Pollen signals of ground flora in managed woodlands

Bunting, M.J.[a*], Grant, M.J.[b] and Waller, M.[c]

[a] Department of Geography, Environment and Earth Sciences, University of Hull, Cottingham Road, Hull, HU6 7RX. E-mail: M.J.Bunting@hull.ac.uk

[b] Coastal and Offshore Archaeological Research Services (COARS), Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, European Way, Southampton, SO14 3ZH

[C] Department of Geography and Geology, Kingston University, Penrhyn Road, Kingston upon Thames, Surrey, KT1 2EE, UK

Abstract

This paper explores the vegetation signals contained in the non-arboreal pollen and spore (NAPS) components of pollen assemblages from Tauber traps placed in woodlands subject to rotational cutting (coppicing) in lowland England. Sets of three Tauber traps were placed in compartments of different ages at multiple locations within each woodland for one year, and pollen assemblages recorded along with a vegetation survey using a modified pin-frame method in an area of 10m radius around each trap array. Cluster analysis suggests that, as expected, the ground layer vegetation broadly reflects the different environmental conditions in the three woods, with the main subdivisions within woods apparently driven by changes in ground cover between the early and late stages of the coppice cycle. Non-arboreal pollen and spores (NAPS) assemblages group according to woodland of origin, with subdivisions which relate to pollen abundance but lack a simple relationship with years since cutting. Indices of Association between NAPS records and plant presence in the area around each array were calculated using presence-absence data for multiple distances of vegetation survey. All values tend towards an asymptote, which is interpreted as implying an effective source area for the single taxon presence-absence indicator values of ground flora taxa in coppiced woodlands on the order of a 10m radius. Only four taxa, Poaceae, *Ranunculus acris*-type, Cyperaceae and *Scilla*-type, have an Index of Association (A) greater than 0.5, implying that the presence of pollen can be interpreted in terms of the local presence of the relevant plant taxon with some confidence. Estimates of Pollen Productivity relative to Poaceae are presented for five taxa, Apiaceae, Asteraceae (Cardueae), Cyperaceae, *Mercurialis perennis*, and *Scilla*-type. Years since cutting does affect the ground vegetation and NAPS assemblage trapped in these woods, but that the effect is more clearly seen at an assemblage level in the vegetation than in the pollen assemblages. The interpretative significance of NAPS taxa does not seem to be in providing information about the local conditions around the sampling point, but in reflecting the ground flora of the wider woodland.

Key words: coppicing, ground flora, pollen-vegetation relationships, Tauber traps, woodland

Highlights:

- Non-arboreal pollen and spore (NAPS) influx in coppiced woodlands is studied
- NAPS/plant presence Association Indices calculated for several survey distances
- Indices imply effective source area for ground flora is approx. 10m radius
- Estimates of Pollen Productivity are presented for five taxa
- NAPS record reflects ground flora of wider woodland not of local compartment

1. Introduction

Pollen analysis is the main technique used to reconstruct past vegetation on Holocene timescales, from the simplest broad brush identification of whether trees are present in a landscape through to increasingly sophisticated reconstructions of vegetation composition (Trondman, et al. 2015), land-use (e.g. Court-Picon, 2006) and the spatial patterning of vegetation (Hellman, et al. 2009a, 2009b). At the landscape scale fluctuations in the ratio of pollen from non-tree plant sources (non-arboreal pollen, NAP or non-arboreal pollen and spores, NAPS) to pollen from tree and shrub functional types (arboreal pollen, AP) are usually interpreted as indicating changes in the proportion of openness in vegetation communities (e.g. Berglund, et al. 1991, 1996). Given differences within and between communities in the amount of pollen produced and its dispersibility, translation of the ratio into land cover estimates is not trivial (e.g. Sugita, et al. 1999), but the use of taxon-specific pollen dispersal and deposition models has offered an approach for improving reconstructions of landscape openness (Gaillard, et al. 2008, Trondman, et al. 2015).

However, woodland communities also contain plants which produce NAP(S) types. The pollen signal of these types is usually assumed to be minor compared with the AP component, but can fluctuate depending on the canopy density and species and on manipulations of the canopy by disturbance factors such as human management. Coppicing, the practice of cutting some trees to the base to encourage resprouting, yielding even-aged new shoots which can be harvested repeatedly (and sequentially in different compartments), is a widely used traditional woodland management method in north-west Europe (Ellenberg, 1988; Rackham, 2003). When coppicing is undertaken in conjunction with allowing some trees to grow to maturity (standards), a woodland can produce both large timber and underwood for construction, fuel, fencing and other uses. Coppiced woodlands also provide a range of non-timber resources such as fungi, berries, nuts, pannage and other livestock forage, and habitat to support prey animals for hunting for food or sport. Archaeological evidence for the practice of coppicing is extensive and goes back to the Mesolithic period (e.g. Rackham, 1979; Malmros, 1986; Rasmussen, 1993; Pedersen, et al., 1997; Favre and Jacomet, 1998), and its importance for the production of high-quality charcoal meant it remained an important practice in some areas into the industrial era. Like most traditional land management practices it began to fall out of use in the nineteenth century, but the restoration or introduction of coppicing became a valued conservation management tool in the later twentieth century (e.g. Rackham, 2003), and is also practiced in an intensive form as a source of carbon-neutral biofuel for power production. Ecologically, the variation in canopy cover and therefore light reaching the ground layer of the woodland is a key characteristic of the coppiced woodland (Rackham, 1990), which will lead to changes in the flowering and pollen production of the NAPS-producing species as well as the coppiced tree species (Waller, et al. 2012). Over a whole landscape, this effect will average out, but when pollen sites with relatively small source areas such as ponds, small mires or forest hollows (e.g. Sugita, 1994) are considered, fluctuations in the pollen record of NAP(S) taxa may be the result of coppicing rather than reflecting changes in the woodland: open land ratio.

There are multiple possible causes of variations in the proportion of NAP(S) in a woodland pollen assemblage during a coppice cycle. These increases could result from increased pollen production by ground cover plants, through an increase in area covered by those species or greater flowering of existing plants in response to increased light levels reaching the ground. Alternatively, the woodland NAP(S) influx could remain near-constant, but apparent fluctuations be caused by the effects of coppicing on the AP components of the local pollen rain, along with the more open canopy allowing greater input of pollen from a wider landscape, including open communities, during the early stages of the cycle, which later on is intercepted by the increasingly dense and tall canopy of regrowths. The situation is further complicated for pollen types which can originate from multiple plant species. For example, a variation in Poaceae proportions could reflect differences in grass abundance, in the species mixture present, in the long-distance pollen component from open land beyond the woodland, or facultative switching between vegetative and sexual reproduction due to light availability or other disturbance pressures such as grazing (Baker, 2012).

This paper uses data from a study of pollen influx into Tauber traps in coppiced woodlands (Waller, et al. 2012) to investigate the pollen representation of the ground flora components of the vegetation. We aim to determine the representation of changes in ground flora through the coppice cycle in the pollen record of NAPS types, as a tool for extracting better information about past land management practice from the pollen assemblages produced by complex cultural landscapes and to improve the detection of coppice management in long-term pollen records from woodland hollows, small ponds or mires, or in peat forming beneath wet woodlands.

2. Methods

2.1. Field sites

Three woodlands in East Anglia, UK (Figure 1) which are currently subject to coppice management were selected for investigation (for more information, see Waller, et al. 2012). At Bradfield Woods (52°9'N 0°6'W) in Suffolk (Fig 1b), the coppiced stools consist predominantly of *Corylus avellana* and *Fraxinus excelsior*, with *Alnus glutinosa* co-dominant over an area of about 40 ha. *Primula elatior*, *Filipendula ulmaria* and *Mercurialis perennis* are common in the ground flora where the wood overlies boulder clay and *Rubus* spp., *Pteridium aquilinum* and *Hyacinthoides non-scripta* dominate in areas overlying sand. The standards are largely *Quercus robur* and *Betula* spp., mostly less than 70 years old. The majority of Bradfield Woods is managed on a 20+ year rotation. At Chalkney Wood (51°54'N 0°43'E; Fig 1c) in central Essex, *Tilia cordata* is the main coppiced species but in some parts of the wood it is co-dominant with coppiced *Castanea sativa* and less commonly with coppiced *Carpinus betulus*, *Fraxinus excelsior*, *Acer campestre* or *Corylus avellana*. *Quercus robur* is the main standard species, though other species, including *Tilia cordata*, were recorded as 'maidens' in 2007/8. The ground vegetation is dominated by *Hyacinthoides non-scripta* with *Rubus* spp. and *Pteridium aquilinum*. The site is cut on an approximately 25 year rotation. At Hayley Wood (52°10'N 0°49'E) in Cambridgeshire (Fig. 1d), *Corylus avellana* forms the bulk of the coppiced stools with some *Fraxinus excelsior* (ash) and *Acer campestre* (sycamore) coppice beneath a thin canopy of *Quercus* *robur* (oak) standards (Rackham, 1990). *Prunus spinosa* and *Crataegus monogyna* are common as under-storey shrubs. The ground flora is dominated by *Primula elatior* and *Filipendula ulmaria* in central and northern areas, while *Hyacinthoides non-scripta* and *Mercurialis perennis* dominate or co-dominate towards the western, southern and eastern boundaries. Coppicing was reintroduced in part of the wood for conservation purposes in 1963-4, with relatively small plots (0.41 ha) cut on a 14 year rotation.

[INSERT FIGURE 1 HERE]

In all three woods, contemporary (annual) pollen deposition at ground level was investigated using 'Tauber' traps, following the design of Hicks and Hyvärinen (1999). Three traps were placed in a cluster (< 1 m apart) near to the centre of 14 compartments in each wood, a minimum of 20 m from the compartment edge. The compartments sampled were those coppiced in the previous year and compartments 'aged' up to 7 years (when available) and thereafter at age intervals of approximately three years. Traps were set up in October 2006 and collected after a full year.

2.2. *Vegetation data*

Vegetation data were collected from the compartments in which the traps were set. The ground flora was sampled in March-April 2007 using a modified pin-frame method in concentric rings around the centre of the trap array. Four concentric rings (at 1, 2, 4 and 10 m from the traps) were defined, and each ring was sampled in eight locations aligned 45° to the centre of the traps, with a final sampling location in the centre of the ring by the traps, giving a total of 33 locations. Five points were sampled at each location (the centre and four cardinal points at 30 cm from the centre) giving a total of165 sample points (see Figure 2). Species present at each point were recorded on a first hit basis. Any species occurring within 10 m of the centre of the circle but not recorded at any of the points were also noted as present in the relevant distance zone and included in the calculation of the indices of association. The area of survey was chosen for efficiency and on the assumption that the pollen source area for ground cover plants under a woodland canopy would be short, since minimal opportunities for wind entrainment would occur.

[INSERT FIGURE 2 HERE]

Plants were grouped into palynological equivalent (pe) taxa (see Table 1), and percentage cover within each ring calculated.

2.3. Pollen data

This study used pollen assemblages from Tauber traps which were deployed for a single year, allowing precise relationships between the stage of the coppice compartment and the pollen assemblage deposited within it to be studied. Most surface sample studies (see e.g. Broström, et al. 2008) use moss samples which average pollen deposition over an unspecified number of years (e.g. Räsänen, et al. 2004), or averaged pollen influx from multiple years of Tauber trap deployment (e.g. Sugita, et al. 2010). Whilst these methods do reduce the effects of climate-related inter-annual variability in plant flowering (e.g. Huusko and Hicks, 2009; Jackson and Kearsley, 1998), they would have blurred the signal of the coppice cycle which we seek to study due to variability in the ground vegetation throughout a coppice cycle being greater than the climatic influence between consecutive years (e.g. Waller, at al. 2012). Three closely grouped traps were deployed at each location, which enabled us to both include some replication within our analyses and screen our data for possible distortion from non-airborne modes of pollen deposition, e.g. from anthers or pollen-bearing insects falling into the trap.

All pollen samples were processed following the methodology of Hicks et al. (1996) for Tauber traps, including the addition of tablets of exotic pollen to allow the calculation of pollen influx. A minimum of 1000 total land pollen (TLP) grains were counted from each trap and influx calculated in grains cm^{-2} yr^{-1}. For most analyses in this paper, influx from the traps in each array was summed to give a basic count of 3000 grains which ensured a minimum non-arboreal pollen and spores (NAPS) count of 300, and generally gave counts in excess of 500 grains for analysis. The only exception was the calculation of Relative Pollen Productivity (RPP) using the raw influx data (see 2.4.2 below). We screened our data for anomalous values in individual taxa by removing the data for any trap where the difference in influx of a taxon was greater than an order of magnitude different from the values for the same taxon in the other two traps, except at low influxes where the calculation of influx depended on counts of 1-2 grains, such that counting errors (Maher, 1972, 1981) are larger than differences in the estimated influx. 6% of traps were removed from analysis on this basis for *Filipendula*, fewer than 5% for Apiaceae, Asteraceae (Cardueae), Cyperaceae, *Lonicera periclymneum*, Poaceae and *Ranunculus acris*-type, and no outliers were detected for *Mercurialis perennis*, *Rubus* and *Scilla*-type.

2.4. Data analysis

WINTwins, the windows version of TWINSPAN (Hills and Šmilauer, 2005), was used to investigate the underlying structure within the two datasets (pollen and spore assemblages and vegetation survey data) separately and provide an initial overview. Two approaches were then taken to exploring how well the pollen assemblages represented the vegetation: Indices of Representation (after Davis, 1984) and estimation of Pollen Productivity relative to Poaceae (hereafter $RPP_{Poaceae}$).

2.4.1. Indices of representation

The index of association approach (e.g. Davis, 1984; Hjelle, 1997; Bunting, 2003; Fontana, 2005; Li, et al. 2005; Schofield, et al. 2007) offers a simple method for investigating the vegetation signal contained within the pollen signal of taxa present in small amounts in pollen records, especially in contexts where the source area is believed to be small. For this study, all ground layer taxa which were recorded as present at least once in both the vegetation and pollen assemblages across the three study sites were investigated. Indices of association (A: reflects the co-occurrence of plant and pollen in a sample), over-representation (O: type present in the pollen assemblage but not the local vegetation) and under-representation (U: plant present without being recorded in the pollen sample) were calculated as follows:

$$A = B_0 (P_0 + P_1 + B_0)^{-1} \qquad \text{(equation 1)}$$

$$O = P_0 (P_0 + B_0)^{-1} \qquad \text{(equation 2)}$$

$$U = P_1 (P_1 + B_0)^{-1} \qquad \text{(equation 3)}$$

where B_0 = number of samples where pollen type is present and associated plant taxon is present within a defined distance, P_0 = number of samples where the pollen type is present in the surface sample but the plant taxon is not present in the vegetation within the defined area, P_1 = number of samples where the pollen type is not present in the surface sample but the plant taxon is present in the vegetation within the defined area.

Since the vegetation data had been collected in concentric rings, it was possible to calculate these indices using vegetation data with four different spatial resolutions (presence within radii 1m, 2m, 4m and 10m from the centre of the trap array). We hypothesised that as the area increased and more plants were sampled, the trends in the indices could be used like other indications of ‘fit’ between pollen and vegetation data (e.g. correlation coefficient, likelihood function score) to provide an indication of a pollen source area for the taxon as an indicator species. It is assumed that the ‘goodness of fit’ between pollen and vegetation, as measured in any given model of the relationship, increases with increasing area of vegetation surveyed until a pollen source area distance is reached. It is also assumed that adding more vegetation information from beyond this distance either has no effect on the measure of fit or causes it to worsen, giving an asymptote or inflection in the plot of fitness measure against distance of vegetation survey used in its calculation, therefore the position of the asymptote or inflection indicates a pollen source area for the particular combination of trap and plant type.

2.4.2. Relative Pollen Productivity and background pollen influx

The pollen and spore data available in this study are influx data and therefore the values for each taxon are independent. This allows estimates of the parameters of the relationship between pollen and spore influx (hereafter 'influx') and distance-weighted plant abundance (dwpa) to be made separately for each taxon via linear regression analysis. Relative Pollen Productivity can then be calculated by taking the ratio of the slope term between the taxon of interest and the reference taxon ($RPP_{reference}$). Each trap in a trap array was treated as a separate estimate of the influx, therefore most sample points had multiple 'y' values. Data pairs with zero values for both pollen and vegetation were removed from the dataset to avoid these samples having an undue influence on the model fitting process, and taxa present in both pollen and plant datasets from at least four trap arrays were selected for further analysis.

Vegetation data for the selected taxa were distance-weighted using the taxon-specific Sutton distance-weighting term (Sutton, 1953; Sugita, 1993) for neutral atmospheric conditions (but see Jackson and Lyford, 1999):

$$g_i(z) = b_i \gamma z^{\gamma-1} e^{-b_i z^{\gamma}} \qquad \text{(equation 4)}$$

Where z = distance to mid-point of ring, $\gamma = 0.125$ (Prentice, 1985) and b_i is defined as:

$$b_i = 75.2 \frac{v_{si}}{u} \qquad \text{(equation 5)}$$

Where v_{si} is the sedimentation velocity (fall speed) of taxon i and u is the windspeed (3 m s^{-1} was used throughout this paper). Fall speed estimates for the taxa analysed in this paper are summarised in Table 2. Where necessary, fall speeds were estimated using Stoke's Law along with measurements of the a and b axes of the taxon (Gregory, 1973) taken from the images in Moore et al. (1991). The sampling trap was treated as a single point with radius zero, since traps were not positioned within canopy openings of any kind. Cumulative distance-weighted plant abundance from the trap was then calculated for each ring.

A one tailed null hypothesis of no positive linear relationship between dwpa and influx was tested using the Pearson correlation coefficient and, where the probability of the null hypothesis was < 0.05, regression analysis was carried out to estimate the slope term (taxon pollen productivity: PP_{taxon}) and intercept (background pollen influx of the taxon). This analysis was carried out for the cumulative dwpa at each ring.

Poaceae was chosen as the reference taxon for the ground flora taxa, since it occurs widely in the dataset and showed statistically significant linear correlation between cumulative dwpa and influx at all distances used in their respective analyses. Pollen Productivity relative to Poaceae – hereafter $RPP_{Poaceae}$ - was calculated by taking the ratio of the slope terms, and the standard errors on the slopes combined using propagation of errors. As the area of vegetation included in the analysis increases, it is expected that the background influx will decrease and the estimate of RPP stabilise. The correlation coefficient should be highest (the correlation is expected to be strongest) at the distance best approximating the taxon-specific source area. These analyses were carried out using SPSS v.19.

3. Results

Thirty four palynological equivalent taxa were recorded in the vegetation across the three woodland sites (Table 1), and their representation is considered in this paper. Figure 3 summarises the data from both plant surveys and pollen traps in scatter plots. Figure 3a shows the variation in ground cover for each compartment at the three sites plotted against sampled compartment cutting date. Ground cover tends to be highest in the first few years after cutting, but does not show the pattern of decline to a lower steady state over time that might be expected. Bradfield Woods show the nearest to that pattern, with an abrupt drop between the 2000 and 1997 compartments, and a single anomalously high value in the 1983 compartment. The ground cover at Chalkney does not show a clear pattern over time, but is divided into two groups with values around 60% and values below 40% respectively. Hayley Wood generally has the lowest proportion of ground cover, which generally declines with years since cutting with the exception of the 2001 compartment. Figure 3b shows the number of palynological equivalent taxa recorded in each compartment against years since cutting. Values are generally higher in compartments cut since 2000 and lower in older regrowth areas, as expected. The most recent site in each case has very high diversity in Hayley Wood and low diversity in the other two sites, coupled with low ground cover at Bradfield Woods. Hayley Wood has a shorter rotation cycle (c. 14 years) than the other two sites (>25 years) which may support rapid recovery, and the waterlogged nature of the soil at Bradfield Woods may extend the impact of coppicing on ground flora into the following year since damage from compaction, trampling and coverage with discarded material may have a greater effect at this site.

[INSERT TABLE 1 HERE]

[INSERT FIGURE 3 HERE]

Figures 3c-e show summary data for the pollen and spore representation of the same set of taxa. There tends to be a higher proportion of NAPS taxa (Figure 3c) overall in younger compartments, especially in the most recently cut sites at Bradfield Woods, which might be attributable to reduced tree pollen production in those compartments for taxa other than *Corylus* (Waller, et al. 2012), the increase in local pollen-producing surface cover and/or effects of light availability on flowering or increased influx of NAPS from the largely open, agricultural landscape beyond the woodland due to the reduction of canopy cover. Figure 3d presents the total influx of NAPS types and shows a weaker response to time since cutting in variation than seen in the proportion plot, suggesting that such effect as there is largely due to a reduction of tree pollen influx rather than an increase in NAPS influx. The TLP pollen sum was around 1000 for each trap, and results of each trap array were summed for this analysis, giving NAPS counts ranging from around 300 grains to over 2000 grains. Count size is not correlated with number of woodland pe taxa recorded in each assemblage (r=0.087, d.f. = 36, p>0.10 (one-tailed)), suggesting that all counts were large enough to record the majority of taxa present in the sample, even where the assemblages were dominated by AP types. The diversity of pe types in the pollen assemblages (Figure 3e: range 10-20, mean 16) is both higher and more uniform than for the vegetation data (range 1-23, mean 7). This probably reflects the greater spatial sampling area represented by the pollen assemblages, considering both the local pollen component from within the source area and the background pollen component, when compared with the vegetation survey area. Figure 3f shows a clear correlation between % ground cover in the vegetation and % NAPS (r=0.459, d.f. = 36, p < 0.01), but this probably results from the response of both signals to the environmental changes through the coppice cycle in factors such as light competition intensity and canopy openness rather than the pollen signal directly responding to local ground cover.

3.1. Cluster analysis

3.1.1 Ground flora vegetation

Clear differences in the plant lists between the three woods reflect differences in the canopy taxa and environmental setting. TWINSPAN analysis of the vegetation abundance data around each trap site (Figure 4a) clearly separated most samples by woodland, grouping all Bradfield Woods and Hayley Wood samples in the 0xx division and most of the older Chalkney Woods samples in the 1xx division. This first division (0xx versus 1xx) largely seems driven by vegetation (palynological equivalent) diversity, grouping low-diversity samples with strong representation of *Scilla*-type in cluster 1xx. This cluster is further divided according to ground cover and the few other species recorded, but the division seems to reflect geography within the wood rather than years since cutting; cluster 100 collects locations in the northern part of Chalkney Wood, where *Ranunculus* *acris*-type is present and ground cover around 50%, whilst 101 locations are more southerly, lack this taxon and have lower ground cover, around 30%. The 1998 compartment sample is separated off in 11, reflecting lower ground cover here (5%) than elsewhere in Chalkney Wood.

[INSERT FIGURE 4 HERE]

Cluster 00X contains most Bradfield Woods samples, characterised by a greater biodiversity than the Chalkney Wood samples and a ground flora generally dominated by Cyperaceae, *Mercurialis perennis*, Poaceae and *Ranunculus acris*-type; Group 001 has a higher abundance of grasses than group 000 and also has generally greater ground cover (74% versus 58%), and contains four of the five most recently cut compartments along with one of the oldest, that cut in 1985.

Cluster 01x contains Hayley Wood samples grouped with a small number of samples from the other woods. Group 010 has comparatively high ground cover, around 70%, and groups four Chalkney Wood compartments with one Hayley Wood compartment, that cut in 2001, which is also the closest to the secondary woodland of The Triangle. The four Chalkney compartments have high abundance of *Scilla*-type, like the other Chalkney compartments, along with a greater diversity of other taxa; they are four of the five most recently cut, therefore expected to have the best light conditions to support ground flora diversity, and are also all close to the edges of the wood where light penetration is likely to be greater. Group 011 samples have much lower ground cover, averaging 22%, but have similar high floral diversity to the other compartments grouped in 0xx. Group 011 collects all other Hayley Wood samples along with two Bradfield Woods samples, that cut in 1988 and that last cut in 2007. In both cases these compartments have low ground cover compared with the other Bradfield Woods compartments, although the causes are likely to be different. 0110 and 0111 (indicated by underlining on figure 4a) roughly divide more recently cut compartments in Hayley Woods from older ones.

Cluster analysis suggests that, as expected, the ground layer vegetation broadly reflects the different environmental conditions in the three woods, with the main subdivisions within woods apparently driven by changes in ground cover between early and late stages of the coppice cycle.

3.1.2 Pollen assemblages

TWINSPAN analysis (Figure 4b) was carried out using the proportion of woodland NAPS types (hereafter wNAP) relative to the total land pollen and spores sum, since this is the form of data most commonly encountered in the palaeoecological literature. The first division splits moderate abundance samples (average wNAP proportions of 30%, 35% and 40%) from one high abundance sample (Bradfield Woods 2006: 76%) and a group of lower abundance samples (means of 25%, 20% and 15% respectively). Figure 4b shows that the analysis first divided all Hayley Wood samples apart from the compartment cut in 1998 from the other two woods, with the exception of the 2005 compartment from Chalkney Wood, which was grouped with the 2007 and 2006 Hayley Woods compartments (group 011: this group has higher NAP proportion (mean = 40%) and lower average pe diversity (15) than the other Hayley groups). The three subdivisions of Hayley Wood assemblages are broadly on an age basis, although the 2003 assemblage groups with those from 1996-98. Three Bradfield assemblages (those from compartments cut in 2005, 2000 and 1997) are grouped with the bulk of the Chalkney Wood samples in 110, with an average wNAP abundance of 20%. The 1991 and 1978 Chalkney assemblages are separated in group 111 (with the lowest mean proportion of wNAP, 15%) and one Chalkney sample (1983) and one Hayley sample (1998) are grouped with the bulk of the Bradfield Woods samples in cluster 101 (abundance around 25%). The assemblage from the 2006 compartment at Bradfield Woods has a very high wNAP abundance, which sets it apart from all other samples.

Cluster analysis suggests that the wNAPS pollen assemblages can be grouped according to woodland of origin, with subdivisions which relate to pollen abundance and possibly in Hayley Wood also years since cutting (although grouped samples show some geographic grouping, with group 00 containing mostly samples from compartments on the south west of the ride, and the other groups collecting samples from the north-east).

3.2. Indices of Association

Plants were recorded present, but no pollen found in the trap assemblages, for the palynological equivalents *Arum*, *Dactylorhiza*-type and *Sedum*. Both plants and pollen were recorded, but never both in the same compartment, for *Epilobium*-type, *Geum*, *Hypericum perforatum*-type, *Scutellaria*-type, *Stachys*-type, *Veronica* and *Viola*-undiff. Indices of representation were calculated for the remaining 23 ground flora pollen types at multiple distances. Indices based on vegetation presence at a distance of 10m radius around the traps are presented in Table 3. Only four taxa, Poaceae, *Ranunculus acris*-type, Cyperaceae and *Scilla*-type, have an Index of Association (A) greater than 0.5, implying that the presence of pollen can be interpreted in terms of the local presence of the relevant plant taxon with some confidence.

[INSERT TABLE 3 HERE]

3.2.1 Variations in indices of association with increased vegetation survey radius

Since indices could be calculated using vegetation presence in different radii around the traps, plots of changes in index with increasing distance were made. The plots can be grouped into four clusters showing similar patterns with two exceptions (examples shown in Figure 5; all taxa presented in supplementary material 1). Group 1 contains Cyperaceae, Poaceae, *Ranunculus acris*-type and *Scilla*-type. For these taxa, A increases with increasing distance, the rate of increase slows beyond 2m radius, and A is the largest index of representation beyond 4m. The second group shows increasing A with increasing distance, generally levelling off beyond 2m, but the index of over-representation (O) is the highest index. For some taxa, A reaches values around 0.5 and close to the O value by 10m (group 2a: *Mercurialis perennis* and *Rubus*-type), but for most O is always the largest index by some way (group 2b: Apiaceae, Asteraceae (Cardueae), Asteraceae (Lactuceae), Brassicaceae, Caryophyllaceae, *Dryopteris dilatata*-type, *Filipendula*, *Lysimachia vulgaris*-type, *Plantago major/media*, *Rumex sanguineus*-type and *Urtica dioica*). The third group has a similar pattern but the index of under-representation (U) has the highest values beyond 2m (*Lonicera periclymneum*, *Paris quadrifolia*-type, *Primula veris*-type and *Prunella vulgaris*-type). Two taxa did not fall into one of the three clusters; the indices for *Allium*-type had the same values at every distance, and for *Potentilla*-type A decreased and U increased with increasing distance.

[INSERT FIGURE 5 HERE]

The tendency of all values towards an asymptote, with only slight changes between values calculated using vegetation present within 4m of the trap array and that present within 10m of the trap array, is interpreted as implying an effective source area for the taxon presence-absence indicator values of ground flora taxa in coppiced woodlands on the order of 10m radius. Ground flora and vegetation data were recorded in March-April, in order to ensure that spring ephemeral species believed particularly significant in coppice woodlands would be recorded, which may lead to under-recording of the abundance of summer-green taxa and over-recording of the abundance of spring ephemeral taxa compared to studies carried out later in the year. This may have contributed to the high over-represented indices (where pollen is present but not plants), although since the Index analysis uses presence-absence data we consider this to be less significant than under-canopy effects of reduced flowering and limited air movement for pollen transport.

3.3. Abundant taxon RPP values

Those taxa present in at least three compartments in both the vegetation and pollen data sets were considered for estimation of RPP. Scatter plots comparing pollen influx and accumulated distance weighted plant abundance to 10m were created for Apiaceae, Asteraceae (Cardueae), Cyperaceae, *Filipendula, Lonicera periclymneum*, *Mercurialis perennis*, Poaceae, *Ranunculus acris*-type, *Rubus*-type. and *Scilla*-type, and obvious outliers removed where these were small in number.

Some taxa showed scatters which suggested a complex taphonomy (see Figure 6). The basic assumption underlying the approach used to estimate RPP in this paper is that there is a common mode of pollen transport linking all samples with their surrounding vegetation, therefore a singular relationship between pollen and vegetation to be modelled. Where there appeared to be two or more distinct relationships in the plot of pollen influx against dwpa, as in Figure 6, this has been interpreted as implying that different modes dominate at different locations, each producing an approximately linear relationship. The relationship with high levels of influx and low local dwpa is interpreted as being dominated by highly stochastic transport modes such as insects (insects visiting flowers and then visiting the traps, perhaps attracted by the availability of open water, depositing pollen into the traps either during a visit or as a result of becoming incorporated into the pollen assemblage) or gravitic deposition (pieces of anther or clumps of ripened pollen falling directly into the trap rather than being released as individual grains into the air and transported through the trunk and canopy space). These non-aerial modes are also probable causes of some of the samples identified as outliers for having exceptionally high influx and removed from analysis for other taxa. Complex scatters of this type were noted for *Filipendula*, *Lonicera*, *Ranunculus* and *Rubus,* all taxa with insect-attracting flowers, and these were not considered further.

[INSERT FIGURE 6 HERE]

Correlation coefficients for pollen against vegetation at different sampling radii for the remaining six taxa are shown in Figure 7, and suggest some improvement in the relationship with distance for Apiaceae and Cyperaceae, with otherwise little change. $\text{RPP}_{\text{Poaceae}}$ calculated using regression of pollen influx against distance-weighted plant abundance to 10m is summarised in table 4. Most estimates of Relative Pollen Productivity presented in the literature are derived from percentage pollen data by applying ERV analysis (Parsons and Prentice, 1981; Prentice and Parsons, 1983), which uses an iterative approach to identify values of RPP and background pollen influx for all taxa at once. We applied this method to the dataset reported here, but the algorithm failed to find a solution; this is interpreted as showing that there are too few samples where most or all of the taxa are present in both pollen and vegetation to enable the algorithm to be effectively applied.

No published values for *Mercurialis perennis* or *Scilla*-type are available in the literature. Hjelle (1998) used a different field method to estimate $\text{RPP}_{\text{Poaceae}}$ of herb taxa in Norwegian hay meadows, and obtained an estimate of 0.27 for Apiaceae type, about six times lower than the estimate reported here, and an estimate of 0.06 for Asteraceae (Cardueae) (*Cirsium*-type), twice the value reported here. The taxonomic mixture of plants making up the palynological equivalent types were different, including *Aegopodium podagraria*, *Anthriscus sylvestris, Carum carvi*, *Pimpinella saxifrage* and *Sanicula europaea*, as well as *Angelica sylvestris* and *Conopodium majus*, the species present in our woodland sites, for Apiaceae, and *Cirsium palustre* only for Asteraceae (Cardueae) where we also recorded *Arctium minus*, *Cirsium arvense*, *C. vulgare* and *Sonchus* sp. Possible explanations for the differences include the different vegetation survey methods (see e.g. Bunting and Hjelle, 2010), the different time of year of recording vegetation (since Poaceae ground cover in woodlands may be lower in March-April than in June-July, depending on the phenology of the species), and the different species mixtures and flowering conditions for the reference taxon, Poaceae, in hay meadows and in woodlands. Hjelle (1998) does not report a taxonomic list of plants in the palynological equivalent type Poaceae for comparison. Multiple estimates of $\text{RPP}_{\text{Poaceae}}$ (Cyperaceae) have been reported in the literature (see e.g. Broström, et al. 2004, Mazier, et al. 2012), and a range of values are included in table 4. The closest value to this study comes from Hjelle (1998), whose species mixture is listed as including *Carex* spp. *Eriophorum angustifolium*, *E. vaginatum* and *Trichophorum cespitosum*, whereas our estimate is derived from a number of *Carex* species (see table 4). Ground flora vegetation data were recorded in March-April, in order to ensure that spring ephemeral species believed particularly significant in coppice woodlands would be recorded. This may lead to under-recording of the abundance of summer-green taxa and over-recording of the abundance of spring ephemeral taxa compared to studies carried out later in the year which might in turn lead to an over-estimate of $RPP_{Poaceae}$ for *Scilla*-type and under-estimate for *Mercurialis perennis* and other taxa.

[INSERT FIGURE 7 HERE]

[INSERT TABLE 4 HERE]

The total annual pollen influx from these six taxa for the traps studied has a mean of 4530 grains cm^{-2}. The intercept on the regression model indicates the pollen influx when no plants are present within the 10m radius survey area, and therefore estimates the influx from the background vegetation, beyond the studied area. These estimates are given in table 4, and sum to 2240 grains cm^{-2}, c. 49% of the mean total influx for these taxa. Using the proportion-based ERV-analysis, 40-60% of the total pollen typically comes from beyond the Relevant Source Area of Pollen (RSAP) (e.g. Sugita 1994), therefore the assumption of a relatively short source area seems reasonable. However, the range of total influx values from individual traps varies very widely, from 80 grains cm^{-2} to 56700 grains cm^{-2}.

4. Discussion

The assumption made in designing this study was that the vegetation and the NAPS pollen signal within the coppiced compartments would show systematic variation with years since cutting on a scale of a few metres. A general decrease in % ground cover and number of pe taxa recorded in the vegetation data was seen with increasing years since cutting in all three woods, as expected. TWINSPAN cluster analysis of the vegetation data show that the three woods have distinctly different ground floras, as would be expected given different geographical location, dominant species in the canopy as both standards and coppiced stools, and differences in the physical environment. Cluster analysis suggests that the ground layer vegetation broadly reflects the different environmental conditions in the three woods, with the main subdivisions within woods apparently driven by changes in ground cover between early and late stages of the coppice cycle along with some geographic variation in the physical environment within the woods.

The proportion of NAPS pollen types is higher in more recently coppiced compartments, which could reflect the increased ground cover recorded in the vegetation surveys, but could also reflect flowering responses to the increased light availability created by coppicing, decreases in pollen production by newly coppiced AP species, increased influx of pollen sourced from beyond the woods due to the opening up of the canopy, or all of these factors. The plot showing the total influx of NAPS types (Figure 3d) shows a weaker response to time since cutting than seen in the proportion plot, which might imply that such effect as there is, can largely be attributed to a reduction of tree pollen influx rather than an increase in NAPS influx. However, the effect is broadly similar across all three woods, and since Waller et al. (2012) showed that pollen production of *Corylus* actually increased in the first few years after coppicing, differences between the woods would be expected if this was the sole process, therefore further investigation is needed to confidently identify the dominant cause of this pattern. Cluster analysis suggests that the woodland NAPS pollen assemblages can be grouped according to woodland of origin, with subdivisions which relate to pollen abundance and possibly in Hayley Wood also years since cutting. NAPS proportions are all below 50% of the total, apart from three recently cut compartments at Bradfield Woods, and show a broad pattern of decreasing with increasing years since cutting, but there is no clear relationship between ground cover and %NAPS in any one of the woods.

These general patterns suggest that years since cutting does affect the ground vegetation and NAPS assemblage trapped in these woods, but that the effect is more clearly seen at an assemblage level in the vegetation than in the pollen assemblages.

4.1. Signals from individual palynological equivalent taxa

Two approaches were used to investigate the signal contained in the record of individual pollen and spore types, indices of association (after Davis, 1984) and fitting a linear pollen dispersal and deposition model to estimate RPP. Although multiple palynological equivalent plant types are clearly recorded in only one wood (Table 1), the pollen record of none of these types is confined to that wood's pollen assemblages; the pollen and spore types are found more widely. Overall, there was much less variation in the number of NAPS types recorded in pollen assemblages than in vegetation samples (Figure 3). Indices were calculated for all 23 taxa present as both plants and pollen in at least one of the 36 compartments in the dataset. Only 4 of those taxa, Poaceae, *Ranunculus acris*-type, Cyperaceae and *Scilla*-type, have A greater than 0.5, a value which implies that the presence of pollen can be interpreted in terms of the local presence of the relevant plant taxon with moderate confidence – in general, the value of A was low, suggesting that the association between pollen/spore presence and local plant presence is weak. Four out of the ten more abundant taxa considered suitable for analysis using a linear model of pollen dispersal and deposition had data scatters suggesting complex taphonomy, all are taxa with insect-attracting flowers, and these were not considered further. Table 4 presents first estimates of $\mathrm{RPP}_{\mathrm{Poaceae}}$ for *Mercurialis perennis* and *Scilla*-type, and first estimates from woodland for Apiaceae, Asteraceae (Cardueae) and Cyperaceae. As is usually the case with RPP estimates, the use of Poaceae as a reference taxon presents challenges. Poaceae is a pollen type made up of many different plants, which vary according to habitat, and many of the species show facultative switching between vegetative and floral reproductive mechanisms so can show high variation in pollen production in response to local conditions (e.g. Baker, 2012). The values obtained for Cyperaceae and Asteraceae (Cardueae) are broadly comparable to those obtained by Hjelle (1998) from a study in hay meadow communities, and whilst the value for Apiaceae shows a different rank position (higher than Poaceae rather than below it and Cyperaceae) compared with Hjelle's (1998) study, the value is still within a reasonable range, and may reflect the greater height relative to the rest of the ground flora canopy and therefore greater pollen transport of Apiaceae in a woodland ground flora community rather than a grassland or the different species mixes.

This discussion highlights the early state of research into pollen productivity, a very important parameter for pollen dispersal and deposition modelling. Carefully designed studies in multiple habitats subject to different management regimes (e.g. Baker, 2012; Abraham & Kozakova, 2012) and supporting different species mixtures are needed to investigate the environmental variations in pollen production of widely occurring taxa such as Poaceae, in order to compare findings from studies of the same palynological equivalent taxa in e.g. grazed pastures (Broström, et al. 2004; Mazier, et al. 2008), hay meadows (e.g. Hjelle, 1998) and woodlands (this study); such a study in northwest Europe is being carried out by the Crackles Project (see Bunting, et al. 2013; forthcoming). A useful future approach will be to combine direct assessment of flowering with pollen surface sample type studies to gain a better understanding of the micro and meso-scale components affecting pollen production within species and landscapes (e.g. Waller, et al. 2012; Bunting, et al. in prep).

4.2. Source area estimates for NAPS taxa in woodlands

The assumption underlying the design of the vegetation survey was that the pollen source area of the ground flora taxa is on the order of a few metres. This is partly based on analogy with other studies of ground-level vegetation communities (e.g. Bunting and Hjelle, 2010) and partly on extrapolation from the short (50-100m) RSAP (Sugita, 1994) typically reported for tree pollen in closed canopy woodland communities (e.g. Calcote, 1995; Bunting 2005; Sugita, et al. 2010) and also found in this project (Bunting, et al in prep). The RSAP is a source area defined on the basis of a particular assemblage of pollen types using the ERV approach, which was not appropriate for this data set, so the analyses presented here are based on relationships for individual pe taxa, an approach applied to datasets before the development of effective computational methods for carrying out ERV analysis (e.g. Bradshaw, 1981; Jackson, 1990). Studies suggest that the RSAP is determined by the spatial sensing properties of the rarer taxa with the longest individual source areas (Bunting, et al. 2004; Hellman, 2009a), therefore we considered that the published RSAPs were a reasonable estimate of the maximum individual source area we might find, and used them to determine the vegetation survey methods.

The pollen source area concept depends on the division of pollen sources into two components based on their position relative to the sampling point, and therefore is usually expressed as a radial distance around the sample point. Pollen sources within the pollen source area contribute ‘local’ pollen to the assemblage, and those located beyond that distance contribute ‘background’ pollen. A widely used approach to defining this radius is to consider the ‘fit’ between pollen signal and vegetation measured at different distances according to a specified model of the pollen-vegetation relationship, and define the distance at which the fit does not improve on the addition of more vegetation data as the pollen source area (e.g. RSAP; Sugita, 1994). On this basis, the correlation coefficient fit measure used for the RPP estimation (Figure 7) implies that the pollen source area is between 4m and 10m, since adding data from the outer set of pin-frame points to the cumulating dwpa produces either the same coefficient or a slight decrease in correlation.

For the Index approach, various measures of ‘fit’ could be defined, such as the distance with the highest ‘A’ value, or the point at which all three indices first reach constant values. Highest values of A are obtained at the longest survey distance, 10m, and groups 2a and 3 show a clear rise in values of A between 4m and 10m, suggesting that the source area may be further out from the trap. The plots of all the indices for groups 2a and 2b show smaller changes between 4m and 10m than between closer samples, but are not constant – these results suggest a pollen source area slightly beyond 10m. As discussed in the text the indices suggest generally quite poor interpretative links between pollen and vegetation at the species level.

'Background' pollen is clearly an important component of the NAPS pollen assemblage, as shown by the high (and relatively uniform) diversity of pollen types recorded in all three woods (Figure 3). Although a number of palynological equivalent plant types occurred only in one of the three woods studied, this was not seen in the pollen assemblages. This may partly be explained by the presence of ground flora elements in the studied woods other than those recorded in the samples used, and partly by background pollen transported from beyond the studied wood which reflects the presence of pe plants in the wider landscape.

4.3. Limitations

This study has several clear limitations. Tauber traps were only deployed for a single year, and although using three traps at each location allowed some outliers to be identified and removed the results will still have been affected by the particular characteristics of the flowering season sampled. A greater vegetation survey distance, and finer spacing of the modified pin-frame points, would allow clearer identification of possible source areas and probably improve the fit of the various models used here, but within the context of the wider project the effort invested in surveying around individual sampling points had to be balanced against the desire to ensure an adequate number of different sampling points were included in the analysis. Vegetation survey was carried out in the spring; coverage and visibility of ground flora taxa varies across the seasons, so results based on survey in other parts of the year might be different. Developing a vegetation recording strategy which combines survey at multiple seasons without being too time-consuming so that a reasonable number of samples could still be recorded could be a useful development for studies of vegetation communities with strong seasonal variation (e.g. grasslands). Using fewer sites per wood and exploring a wider range of woodlands might increase the applicability of the study, but the chosen strategy allowed us to look at a wide range of coppice stages, which was important since historic and presumably pre-historic coppice practice is known to have included cycles of different lengths, from a few years to several decades.

4.4. *Implications for palaeoecology*

Whilst the pollen source area of the NAPS component in these woodlands seems to be quite small, and it is possible to estimate RPP and background influx for some taxa and therefore apply quantitative vegetation cover reconstruction strategies to their representation in the pollen record, the information on local vegetation contained within this pollen signal is limited. The strong contribution of the background pollen rain means that the suite of species present is quite similar across the wood regardless of coppice stage, although the diversity of ground flora present decreases with increasing years since cut. NAPS proportion does decrease with years since cutting (Figure 3c), and a cyclic rise and fall in % NAPS at an appropriate time interval in a pollen record might be a sign of coppicing. There is no correlation between % NAPS and % ground cover (Figure 3f), so this signal is likely to reflect the behaviour of the AP signal and the changes in physical conditions associated with the progress of the coppice cycle. As regrowths create more shade and shelter, they will reduce the occurrence and strength of below canopy trunk space air movement and therefore pollen transport, as well as creating more sites for impaction to remove pollen from the air stream before it reaches the sampling point, and also reduce light levels therefore supressing flowering in some species.

The interpretative significance of NAPS taxa does not seem to be in providing information about the local conditions around the sampling point, but in reflecting the ground flora of the wider woodland. Identifying the indicator value (see e.g. Court-Picon, 2006) of the different pollen types recorded here will require a wider study of habitats throughout the landscape of interest, and may be inhibited by the heavily managed and industrialised nature of much of the northern European lowlands and by the taxonomic limitations of pollen identification.

5. Conclusions

We set out to determine whether the NAPS component of the pollen record was a useful tool for identifying coppice management in long-term pollen records. Our findings show that there is no unambiguous signal of coppice management. However, there are a few years of increased %NAPS levels immediately following coppicing, which might show up through cyclic oscillations in these values in a pollen diagram of sufficiently high temporal resolution from a site where the spatial sensitivity of the assemblage is comparable to the coppiced unit. $RPP_{Poeaceae}$ values are estimated for five taxa, Apiaceae (1.61 ± 0.40), Asteraceae (Cardueae) (0.03 ± 0.01), Cyperaceae (0.40 ± 0.07), *Mercurialis perennis* (0.24 ± 0.04) and *Scilla*-type (0.34 ± 0.06), which provide a starting point for future investigations using pollen dispersal and deposition models. Indices of representation show quite poor relationships between pollen presence in traps and plant presence in spring vegetation surveys in the immediate area, and imply that the effective source area for these ground flora types is around 10m, but the non-arboreal component of the pollen record mainly reflects the ground flora of the wider woodland, not of the local sampling area.

Glossary

A: Index of Association

AP: arboreal pollen

dwpa: distance-weighted plant abundance

NAP: non-arboreal pollen

NAPS: non-arboreal pollen and spores

O: Index of Over-representation

pe: palynological equivalent

RPP: Relative Pollen Productivity

$\mathrm{RPP}_{\mathrm{Poaceae}}$: Pollen Productivity relative to Poaceae

RSAP: Relevant Source Area of Pollen

U: Index of Under-representation

wNAP: woodland non-arboreal pollen

Acknowledgements

We would like to thank the managers and owners of Hayley Wood (the Cambridgeshire Wildlife Trust), Bradfield Woods (the Suffolk Wildlife Trust) and Chalkney Wood (Essex County Council) for providing access to the sites. Thanks also go to Claire Ivison (Kingston University) for drafting Figure 1. The research was funded by the award of grant from the LeverhulmeTrust (F/00 520/E) to the authors. Anne Birgitte Nielsen and an anonymous referee provided helpful comments on an earlier version of this manuscript.

References

Abraham, V., Kozakova, R., 2012. Relative pollen productivity estimates in the modern agricultural landscape of Central Bohemia (Czech Republic). Review of Palaeobotany and Palynology 179, 1-12.

Baker, A., 2012. Does heavily grazed vegetation show up in the pollen record? Quaternary International 279-80, 34-35.

Bennett, K.D., 1994. Annotated catalogue of pollen and pteridophyte spore types of the British Isles. Unpublished manuscript, Department of Plant Sciences, University of Cambridge.

Berglund, B.E., Birks, H.J.B., Ralska-Jasiewiczowa, M., Wright, H.E., 1996. Palaeoecological events during the last 15,000 years. Wiley, Chichester.

Berglund, B.E., Larsson, L., Lewan, N., Skansjö, S., Riddersporre, M., 1991. The cultural landscape during 6000 years in southern Sweden – the Ystad Project. Ecological Bulletins 41, Mungsgaard, Copenhagen.

Bradshaw, R.H.W., 1981a. Modern pollen representation factors for woods in southeast England, U.K. Journal of Ecology 69, 45-70.

Broström, A., Nielsen, A.B., Gaillard, M.J., Hjelle, K., Mazier, F., Binney, H., Bunting, J., Fyfe, R., Meltsov, V., Poska, A., Räsänen, S., Soepboer, W., von Stedingk, H., Suutari, H., Sugita, S., 2008. Pollen productivity estimates of key European plant taxa for quantitative reconstruction of past vegetation: a review. Vegetation History and Archaeobotany 17, 461-468.

Broström, A., Sugita, S., Gaillard, M-J., 2004. Pollen productivity estimates for reconstruction of past vegetation cover in the cultural landscape of Southern Sweden. The Holocene 14, 371-384.

Bunting, M.J., Hjelle, K.L., 2010. Effect of vegetation data collection strategies on estimates of relevant source area of pollen (RSAP) and relative pollen productivity estimates (relative PPE) for non-arboreal taxa. Vegetation History and Archaeobotany 19, 365–374.

Bunting, M.J., 2003. Pollen-vegetation relationships in non-arboreal moorland taxa. Review of Palaeobotany and Palynology 125, 285-298.

Bunting, M.J., Armitage, R., Binney, H.A., Waller, M., 2005. Estimates of Relative Pollen Productivity and Relevant Source Area of Pollen for major tree taxa in two Norfolk (UK) woodlands. The Holocene 15, 459-465.

Bunting, M.J., Gaillard, M.J., Sugita, S., Middleton, R., Broström, A., 2004. Vegetation structure and pollen source area. The Holocene 14, 651-660.

Bunting, M.J., Farrell, M., Broström, A., Hjelle, K.L., Mazier, F., Middleton, R., Nielsen, A.B., Rushton, E., Shaw, H., Twiddle, C.L., 2013. Palynological perspectives on vegetation survey: a critical step for model-based reconstruction of Quaternary land cover. Quaternary Science Reviews 82, 41-55.

Calcote, R., 1995. Pollen source area and pollen productivity: evidence from forest hollows. Journal of Ecology 83, 591–602.

Carew, T., Meddens, F., Batchelor, R., Branch, N., Elias, S., Goodburn, D., Vaughan-Williams, A., Webster, L., Yeoman, L., 2009. Human–environment interactions atthe wetland edge in East London: trackways, platforms and Bronze Age responses to environmental change. Transactions of the London and Middlesex Archaeological Society 60, 1–34.

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). Vegetation History and Archaeobotany 15, 151-168.

Davis, O.K., 1984. Pollen frequencies reflect vegetation patterns in a Great Basin (USA) mountain range. Review of Palaeobotany and Palynology 40, 295-315.

Ellenberg, H., 1988. Vegetation Ecology of Central Europe, 4th edition. Cambridge University Press, Cambridge.

Favre, P., Jacomet, S., 1998. Branch wood from the lake shore settlements of Horgen Scheller, Switzerland. Evidence for economic specialization in the late Neolithic period. Vegetation History and Archaeobotany 7, 167-178.

Fontana, S.L., 2005. Coastal dune vegetation and pollen representation in south Buenos Aires Province, Argentina. Journal of Biogeography 32, 719-735.

Gaillard, M-J., Sugita, S., Bunting, M.J., Middleton, R., Broström, A., Caseldine, C., Giesecke, T., Hellman, S.E.V., Hicks, S., Hjelle, K., Langdon, C., Nielsen, A-B., Poska, A., von Stedingk, H., Veski, S., PolLandCal members, 2008. The use of modelling and simulation approach in reconstructing past landscapes from fossil pollen data: a review and results from the POLLANDCAL network. Vegetation History and Archaeobotany 17, 419-443.

Gregory, P.H., 1973. The Microbiology of the Atmosphere. Leonard Hill, Aylesbury.

Hellman, S., Bunting, M.J., Gaillard, M-J., 2009a. Relevant Source Area of Pollen in patchy cultural landscapes and signals of anthropogenic landscape disturbance in the pollen record: A simulation approach. Review of Palaeobotany and Palynology 153, 245-258.

Hellman, S., Gaillard, M.-J., Bunting, M.J. and Mazier, F., 2009b. Estimating the Relevant Source Area of Pollen in the past cultural landscapes of southern Sweden – a forward modelling approach. Review of Palaeobotany and Palynology 153, 245-258.

Hicks, S., Ammann, B., Latalowa, M., Pardoe, H., Tinsley, H., 1996. European pollen monitoring programme: project description and guidelines. Technical Report. University of Oulu, Oulu.

Hicks, S., Hyvärinen, H., 1999. Pollen influx values measured in different sedimentary environments and their palaeoecological implications. Grana 38, 228–242.

Hill, M.O., Šmilauer, P., 2005. TWINSPAN for Windows version 2.3. Centre for Ecology & Hydrology and University of South Bohemia, Huntingdon and České Budějovice.

Hjelle, K.L., 1997. Relationships between pollen and plants in human-influenced vegetation types using presence-absence data in western Norway. Review of Palaeobotany and Palynology 99, 1-16.

Hjelle, K.L., 1998. Herb pollen representation in surface moss samples from mown meadows and pastures in western Norway. Vegetation History Archaeobotany 7, 79–96.

Huusko, A., Hicks, S., 2009. Conifer pollen abundance provides a proxy for summer temperature: evidence from the latitudinal forest limit in Finland. Journal of Quaternary Science 4, 522–528.

Jackson, S.T., 1990. Pollen source area and representation in small lakes of the north-eastern United States. Review of Palaeobotany and Palynology 63, 53-76.

Jackson, S.T., Kearsley, J.B., 1998. Representation of local forest composition in moss-polster pollen assemblages. Journal of Ecology 86, 474-490.

Jackson, S.T., Lyford, M.E., 1999. Pollen dispersal models in Quaternary plant ecology: assumptions, parameters and prescriptions. The Botanical Review 65, 39-75.

Li, Y.C., Xu, Q.H., Zhao, Y.K., Yang, X.L., Xiao, J.L., Chen, H., Lu, X.M., 2005. Pollen indication to source plants in the eastern desert of China. Chinese Science Bulletin 50, 1632-1641.

Maher L.J., 1972. Nomograms for computing 0.95 confidence limits for pollen data. Review of Palaeobotany and Palynology 13, 85-93.

Maher L.J., 1981. Statistics for microfossil concentration measurements employing samples spiked with marker grains. Review of Palaeobotany and Palynology 32, 153-191.

Malmros, C., 1986. A Neolithic road built of wood at Tibirke, Zealand, Denmark. Contributionto the history of coppice management in the Sub-Boreal period. Striae 24, 153-156.

Mazier, F., Gaillard, M-J., Kunes, P., Sugita, S., Trondman, A-K., Broström, A., 2012. Testing the effect of site selection and parameter setting on REVEALS-model estimates of plant abundance using the Czech Quaternary Palynological Database. Review of Palaeobotany and Palynology 187, 38-49.

Mazier, F., Broström, A., Gaillard, M-J., Sugita, S., Vittoz, P., Buttler, A., 2008. Pollen productivity estimates and relevant source area of pollen for selected plant taxa in a pasture woodland landscape of the Jura Mountains (Switzerland). Vegetation History and Archaeobotany 17, 479-495.

Meddens, F.M., 1996. Sites from the Thames Estuary wetlands, England, and their Bronze Age use. Antiquity 70, 325–334.

Moore, P.D.,Webb, J.A., Collinson, M.E., 1991. Pollen Analysis, 2nd edition. Blackwell, Oxford.

Parsons, R.W., Prentice, I.C., 1981. Statistical approaches to R-values and the pollen–vegetation relationship. Review of Palaeobotany and Palynology 32, 127–152.

Prentice, I.C., Parsons, R.W., 1983. Maximum likelihood linear calibration of pollen spectra in terms of forest composition. Biometrics 39, 1051–1057.

Pedersen, L., Fischer, A., Aaby, B., 1997. The Danish Storebælt since the Ice Age. A/S Storebæltsforbindelsen, Copenhagen.

Peterken, G., 1993. Woodland Conservation and Management, 2nd edition. Chapman and Hall, London.

Prentice, I.C., 1985. Pollen representation, source area, and basin size: towards a unified theory of pollen analysis. Quaternary Research 23, 76–86.

Rackham, O., 1979. Neolithic woodland management in the Somerset Levels: Sweet Track 1. Somerset Levels Papers 3, 65-72.

Rackham, O., 2003. Ancient Woodland, 2nd edition. Castlepoint Press, Colvend.

Rackham, O., 1990. Hayley Wood: its history and ecology. Cambridge Wildlife Trust Ltd, Cambridge.

Rasmussen, P., 1990. Pollarding of trees in the Neolithic: often presumed — difficult to prove. In: Robinson, D.E. (Ed.), Experimentation and Reconstruction in Environmental Archaeology. Oxbow, Oxford, pp. 77–99.

Rasmussen, P., 1993. Analysis of sheep/goat faeces from Egolzwil 3, Switzerland: evidence for branch and twig foddering of livestock in the Neolithic. Journal of Archaeological Science 20, 479–502.

Räsänen, S., Hicks, S., Odgaard, B.V., 2004. Pollen deposition in mosses and in a modified 'Tauber trap' from Hailuoto, Finland: what exactly do the mosses record? Review of Palaeobotany and Palynology 129, 103-116.

Schofield, J.E., Edwards, K.J., McMullen, J.A., 2007. Modern pollen-vegetation relationships in subarctic southern Greenland and the interpretation of fossil pollen data from the Norse landnám. Journal of Biogeography 34, 473-488.

Stace, C., 1997. New Flora of the British Isles, 2nd edition. Cambridge University Press, Cambridge.

Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. Pollen et Spores 13, 615–621.

Sugita, S., 1993. A model of pollen source area for an entire lake surface. Quaternary Research 39, 239-244.

Sugita, S., 1994. Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. Journal of Ecology 82, 881–897.

Sugita, S., Gaillard, M.-J., Broström, A., 1999. Landscape openness and pollen records: a simulation approach. The Holocene 4, 409-421.

Sugita, S., Hicks, S., Sormunen, H., 2010. Absolute pollen productivity and pollen-vegetation relationships in northern Finland. Journal of Quaternary Science 25, 724-736.

Sutton, O.G., 1953. *Micrometeorology*. McGraw-Hill, New York.

Trondman, A-K., Gaillard, M-J., Mazier, F., Sugita, S., Fyfe, R., Nielsen, A.B., Twiddle, C., Barratt, P., Birks, H.J.B., Bjune, A.E., Bjorkman, L., Broström, A., Caseldine, C., David, R., Dodson, J., Doerfler, W., Fischer, E., van Geel, B., Giesecke, T., Hultberg, T., Kalnina, L., Kangur, M., van der Knaap, P., Koff, T., Kunes, P., Lageras, P., Latalowa, M., Lechterbeck, J., Leroyer, C., Leydet, M., Lindbladh, M., Marquer, L., Mitchell, F.J.G., Odgaard, B.V., Peglar, S.M., Persson, T., Poska, A., Roesch, M., Seppa, H., Veski, S., Wick, L., 2015. Pollen-based quantitative reconstructions of Holocene regional vegetation cover (plant-functional types and land-cover types) in Europe suitable for climate modelling. Global Change Biology 21, 676-697.

Waller, M., Grant, M.J., Bunting, M.J., 2012. Modern pollen studies from coppiced woodlands and their implications for the detection of woodland management in Holocene pollen records. Review of Palaeobotany and Palynology 187, 11-28.

Figure list

Figure 1: location map of field sites

Figure 2: diagram showing the layout of the modified pin-frame used for recording the vegetation in the field (see text for details).

Figure 3: a) % ground cover against year of cutting b) vegetation diversity (number of pe) in 10m radius area against year of cutting c) mean %NAPS in the pollen traps against year of cutting d) mean NAP influx per pollen trap against year of cutting e) number of pe taxa recorded in the pollen traps against year of cutting f) %NAPS against % vegetation cover. Solid circles show locations in Bradfield Woods, grey shaded circles those in Chalkney Wood, and open circles those in Hayley Wood.

Figure 4: WinTWINS cluster diagrams for a) vegetation data (numbers beneath groups show the mean ground cover/number of palynological equivalent taxa in the plant lists for each group) and b) non-arboreal pollen data (numbers beneath groups show the mean %NAPS/ number of palynological equivalent NAPS taxa in the pollen assemblage for each group) - see text for details. Each sample is identified by a letter for the woodland and two digits for the year of cutting: B98 is the sample from the compartment in Bradfield Woods which was cut in 1998. In addition, samples from Bradfield Woods are bolded and those from Hayley Wood are italicised. Underlining within groups shows the next level of division into subgroups, where that was possible.

Figure 5: trends in indices with increasing survey area for ground flora taxa. Plots give examples of the three clusters described in the text.

Figure 6: Filipendula pollen influx against dwpa to 10m – the solid line oval outlines samples with low dwpa and high pollen influx, and the dashed line oval outlines samples with lower influx. These two

groups are considered to reflect two different dominant modes of pollen transport at different pollen traps (see text for details)

Figure 7: Pearson product-moment Correlation coefficients between pollen influx and cumulated dwpa at increasing distances around the pollen traps for ground flora taxa. Asteraceae (Cardueae) correlations are significant with $0.01 < p < 0.05$, and all others at $p < 0.01$

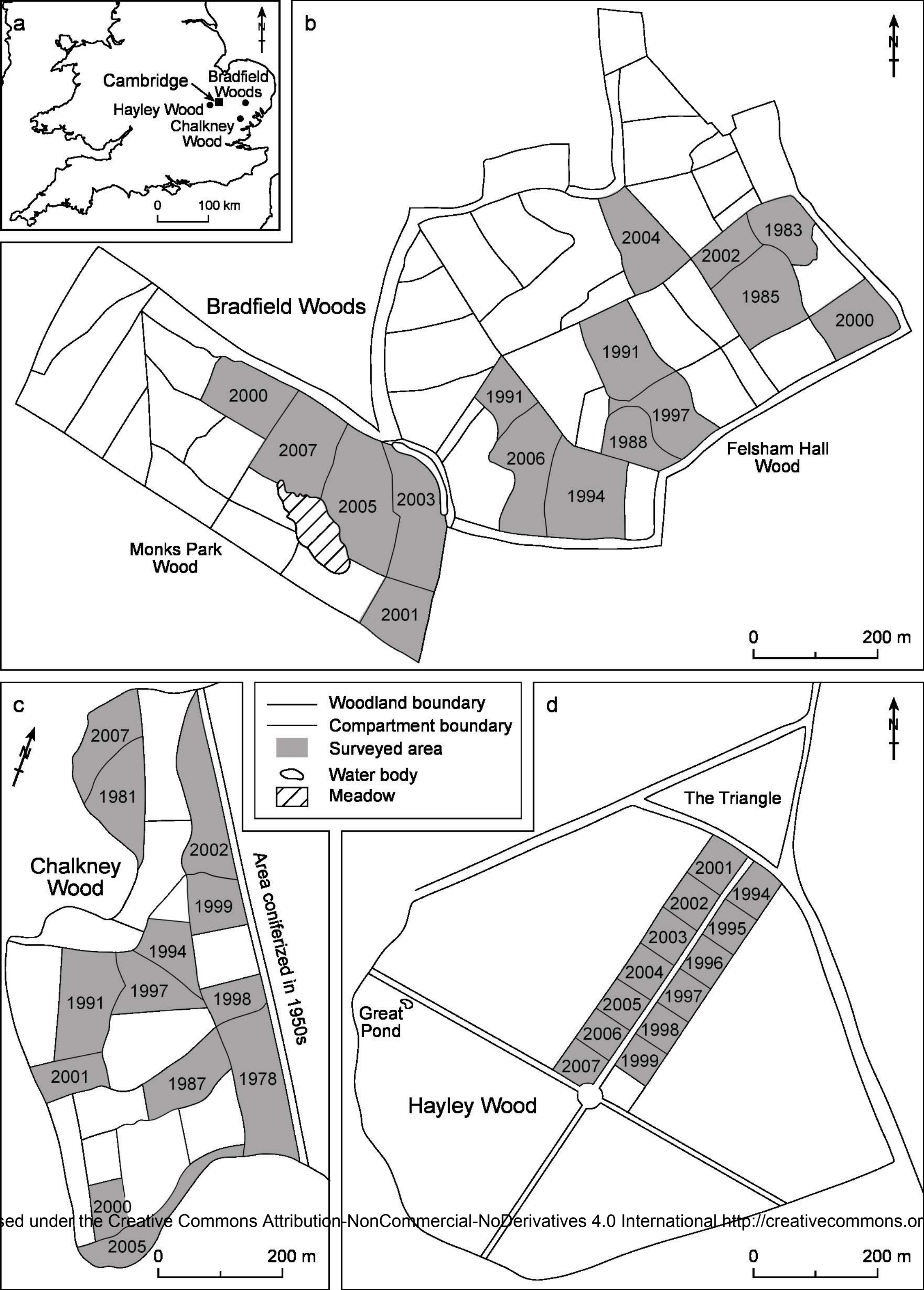
Table list

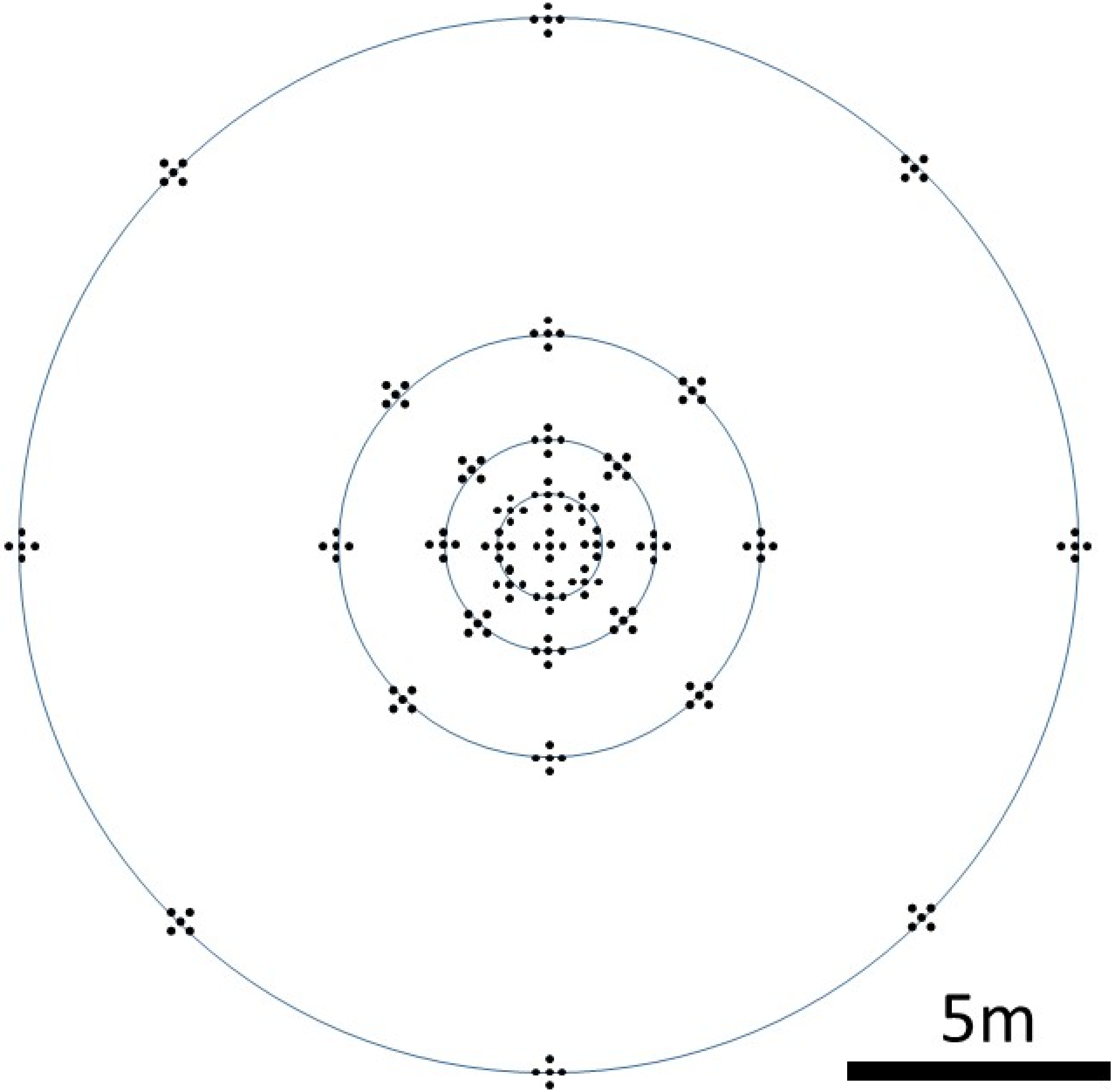
Table 1: plant species recorded and palynological equivalent taxa (after Bennett 1994)

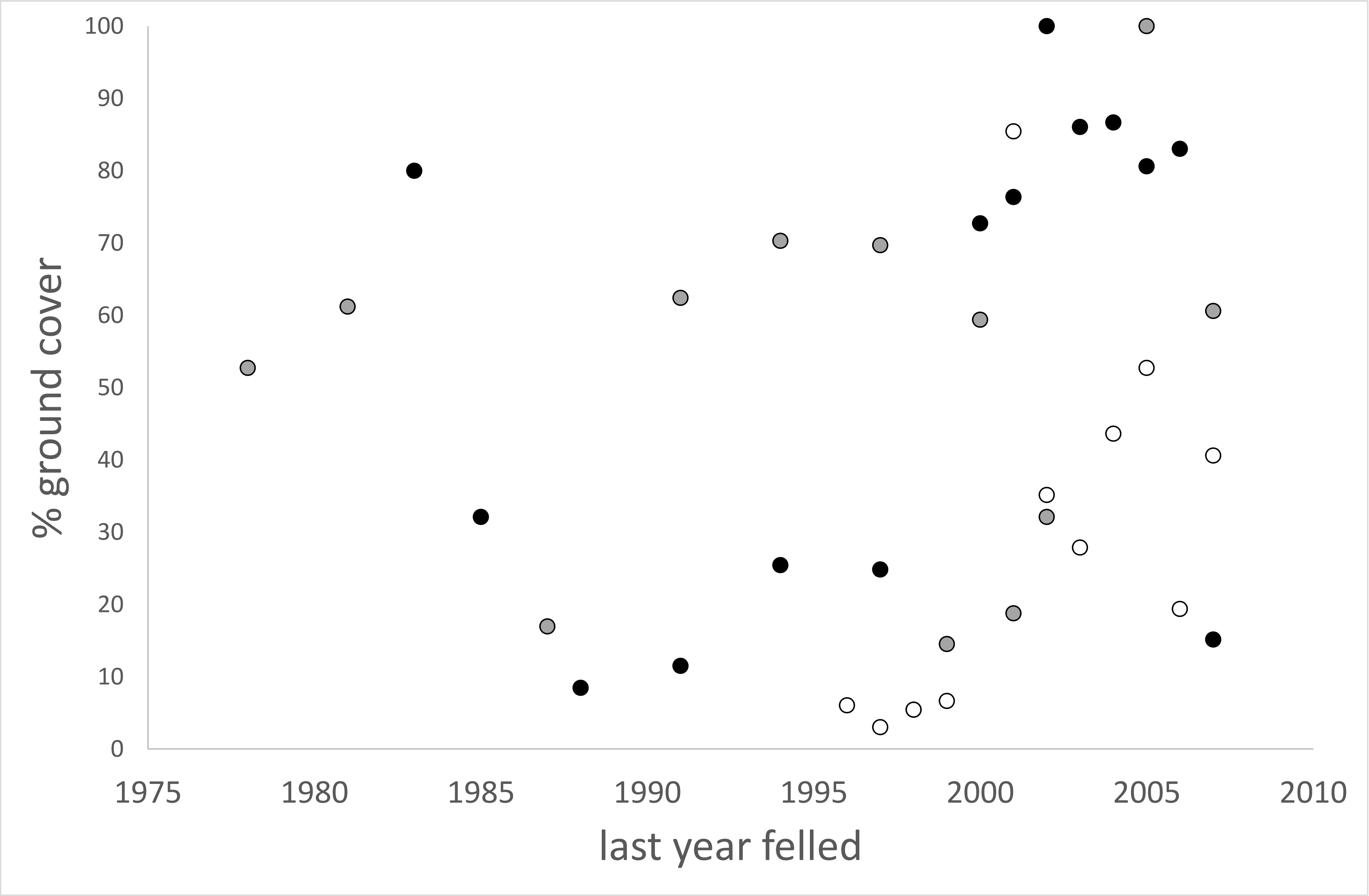
Table 2: fall speed estimates for the ten taxa selected for linear regression analysis (see text for details)

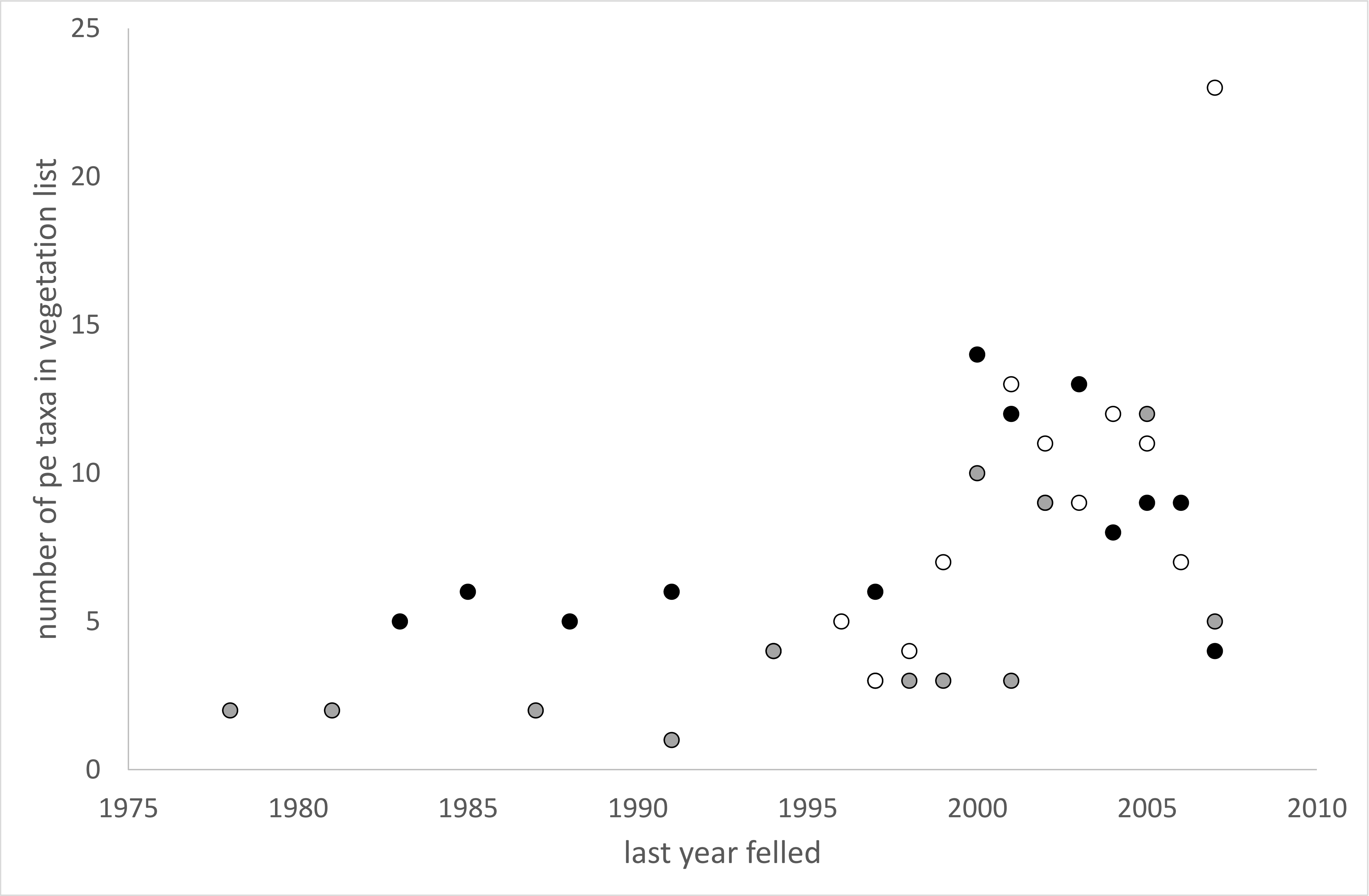
Table 3: indices of association between pollen trap assemblages and vegetation surveyed within 10m of the centre of the trap array for ground flora species

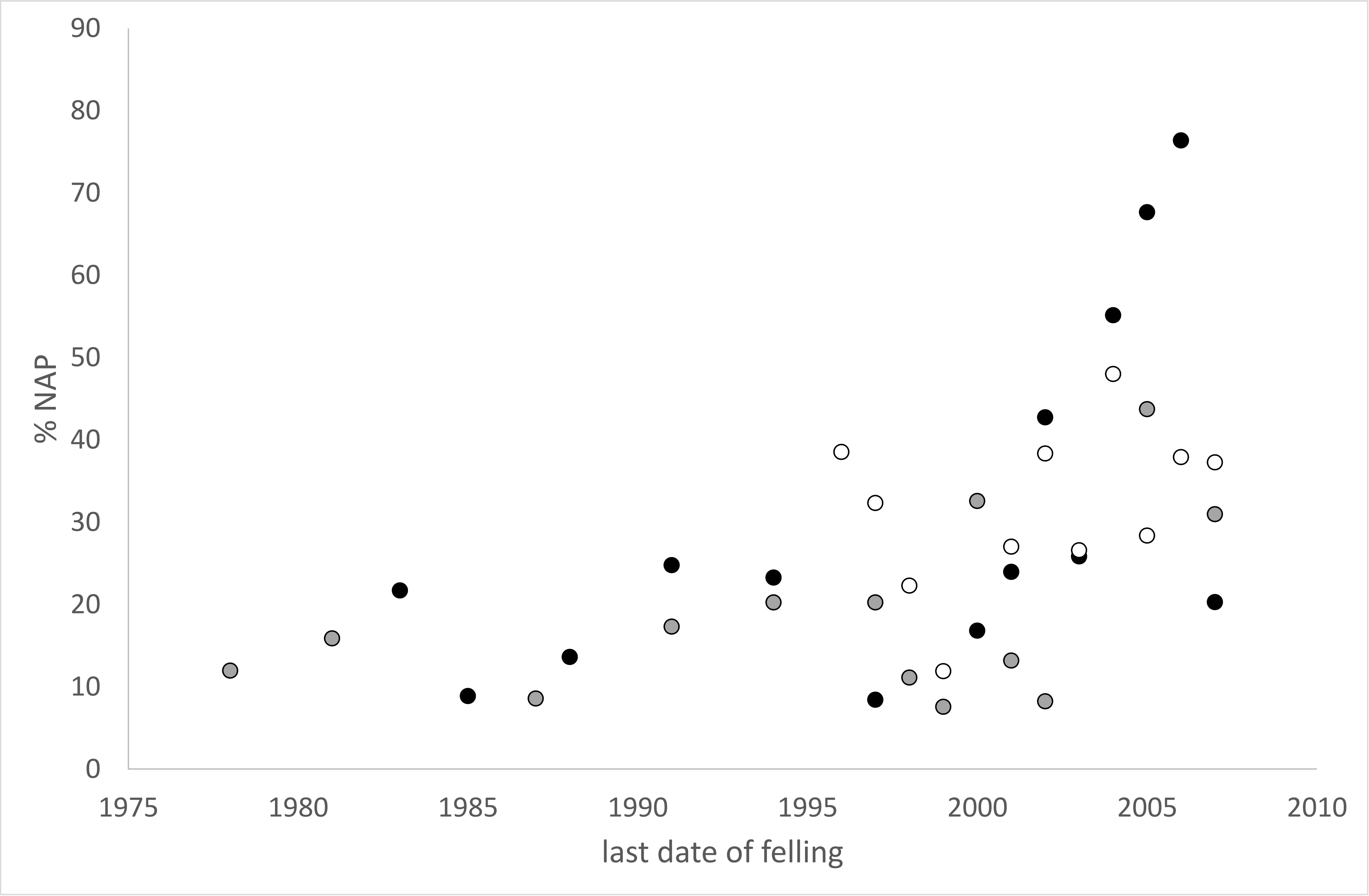
Table 4: summary of estimated pollen productivity values relative to Poaceae for the main six ground flora taxa (see text for details)

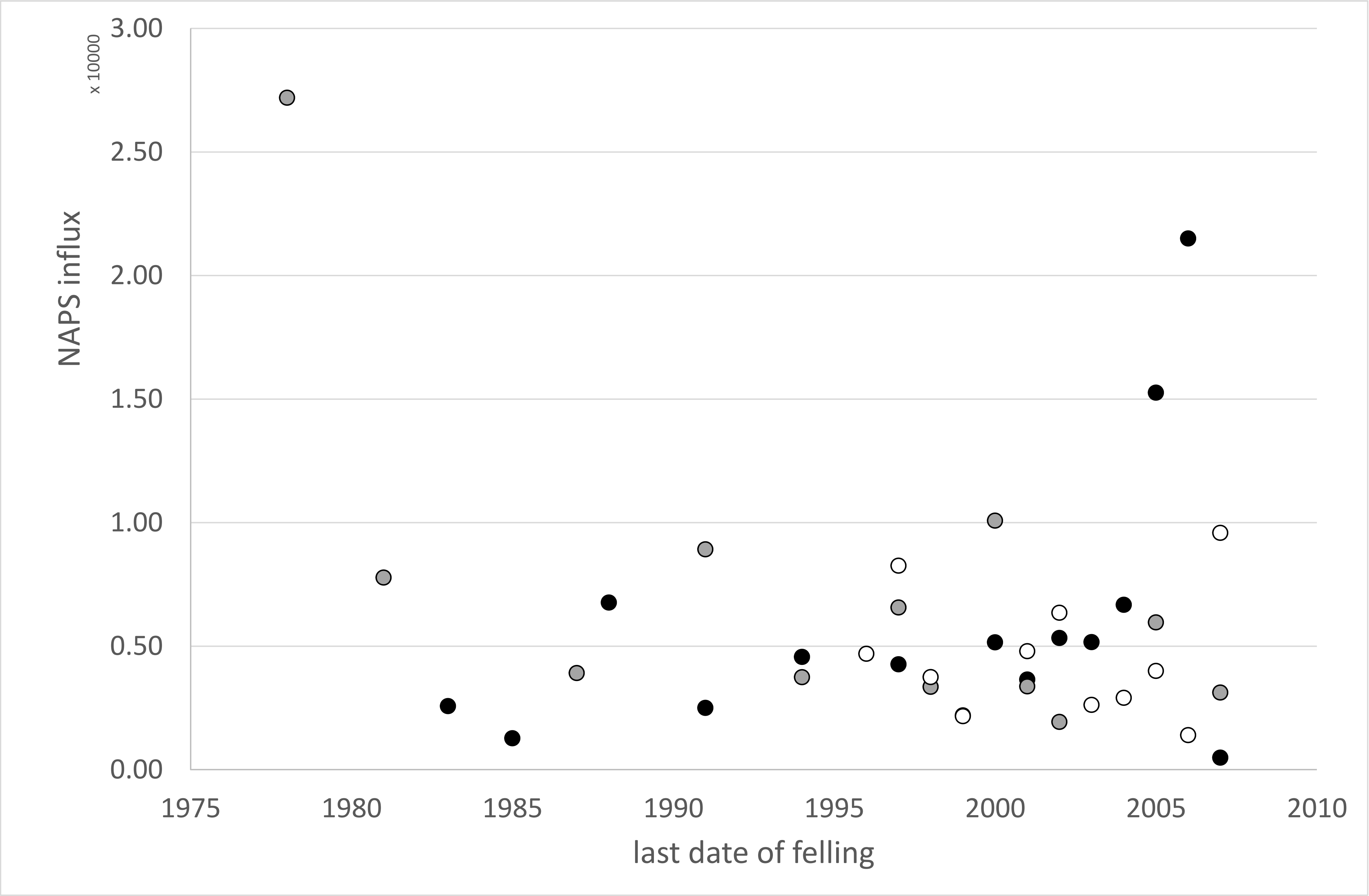

a
Cambridge
Bradfield Woods
Hayley Wood
Chalkney Wood
N
0
100 km
b
N
Bradfield Woods
2004
1983
2002
1985
2000
1991
2000
1991
1997
2007
1988
2006
Felsham Hall Wood
2005
2003
1994
Monks Park Wood
2001
0
200 m
c
2007
1981
2002
Chalkney Wood
1999
Area coniferized in 1950s
1994
1991
1997
1998
2001
1987
1978
2000
2005
0
200 m
Woodland boundary
Compartment boundary
Surveyed area
Water body
Meadow
d
N
The Triangle
2001
1994
2002
1995
2003
1996
2004
1997
Great Pond
2005
1998
2006
1999
2007
Hayley Wood
0
200 m

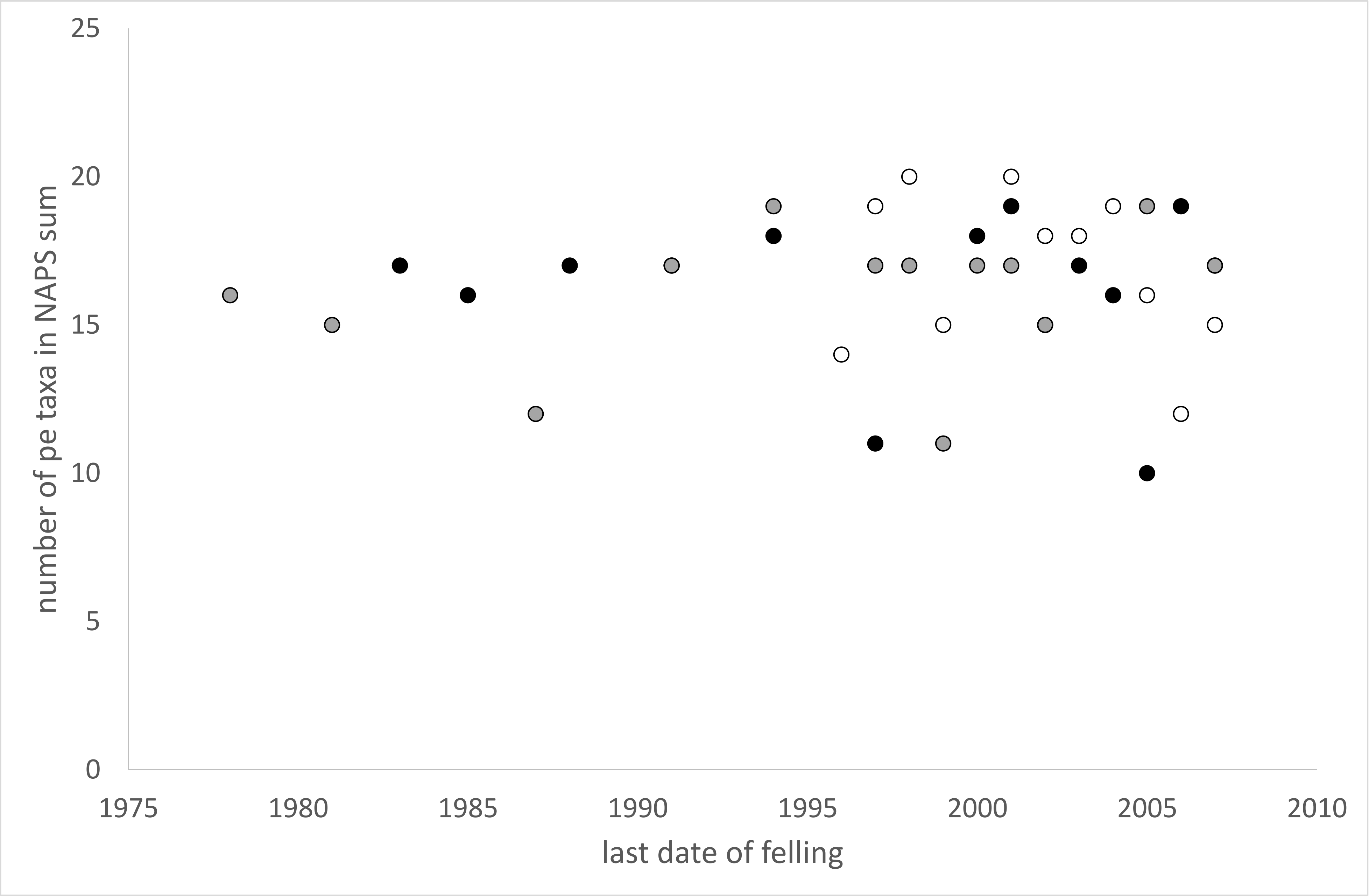

5m

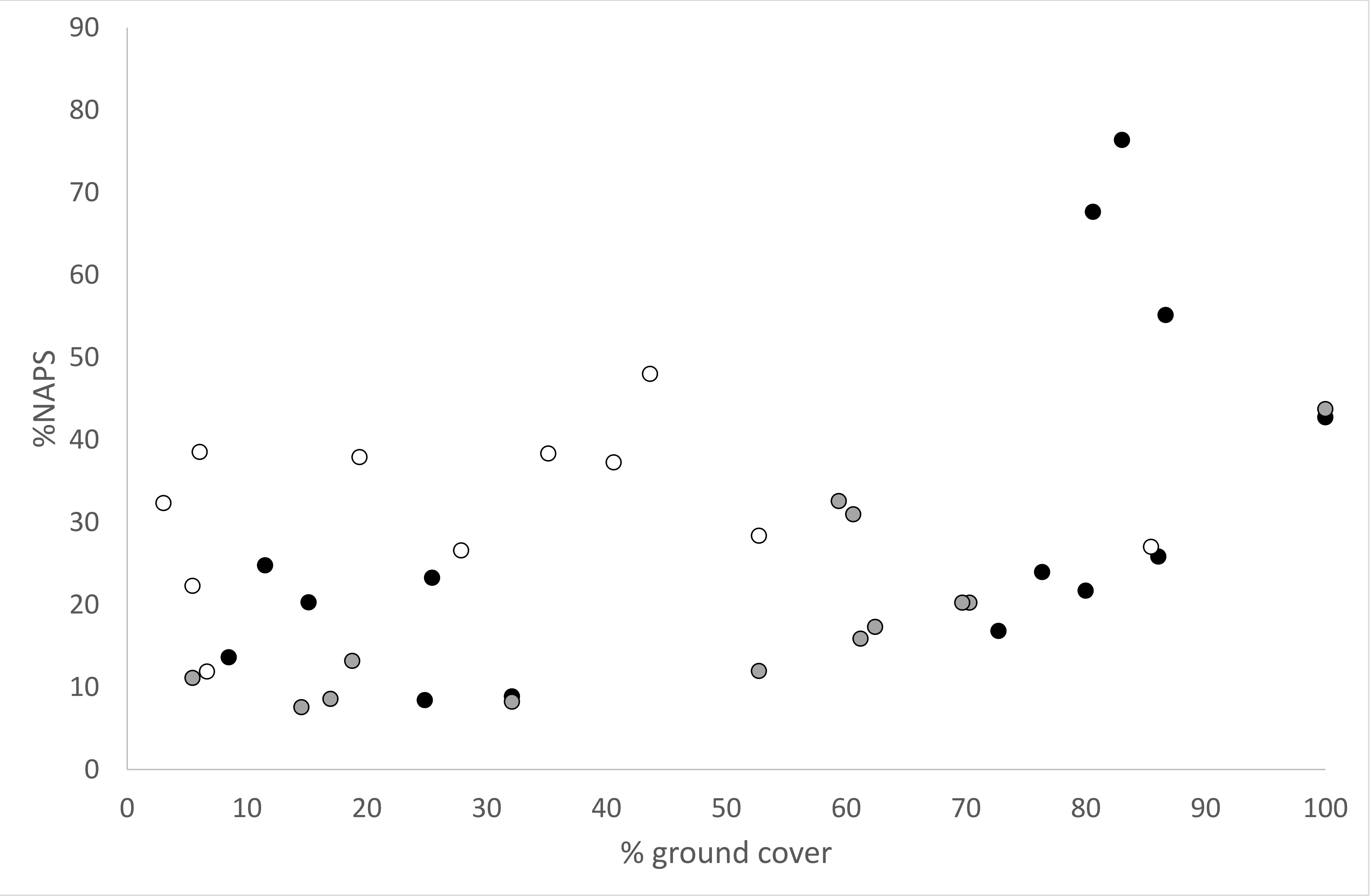

% ground cover
0
10
20
30
40
50
60
70
80
90
100
1975
1980
1985
1990
1995
2000
2005
2010
last year felled

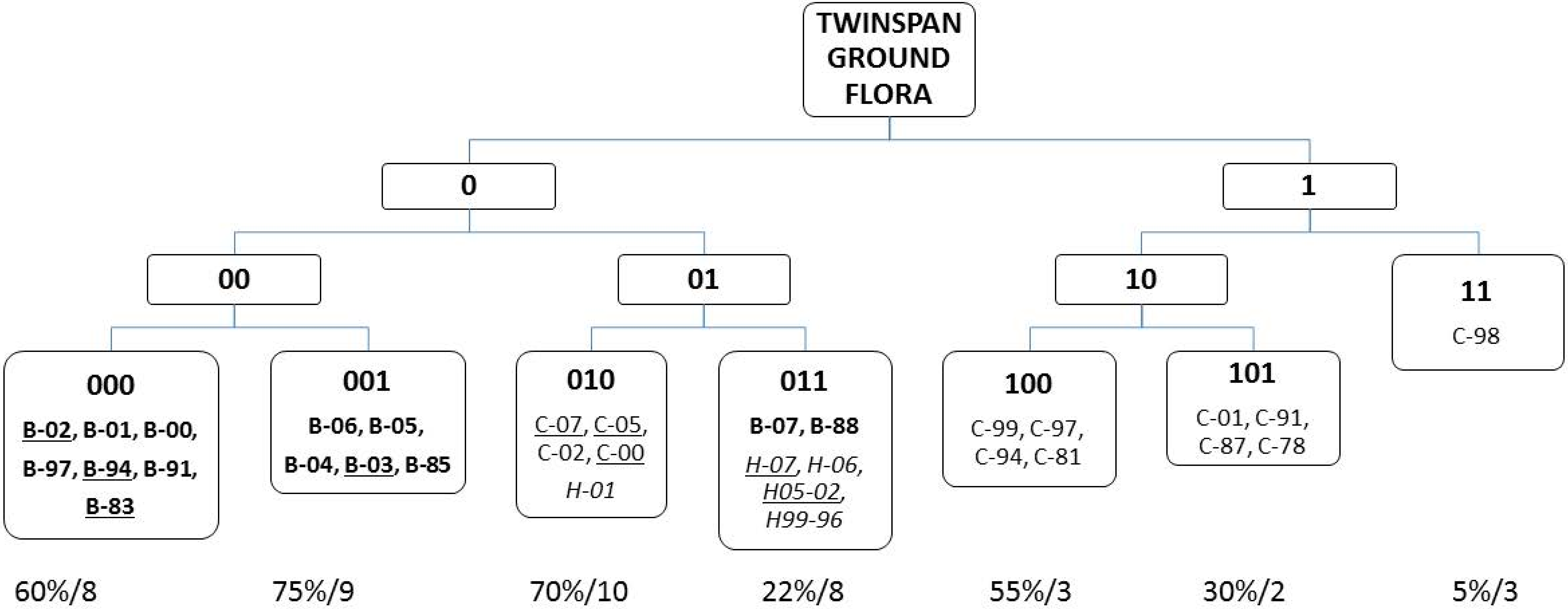

25
20
15
10
5
0
number of pe taxa in vegetation list
1975
1980
1985
1990
1995
2000
2005
2010
last year felled

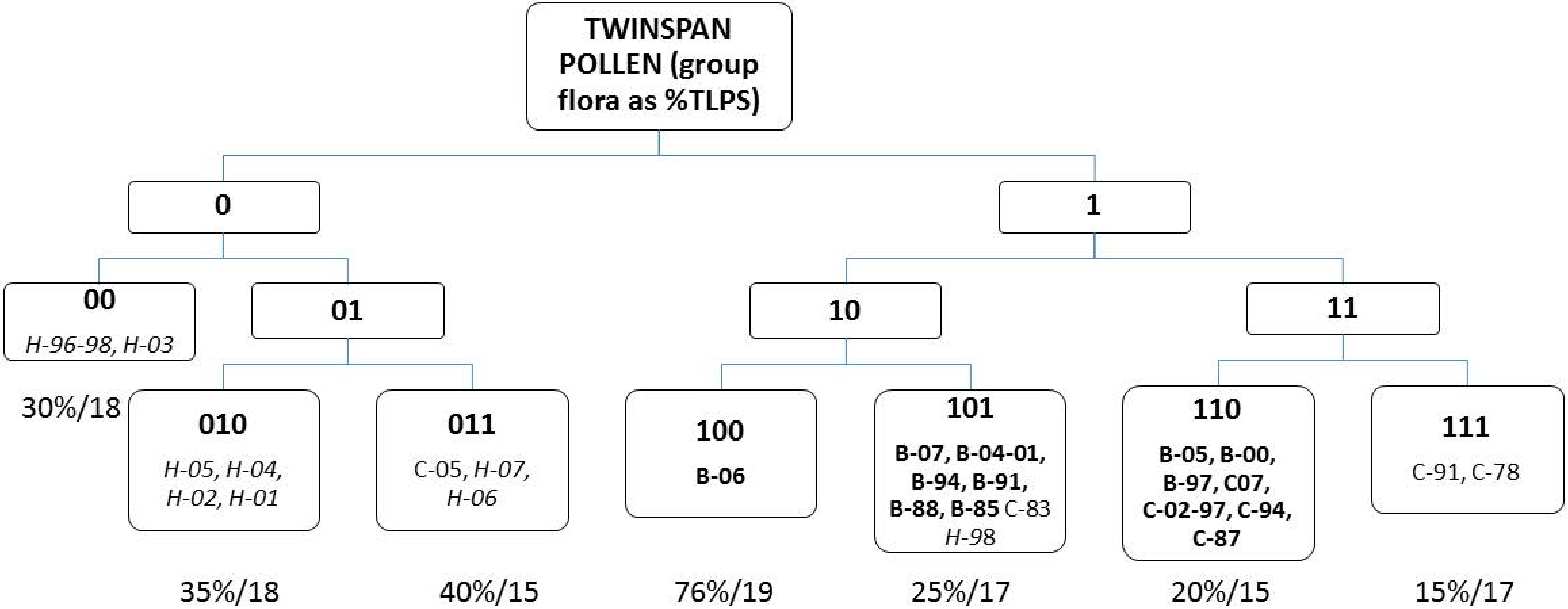

90
80
70
60
50
40
30
20
10
0
% NAP
1975
1980
1985
1990
1995
2000
2005
2010
last date of felling


3.00
2.50
2.00
1.50
1.00
0.50
0.00
x 10000
NAPS influx
1975
1980
1985
1990
1995
2000
2005
2010
last date of felling


25
20
15
10
5
0
number of pe taxa in NAPS sum
1975
1980
1985
1990
1995
2000
2005
2010
last date of felling


%NAPS
% ground cover
0
10
20
30
40
50
60
70
80
90
100


TWINSPAN GROUND FLORA
0
1
00
01
10
11
C-98
000
B-02, B-01, B-00, B-97, B-94, B-91, B-83
001
B-06, B-05, B-04, B-03, B-85
010
C-07, C-05, C-02, C-00
H-01
011
B-07, B-88
H-07, H-06, H05-02, H99-96
100
C-99, C-97, C-94, C-81
101
C-01, C-91, C-87, C-78
60%/8
75%/9
70%/10
22%/8
55%/3
30%/2
5%/3



TWINSPAN POLLEN (group flora as %TLPS)

0

00

H-96-98, H-03

30%/18

01

010

H-05, H-04, H-02, H-01

35%/18

011

C-05, *H-07, H-06*

40%/15

1

10

100

B-06

76%/19

101

B-07, B-04-01, B-94, B-91, B-88, B-85 C-83 *H-98*

25%/17

11

110

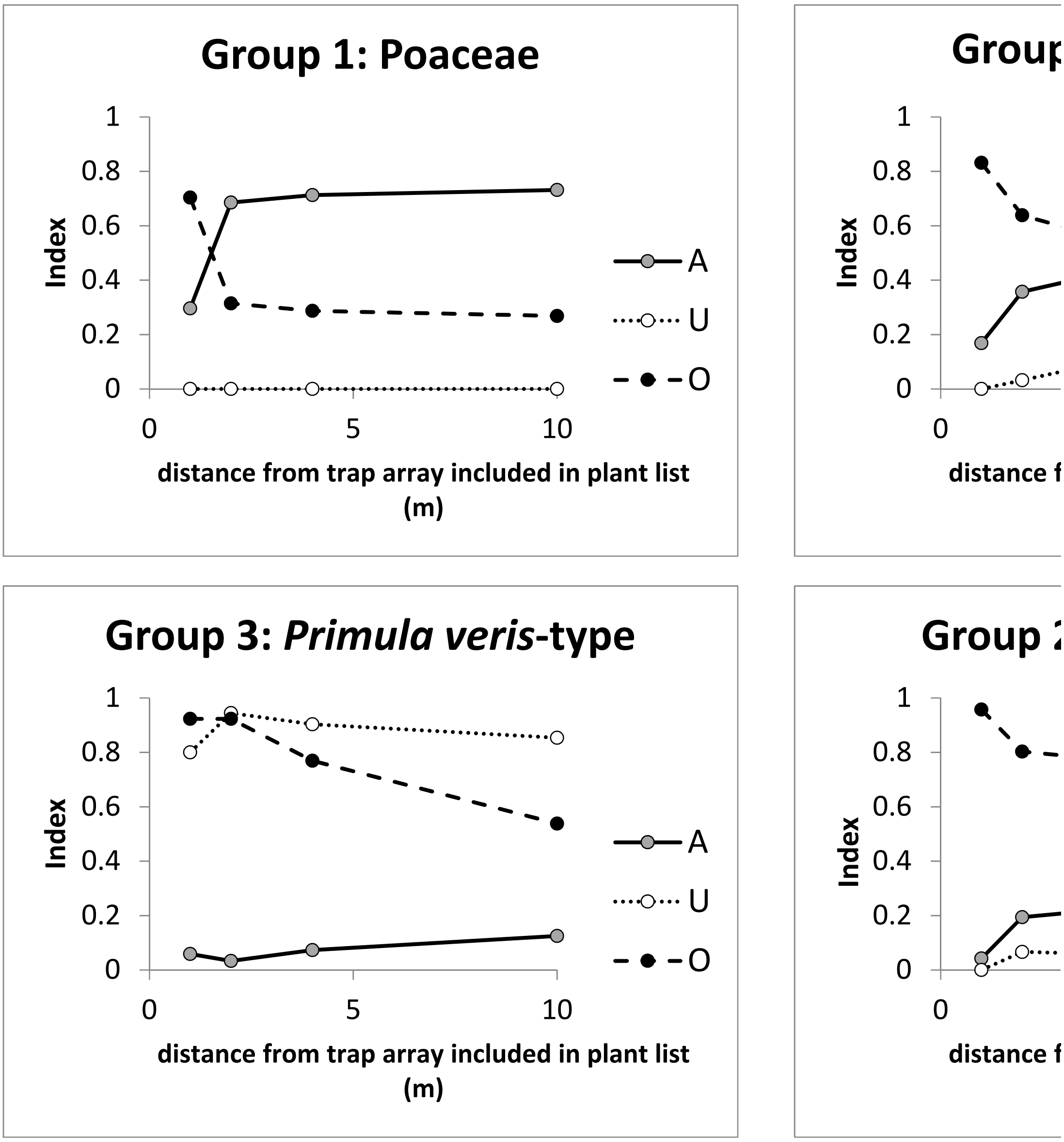
B-05, B-00, B-97, C07, C-02-97, C-94, C-87

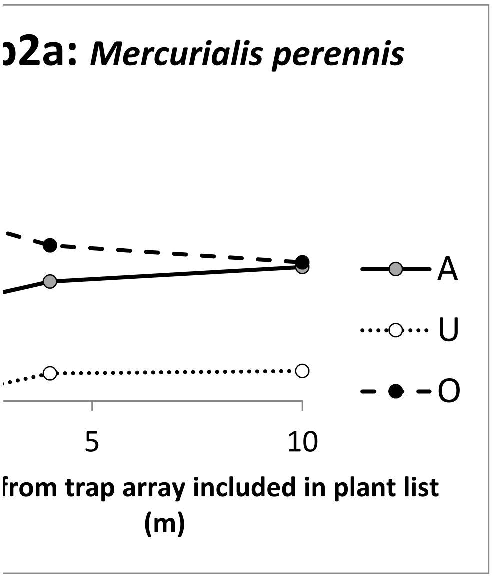
20%/15

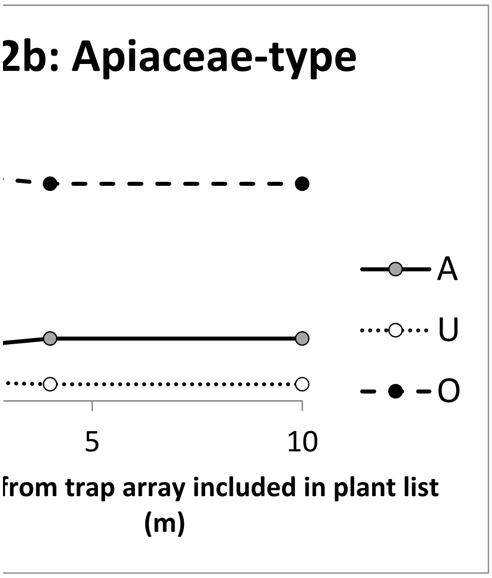
111

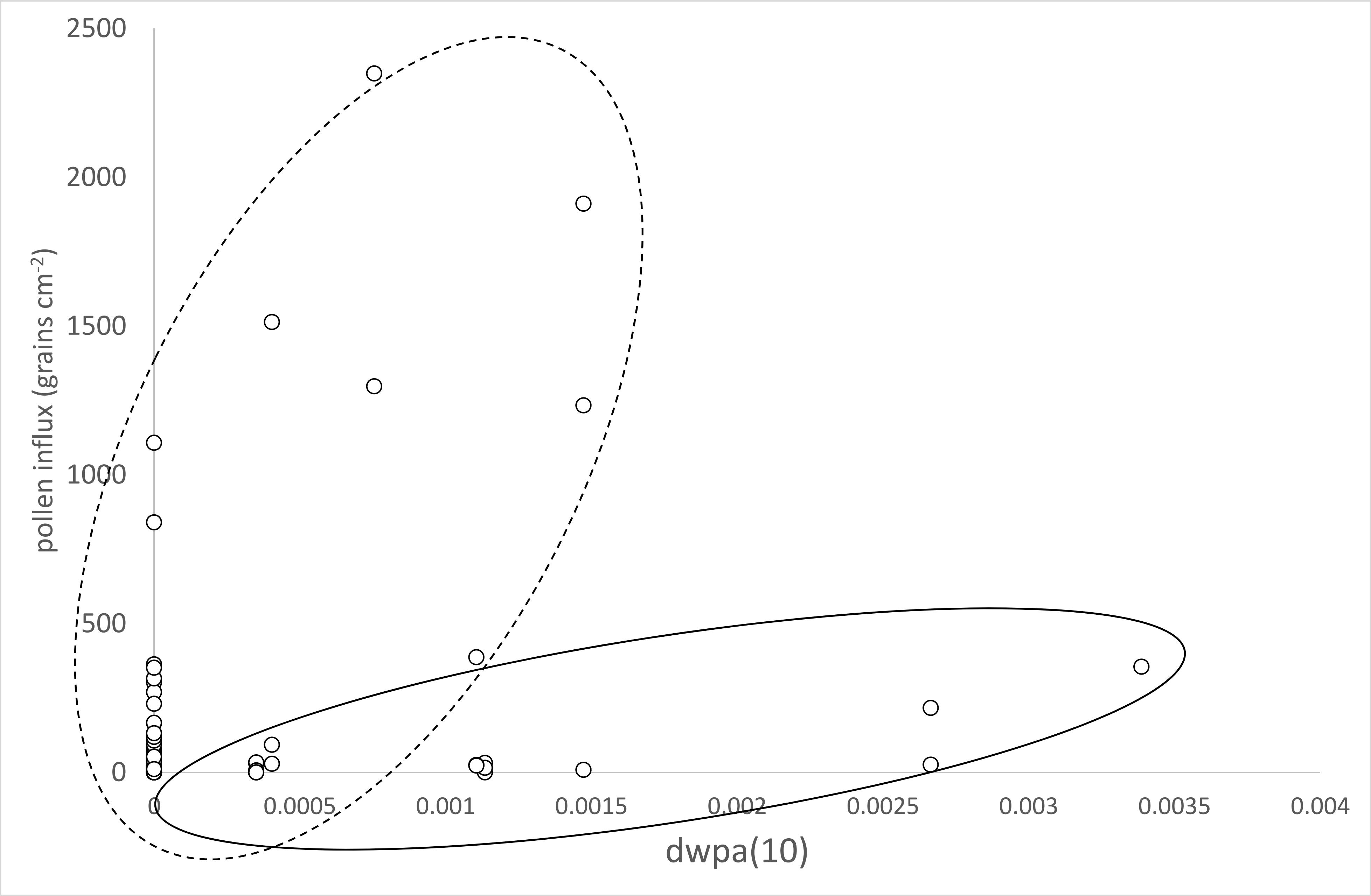
C-91, C-78

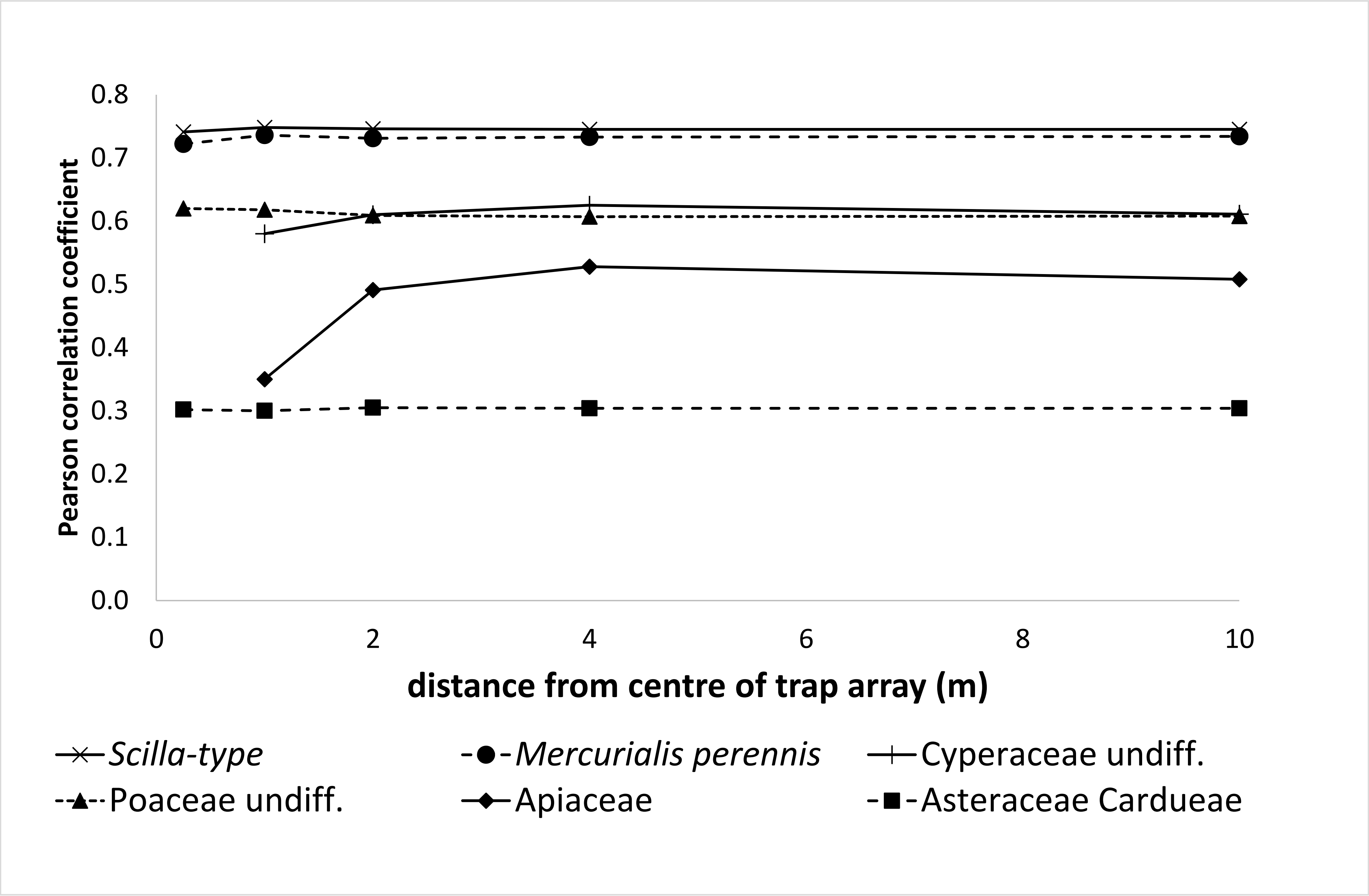
15%/17


Group 1: Poaceae
Index
0
0.2
0.4
0.6
0.8
1
0
5
10
distance from trap array included in plant list (m)
A
U
O
Group
Index
0
0.2
0.4
0.6
0.8
1
0
distance f
Group 3: *Primula veris*-type
Index
0
0.2
0.4
0.6
0.8
1
0
5
10
distance from trap array included in plant list (m)
A
U
O
Group
Index
0
0.2
0.4
0.6
0.8
1
0
distance f


2a: *Mercurialis perennis*
A
U
O
5
10
from trap array included in plant list
(m)


2b: Apiaceae-type
A
U
O
5
10
from trap array included in plant list
(m)


2500
2000
1500
1000
500
0
pollen influx (grains cm-2)
0
0.0005
0.001
0.0015
0.002
0.0025
0.003
0.0035
0.004
dwpa(10)



Pearson correlation coefficient
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
2
4
6
8
10
distance from centre of trap array (m)
Scilla-type
Mercurialis perennis
Cyperaceae undiff.
Poaceae undiff.
Apiaceae
Asteraceae Cardueae

- Non-arboreal pollen and spore (NAPS) influx in coppiced woodlands is studied
- NAPS/plant presence Association Indices calculated for several survey distances
- Indices imply effective source area for ground flora is approx. 10m radius
- Estimates of Pollen Productivity are presented for five taxa
- NAPS record reflects ground flora of wider woodland not of local compartment

Table 1: plant species recorded and palynological equivalent taxa (after Bennett 1994)

	actual plant species recorded		
Palynological equivalent	**Bradfield Woods**	**Chalkney Woods**	**Hayley Wood**
Allium-type	*Allium ursinum*		
Apiaceae	*Conopodium majus*		*Angelica sylvestris*
Arum	*Arum maculatum*		*Arum maculatum*
Asteraceae (Cardueae)	*Arctium minus, Cirsium arvense, C. palustre, C. vulgare*	*Cirsium arvense, Sonchos* sp.	
Asteraceae (Lactuceae)	*Taraxacum oblogatum*		*Taraxacum oblongatum*
Brassicaceae		*Cardamine pratensis*	
Caryophyllaceae		*Cerastium fontanum, Silenedioica*	
Cyperaceae	*Carex pendula, C. strigosa, C. strigosa/sylvatica, C. sylvatica*	*Carex pendula, C. sylvatica*	*Carex flacca, C. pendula, C. riparia,*
Dactylorhiza-type			*Orchis fuchsii*
Dryopteris dilatata		*Dryopteris dilatata*	
Epilobium-type		*Epilobium* sp	*Epilobium* sp
Filipendula	*Filipendula ulmaria*		*Filipendula ulmaria*

Geum	*Geum* undif.		*Geum urbanum*
Hypericum perforatum-type	*Hypericum hirsutum, H. humifusum*		*Hypericum hirsutum, H. humifusum, H. tetrapterum*
Lonicera periclymenum	*Lonicera periclymenum*	*Lonicera periclymenum*	*Lonicera periclymenum*
Lysimachia vulgaris type		*Lysimachia nemorum*	
Mercurialisperennis	*Mercurialis perennis*	*Mercurialis perennis*	*Mercurialis perennis*
Paris quadrifolia-type	*Paris quadrifolia*		*Paris quadrifolia*
Plantago major/media			*Plantago major*
Poaceae	*Agrostis stolonifera, Brachypodium sylvatica, Deschampsia caespitosa, Poa annua, P.* undif.	*Agrostis stolonifera, Poa annua, P. trivialis, P.* undif.	*Agrostis stolonifera, Deschampsia caespitosa, Holcus mollis, Poa trivialis, P.* undif.
Potentilla-type	*Potentilla sterilis*	*Potentilla sterilis*	*Potentilla sterilis*
Primula veris-type	*Primula elatior*		*Primula elatior*
Prunella vulgaris-type	*Prunella vulgaris*	*Prunella vulgaris*	*Glechoma hederacea*
Ranunculus acris-type	*Anemone nemorosa, Ranunculus ficaria*	*Anemone nemorosa, Ranunculus ficaria, R. repens*	*Anemone nemorosa, Ranunculus ficaria*
Rosaceae indet.			*Rosa* sp.
Rubus undiff.	*Rubus fruticosus* agg., *R. idaeus*	*Rubus caesius, R. fruticosus* agg., *R. idaeus*	*Rubus caesius, R. fruticosus* agg., *R. idaeus*
Rumex sanguineus type		*Rumexcrispus*	
Scilla-type		*Hyacinthoides non-scripta*	*Hyacinthoides non-scripta*
Scutellaria-type	*Ajuga reptans*	*Ajuga reptans*	*Ajuga reptans*

Sedum			*Sedum telephium*
Stachys-type	*Stachys sylvatica*		*Lamium sp.*
Urtica dioica	*Urtica dioica*	*Urtica dioica*	*Urtica dioica*
Veronica		*Veronica chamaedrys, V.*undif	
Viola undiff.	*Viola* undif.	*Viola* undif.	*Viola reichenbachiana*

Table 2: fall speeds of abundant pollen types

Taxon	Fallspeed (m/s)	source
Apiaceae	0.021	this paper
Asteraceae (Cardueae)	0.067	this paper
Cyperaceae	0.035	Sugita et al 1999
Filipendula	0.006	Broström et al. 2004
Lonicera periclymenum	0.158	this paper
Mercurialis perennis	0.024	this paper
Poaceae	0.035	Sugita et al 1999
Ranunculus acris-type	0.014	Broström et al. 2004
Rubus undiff.	0.019	this paper
Scilla-type	0.088	this paper

Table 3: indices of association between pollen trap assemblages and vegetation surveyed within 10m of the centre of the trap array for ground flora species

Taxon	Index of Association	Index of Under-representation	Index of Over-representation	
A>0.5: Associated				
Poaceae undiff.	0.73	0.00	0.27	
Ranunculus acris-type	0.65	0.24	0.18	
Cyperaceae	0.63	0.03	0.35	
Scilla-type	0.60	0.13	0.34	
A>0.25: weakly associated				
Mercurialis perennis	0.48	0.11	0.49	
Rubus undiff.	0.46	0.23	0.46	
Filipendula	0.31	0.22	0.66	over-represented?
Asteraceae (Cardueae)	0.26	0.17	0.73	over-represented?
Lonicera periclymenum	0.25	0.68	0.46	
Allium-type	0.25	0.00	0.75	
A<0.25, U>O: under-represented				
Prunella vulgaris-type	0.04	0.96	0.75	poor
Potentilla-type	0.08	0.88	0.79	poor
Primula veris-type	0.13	0.85	0.54	poor
Paris quadrifolia-type	0.20	0.78	0.33	
A<0.25, O>U: Over-represented				
Plantago major/media	0.04	0.67	0.95	

Lysimachia vulgaris type	0.03	0.67	0.96	
Rumex sanguineus type	0.08	0.33	0.91	
Dryopteris dilatata	0.04	0.33	0.96	
Caryophyllaceae	0.15	0.17	0.84	
Urtica dioica	0.08	0.13	0.92	
Apiaceae	0.22	0.06	0.77	
Asteraceae (Lactuceae)	0.05	0.00	0.95	
Brassicaceae	0.03	0.00	0.97	

Table 4: estimated pollen productivity values relative to Poaceae for the main six ground flora taxa (see text for details).

	$RPP_{Poaceae}$ regression method	Background pollen influx (grains cm^{-2}) rounded to nearest 10 grains	Broström et al. 2004 values	Mazier et al 2012 PPE.st2 dataset	Hjelle 1998
Apiaceae	1.61 ± 0.40	50		0.26	0.27
Asteraceae Cardueae	0.03 ± 0.01	30			0.06 (*Cirsium* type)
Cyperaceae	0.40 ± 0.07	50	1.0	0.87	0.29
Mercurialis perennis	0.24 ± 0.04	70			
Poaceae	1	1950	1	1.0	1
Scilla-type	0.34 ± 0.06	80			