen grains affects the presence of any particular pollen type in the assemblages. This fact necessitates the establishment of specific pollen indicator taxa for each of these plant communities.

Association and representation indices

The previous analyses have shown serious problems of under- and over-representation of some pollen types. The association, under- and over-representation of pollen types can be identified and explored with Davis indices (A, U and O). It is therefore possible to identify two new categories of pollen indicators in addition to the first category (1) strong indicators of human activities. They are:

(2) indicators which are more or less specific for the investigated environments, cultivated fields or ruderal habitats;

(3) local or regional indicators of human presence, according to their indices of association and representation

Table 1 Pollen types which represent only archaeophyte plant species in eastern France

Period	Time range	Pollen types indicating cultivated habitats	Pollen types indicating ruderal habitats	Pollen types indicating both
Neolithic	5500–2200 b.c.	2 <i>Agrostemma githago, Papaver argemone</i>	5 <i>Hyoscyamus niger, Malva sylvestris-t., Verbena officinalis</i>	2 <i>Fallopia, Polygonum aviculare-t.</i>
Bronze Age	2200–750 b.c.	4 <i>Centaurea cyanus, Chaenorhinum minus, Kickxia, Scleranthus</i>	2 <i>Omphalodes-t.</i>	1 <i>Papaver rhoeas</i> group
Iron Age	750 b.c.–A.D. 52	4 <i>Adonis aestivalis-t., Fumaria, Lithospermum arvense, Spergula arvensis</i>	2 <i>Reseda, Xanthium strumarium-t.</i>	–
Roman period	A.D. 52–500	2 <i>Ranunculus arvensis</i> group, <i>Vaccaria hispanica</i>	0 –	–
Medieval period	A.D. 500–1500	2 <i>Legousia-t., Melampyrum</i>	3 <i>Chelidonium majus, Medicago sativa-t.</i>	1 <i>Mercurialis annua</i>
No data available		7 <i>Antirrhinum-t., Erodium, Heliotropium europaeum-t., Lycopsis arvensis-t., Nigella, Polycnemum, Sagina apetala-t.</i>	3 <i>Echium, Malva neglecta-t., Marrubium</i>	1 <i>Aconitum</i> group
Total		21	15	5

The determination of the probable introduction period of each species, based on macro-remains, pollen and historical records, is used to classify pollen types according to their probable period of appearance in fossil pollen assemblages. When no data were available for the introduction period of a plant species, the pollen types are put in the category “No data available”. They are also classified according to the environment to which the species they represent belong (cultivated fields, ruderal or both habitats). Relationships between pollen types and species are given in Appendix A (Supplementary material), t = type

values, so that these pollen types show the presence of the species near to or far from the sampling point. The classification as local or regional pollen indicators was made by comparing the results obtained for the Davis indices with those of similar studies made in other regions (Hjelle 1997; Mazier et al. 2006, see Appendix B in Supplementary material) and by taking into account the production and dispersal of the pollen types. As a mixture of open and wooded landscape has been sampled in this study, the classification as local or regional indicator should be considered as a summarized proposal for the studied area.

Integration of pollen types in these two categories brings to light the characteristics of arable and ruderal habitats of the study area. These results are presented in Table 2 and Appendix B (Supplementary material).

Comparison of the list of strong indicators and the study of modern pollen rain and vegetation

The comparison of the three categories of indicator values allows the following observations to be made:

First, the majority of the strong indicator taxa, that enable an immediate identification of cultivated fields, ruderal habitats or both, are local indicators, so they reflect the presence of vegetation communities influenced by humans close to the sampling point (Table 2, in bold).

In addition, the absence from the modern pollen rain of a large number of the expected pollen indicators, especially in fields and among the strong indicators, is mainly due to their rarity in the investigated environments and not to the impossibility of finding them in pollen assemblages, even if the species represented by the absent pollen types have a generally low pollen production and dispersal.

Finally, other indicator pollen type, composed of native species or a mixture of indigenous species, archaeophytes and neophytes, are less often found in a precise anthropogenic vegetation type and rather reflect a regional presence of these environments. As could be expected, regional indicators principally consist of pollen types which represent taxa with high pollen production and wind distribution such as *Plantago*, *Rumex*, *Chenopodiaceae*, *Artemisia* spp. etc. Consequently, they will be more frequently found in the pollen rain.

Table 2 Anthropogenic indicators in pollen diagrams for eastern France

	Local pollen indicators	Regional pollen indicators	Pollen types never found in the pollen rain
Cultivated habitats	<i>Anagallis</i> -t., <i>Antirrhinum</i> -t., <i>Centaurea cyanus</i> , <i>Cerealia</i> -t. <i>Kickxia</i> , <i>Scleranthus</i> , <i>Sinapis</i> , <i>Valerianella</i> , <i>Viola tricolor</i> -t.		<i>Adonis aestivalis</i> -t., <i>Agrostemma githago</i> , <i>Aphanes arvensis</i> -t., <i>Arnoseris minima</i> , <i>Chaenorhinum minus</i> , <i>Erodium</i> , <i>Gagea</i> -t., <i>Heliotropium europaeum</i> , <i>Legousia</i> -t., <i>Lithospermum arvense</i> , <i>Lycopsis arvensis</i> -t., <i>Melampyrum</i> , <i>Mercurialis annua</i> , <i>Myosotis discolor</i> , <i>Nigella</i> , <i>Odontites</i> -t., <i>Ornithogalum umbellatum</i> -t., <i>Ornithopus</i> , <i>Papaver argemone</i> , <i>Polyicum</i> , <i>Ranunculus arvensis</i> group, <i>Sagina apetala</i> -t., <i>Spergula arvensis</i> , <i>Thymelaea passerina</i> , <i>Vaccaria hispanica</i>
Ruderal habitats	<i>Bryonia</i> , <i>Calystegia</i> , <i>Chelidonium majus</i> , <i>Dipsacus/Cephalaria</i> , <i>Echium</i> , <i>Geum</i> -t., <i>Lamium album</i> -t., <i>Linaria</i> -t., <i>Malva sylvestris</i> -t., <i>Medicago lupulina</i> -t., <i>Mentha</i> -t., <i>Rubus</i> , <i>Solanum dulcamara</i> , <i>Verbascum</i> , <i>Verbena officinalis</i>	<i>Artemisia</i> , <i>Urtica</i>	<i>Agrimonia</i> -t., <i>Astragalus</i> -t., <i>Cuscuta europaea</i> -t., <i>Cynoglossum</i> , <i>Hyoscyamus niger</i> , <i>Lactuca</i> -t., <i>Lappula</i> , <i>Lavatera</i> -t., <i>Marrubium</i> , <i>Medicago sativa</i> -t., <i>Omphalodes</i> -t., <i>Reseda</i> , <i>Saussurea</i> -t., <i>Sympytum</i> , <i>Xanthium strumarium</i> -t.
Both	<i>Convolvulus arvensis</i> -t., <i>Euphorbia</i> , <i>Fallopia</i> , <i>Fumaria</i> , <i>Galeopsis/Ballota</i> group, <i>Geranium</i> , <i>Malva neglecta</i> -t., <i>Papaver rhoes</i> group, <i>Persicaria maculosa</i> -t. (= <i>Polygonum persicaria</i> -t.), <i>Sanguisorba minor</i> , <i>Solanum nigrum</i> -t.	<i>Chenopodiaceae/</i> <i>Amaranthus</i> , <i>Polygonum aviculare</i> -t.	<i>Aconitum</i> group , <i>Herniaria glabra</i> -t., <i>Sonchus</i> -t., <i>Spergularia</i> -t.
All anthropogenic habitats	<i>Cirsium</i> , <i>Trifolium repens</i> -t., <i>Veronica</i> -t.,	<i>Plantago lanceolata</i> -t., <i>Plantago major/media</i> -t., <i>Rumex acetosa</i> -t., <i>Rumex obtusifolius</i> -t.	

Pollen types are classified according to the environment to which the species they represent belong (cultivated fields, ruderal or both habitats and all anthropogenic habitats) and according to their indices of association and representation values, as local or regional pollen indicators. Pollen types never found in the pollen rain are also shown. Strong indicator pollen taxa are shown in bold. Some pollen types found in ruderal habitats are also typical of woodland edges, and they are underlined. Relationships between pollen types and species are given in Appendix A (Supplementary material), t = type

Comparison between the anthropogenic pollen indicators from Behre (1981) and our results

For some of the pollen types, we arrived at the same conclusions as Behre: *Centaurea cyanus*, *Lychnis-Agrostemma*-type, *Scleranthus annus* and *Spergula arvensis* are pollen types found only in cultivated fields. *Urtica* and *Artemisia* are more specifically confined to ruderal places. *Fallopia convolvulus*, *Polygonum persicaria*-type and Chenopodiaceae are found in cultivated fields as well as in ruderal habitats. *Trifolium repens*-type is found in all kinds of anthropogenic habitats.

For some other pollen types, our results were different from those already published: *Plantago lanceolata* is indicated by Behre as a preferential marker of wet meadows and pastures. The author adds that this species should be used with caution because it is also likely to indicate cultivated fields in ancient periods (Behre 1981, p. 235). These conclusions are similar to ours as we determined this species as an indicator of all types of anthropogenic habitats. *Plantago major/media*-type is preferentially associated by Behre with trampled and ruderal places. The specificity of this marker has often been discussed. For example, strong correlations have been found between this pollen type and the increase of livestock in particular fossil contexts as in the detailed study of pollen sequences in lake Chalain (Richard and Gery 1993). In our study, we found it everywhere and it indicates any type of anthropogenic locality. The pollen of *Rumex* is difficult to identify more exactly, and the author suggests two different types, *Rumex cf. acetosella* and *R. cf. acetosa*. We did not identify the first one and *Rumex acetosa*-type includes, among others, two different species, *R. acetosella* and *R. acetosa*. Therefore, our interpretations are not comparable and in our study, *Rumex acetosa*-type reflects all types of anthropogenic localities. *Polygonum aviculare*-type is the one for which our conclusions differ the most. Indeed, Behre indicates its presence in all types of anthropogenic habitats and considers it as an apophyte (native, in habitats created by humans). On the contrary, the approach we used to determine its status enables us to show that in our study region this species and its subspecies is an alien, an archaeophyte present since the Neolithic, particularly associated with cultivated fields and ruderal habitats (see Brun 2009).

Discussion

From a phytosociological point of view, our study proceeds in the same way as that of Behre, even if it only deals with two types of anthropogenic habitats, but it also includes historical, ecological and phytogeographical analyses (see

Brun 2009) as well as field work and comparison of the vegetation and its pollen rain (Brun et al. 2007, 2008). In this respect, it is a confirmation of Behre's results. However, it can provide a greater degree of precision and reveal some discrepancies in the identification of anthropogenic markers and the limits of Behre's classification for the studied area. The differences are threefold:

(1) First of all, the vast geographical area of Europe north of the Alps chosen in Behre's study makes the identification of native and alien taxa difficult; note that today there is still no synthesis on this subject for this area. Consequently, this differentiation is not incorporated into the classification. Even though the author introduces it into the text for some species of *Polygonum*, *Chenopodium* and *Tripleurospermum* for example (Behre 1981, p. 237), he does not clarify which taxa or pollen types are classified in each category. It is nevertheless essential to assert precisely the indicator value of the species and exceed a limit often invoked by some authors, which indicates that this value is difficult to determine since the species often grow in both natural and anthropogenic environments (Vorren 1986; Fægri and Iversen 1989).

By determining the status of species as native or alien, archaeophyte or neophyte, one can discover the possible period of arrival of aliens. By studying their characteristics, we can, indeed, understand the history of these particular vegetation types and give a different weight to the aliens and native plants. So, we can distinguish alien species and alien pollen types which have a more restricted ecological spectrum and which grow only in anthropogenic habitats. This is the identification of strong indicator taxa.

(2) Secondly, the accurate identification of the species that are or were present in anthropogenic floras in cultivated fields and ruderal habitats as well as their life form characteristics highlights the floral characteristics of the study area, and in particular the presence of taxa with a southern distribution which are absent from more northern Europe. This allows us to obtain a more precise and complete list of indicator taxa.

(3) Finally, the field work enables us to validate the link between a vegetation type and its pollen representation, and to determine indicator pollen taxa which are characteristic of each studied habitat. The comparison between the vegetation and the pollen data allows us to prioritize and emphasize the importance of strong indicator taxa which allow an immediate identification of the different types of anthropogenic habitats. Thus we can distinguish the strong indicators previously identified and take into account some of the factors that influence their pollen representation such as mode of pollination and size of pollen grains. This enables us to attribute a local or regional value to the indicator taxa seen in the pollen rain from these environments.

Conclusion

The process used proves to be viable and this study confirms that the systematic use of the classical indicators of human activities defined for central and northern Europe (Behre 1981) is not appropriate for reconstructing human activities in more southern areas. Our study stresses that the interpretation of pollen diagrams needs knowledge of local vegetation in order to provide evidence of vegetation and land-use changes in the fossil pollen assemblages.

The completed list of anthropogenic pollen indicators could be used to reconstruct human activities from fossil pollen records in the study area. Indicator taxa that would be the most easily identified in the fossil assemblages are those that are well dispersed and they therefore reflect a regional presence of anthropogenic habitats. The study shows that all these markers indicate ruderal localities or ruderal and arable environments or any type of anthropogenic habitat. So, the differing pollen composition of ruderal and arable weed vegetation relies on strong indicator types which are local markers. Consequently, only those activities, especially farming, occurring in the immediate vicinity of the sampling site will be strongly recorded.

Finally, for better detection of human activities, the most suitable sampling sites are those which enable us to reconstruct local vegetation, such as former channels, sediment samples from archaeological sites, minor watercourses, small lakes and kettle-hole bogs. In these cases, it would be particularly useful to make large pollen counts with a minimum of 400 NAP and to improve the identification level of pollen types. The recognition from their pollen of more precise taxa, usually not made by palynologists, would be of great interest; for example, *Agrostemma githago* which is sometimes seen in pollen assemblages is generally included within the Caryophyllaceae pollen type, but it is a strong indicator of cornfields.

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References

- Behre K-E (1981) The interpretation of anthropogenic indicators in pollen diagrams. *Pollen Spores* 23:225–245
- Behre K-E (1988) The role of man in European vegetation history. In: Huntley BW, Webb T III (eds) *Vegetation history*. Kluwer, Dordrecht, pp 633–672
- Behre K-E (2007) Evidence for Mesolithic agriculture in and around Central Europe? *Veget Hist Archaeobot* 16:203–219
- Behre K-E (2008) Comment on: “Mesolithic agriculture in Switzerland? A critical review of the evidence” by W. Tinner, E.H. Nielsen and A.F. Lotter. *Quat Sci Rev* 27:1,467–1,468
- Berglund BE, Ralska-Jasiewiczowa M (1986) Pollen analysis and pollen diagrams. In: Berglund BE (ed) *Handbook of Holocene palaeoecology and palaeohydrology*. Wiley, Chichester, pp 155–484
- Beug H-J (2004) *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete*. Pfeil, Munich
- Bock B (2005) Base de données Nomenclature de la Flore de France—BdNFF version 4.02—mars 2005. Tela Botanica. <http://www.tela-botanica.org/eflore> (From Kerguélen, M. 1999: Index Synonymique de la Flore de France. Version 1999)
- Broström A, Gaillard M-J, Ihse M, Odgaard B (1998) Pollen-landscape relationships in modern analogues of ancient cultural landscapes in southern Sweden—a first step towards quantification of vegetation openness in the past. *Veget Hist Archaeobot* 7:189–201
- Broström A, Nielsen AB, Gaillard M-J, Hjelle K, Mazier F, Binney H, Bunting J, Fyfe R, Meltsøv V, Poska A, Räsänen S, Soepboer W, von Stedingk H, Sutari H, Sugita S (2008) Pollen productivity estimates of key European plant taxa for quantitative reconstruction of past vegetation: a review. *Veget Hist Archaeobot* 17:461–478
- Brun C (2009) Biodiversity changes in highly anthropogenic environments (cultivated and ruderal) from the Neolithic to present day in the eastern part of France. *Holocene* 19:861–871
- Brun C, Dessaint F, Richard H, Bretagnolle F (2007) Arable-weed flora and its pollen representation: a case study from the eastern part of France. *Rev Palaeobot Palynol* 146:29–50
- Brun C, Dessaint F, Richard H, Bretagnolle F (2008) La flore des milieux rudéraux et sa représentation pollinique: une nouvelle approche pour la reconstruction des paléoenvironnements humains. In: Galop D (ed) *Paysages et environnement. De la reconstitution du passé aux modèles prospectifs*. Presses universitaires de Franche-Comté, Besançon (Annales littéraires. Série Environnement, sociétés et archéologie), pp 193–204
- Bunting MJ (2003) Pollen–vegetation relationships in non-arboreal moorland taxa. *Rev Palaeobot Palynol* 125:285–298
- Court-Picon M, Buttler A, de Beaulieu J-L (2006) Modern pollen/vegetation/land-use relationships in mountain environments: an example from the Champsaur valley (French Alps). *Veget Hist Archaeobot* 15:151–158
- Davis OK (1984) Pollen frequencies reflect vegetation patterns in a Great Basin (U.S.A.) mountain range. *Rev Palaeobot Palynol* 40:295–315
- Dray S, Chessel D, Thioulouse J (2003) Procrustean co-inertia analysis for the linking of multivariate datasets. *Écoscience* 10:110–119
- Ellenberg H (1979) Zeigerwerte der Gefäßpflanzen Mitteleuropas. *Scripta Geobotanica* 9, Göttingen
- Fægri K, Iversen J (1989) *Textbook of pollen analysis*, 4th edn. by Fægri K, Kaland PE, Krzywinski K. Wiley, Chichester
- Gaillard M-J, Birks HJB, Emanuelsson U, Berglund BE (1992) Modern pollen/landuse relationships as an aid in the reconstruction of past land-uses and cultural landscapes: an example from south Sweden. *Veget Hist Archaeobot* 1:3–17
- Gaillard M-J, Birks HJB, Emmanuelson U, Karlsson S, Lagerås P, Olausson D (1994) Application of modern pollen/land-use relationships to the interpretation of pollen diagrams—reconstructions of land-use history in south Sweden, 3000–0 BP. *Rev Palaeobot Palynol* 82:47–73
- Galop D (1998) La forêt, l’homme et le troupeau dans les Pyrénées. 6000 ans d’histoire de l’environnement entre Garonne et Méditerranée. Contribution palynologique, Framespa, Toulouse

- Galop D, Mazier F, Lopez-Saez J-A, Vannière B (2003) Palynologie et histoire des activités humaines en milieu montagnard. Bilan provisoire des recherches et nouvelles orientations méthodologiques sur le versant nord des Pyrénées. Archéologie du midi médiéval 21:159–170
- Gauthier E (2004) Forêts et agriculteurs du Jura: les quatre derniers millénaires. (Annales littéraires. Série Environnement, sociétés et archéologie, 6) Presses universitaires franc-comtoises, Besançon
- Hicks S (1988) The representation of different farming practices in pollen diagrams from northern Finland. In: Birks HH, Birks HJB, Kaland PE, Moe D (eds) The cultural landscape—past present and future. Cambridge University Press, Cambridge, pp 188–207
- Hjelle KL (1997) Relationships between pollen and plants in human influenced vegetation types using presence-absence data in western Norway. Rev Palaeobot Palynol 99:1–16
- Hjelle KL (1999) Modern pollen assemblages from mown and grazed vegetation types in western Norway. Rev Palaeobot Palynol 107:55–81
- Holub J, Jirásek V (1967) Zur Vereinheitlichung der Terminologie in der Phytogeographie. Folia Geobot Phytotax 2:69–113
- Jalut G (1991) Le pollen, traducteur du paysage agraire. In: Guilaine J (ed) Pour une archéologie agraire. Armand Collin, Paris, pp 345–368
- Julve P (1998) Baseflor. Index botanique, écologique et chorologique de la flore de France. <http://perso.wanadoo.fr/philippe.julve/catminat.htm>. Accessed 9 April 2007
- Marguerie D (1992) Evolution de la végétation sous l'impact anthropique en Armorique du Méolithique au Moyen Âge: étude palynologiques et anthracologiques des sites archéologiques et des tourbières associées. Doctoral thesis, Université de Rennes, Rennes
- Mazier F, Galop D, Brun C, Buttler A (2006) Modern pollen assemblages from grazed vegetation in the western Pyrenees, France: a numerical tool for more precise reconstruction of past cultural landscapes. Holocene 16:91–103
- Oberdorfer E (1970) Pflanzensoziologische Exkursionsflora für Süddeutschland. Ulmer, Stuttgart
- Preston CD, Pearman DA, Hall A (2004) Archaeophytes in Britain. Bot J Linn Soc 145:257–294
- Proctor M, Yeo P, Lack A (1996) The natural history of pollination. Harper Collins, London
- Pyšek P, Sádlo J, Mandák B (2002) Catalogue of alien plants of the Czech Republic. Preslia 74:97–186
- Pyšek P, Richardson DM, Rejmánek M, Webster GL, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53:131–143
- Reille M (1992) Pollen et spores d'Europe et d'Afrique du Nord. Laboratoire de Botanique Historique et Palynologie, Marseille
- Reille M (1995) Pollen et spores d'Europe et d'Afrique du Nord—Supplément 1. Laboratoire de Botanique Historique et Palynologie, Marseille
- Reille M (1998) Pollen et spores d'Europe et d'Afrique du Nord—Supplément 2. Laboratoire de Botanique Historique et Palynologie, Marseille
- Richard H, Gery S (1993) Variations in pollen proportions of *Plantago lanceolata* and *P. major/media* at a Neolithic lake dwelling, Lake Chalain, France. Veget Hist Archaeobot 2:79–88
- Tinner W, Nielsen EB, Lotter AF (2007) Mesolithic agriculture in Switzerland? A critical review of the evidence. Quat Sci Rev 26:1,416–1,431
- Tinner W, Nielsen EB, Lotter AF (2008) Evidence for Late-Mesolithic agriculture? A reply to Karl-Ernst Behre. Quat Sci Rev 27:1,468–1,470
- Vorren K-D (1986) The impact of early agriculture on the vegetation of Northern Norway. A discussion of anthropogenic indicators in biostratigraphical data. In: Behre K-E (ed) Anthropogenic indicators in pollen diagrams. Balkema, Rotterdam, pp 1–18