Approaches to quantitative reconstruction of woody vegetation in managed woodlands from pollen records

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Abstract

There has been increasing interest in developing quantitative methods for reconstructing the dynamics of cultural landscapes over the last 15 years. This paper adds to this literature by using various approaches to reconstruct the vegetation of two woodlands subject to rotational coppicing (the periodic cutting of broadleaved trees and shrubs for wood products). Pollen deposition at ground level was determined at both sites using 'Tauber' traps placed near to the centre of 14 compartments of differing age in the coppice rotation. For the main woody taxa, Relative Pollen Productivity (RPP) estimates were derived using linear regression for pollen influx data and Extended R-value analysis for percentage data. The vegetation around three ponds was reconstructed by applying four methods (inverting the two RPP estimate approaches, the modern analogue technique and correction for pollen productivity using the linear regression estimated RPP values) to pollen data obtained from the uppermost sample of sediment from the ponds. To determine whether these methods gave better estimates of the vegetation composition than the original pollen proportions, the results were compared with the surveyed vegetation around each pond using the Bray-Curtis Index. Linear regression of pollen influx produced RPP values which are comparable with previous European studies, while for some taxa the Extended R-value analysis produced estimates which are orders of magnitude different both from values derived from the linear regression and previous work. No single approach performed equally well at reconstructing the vegetation around the ponds, and at two of the three locations the uncorrected pollen proportions were most similar to the surveyed vegetation. We conclude that applying quantitative reconstruction methods to individual small sites is, currently, not likely to be useful in complex cultural landscapes. In the context of coppiced woodland, deficiencies in our understanding of pollen taphonomy and the impact of the practice on pollen production first need to be rectified, and we identify strategies to address this situation.

Keywords: coppicing, modern pollen–vegetation relationships, palaeoecology, pollen dispersal and deposition models, woodland management

Highlights

- $\mathrm{RPP}_{Quercus}$ values for 8 tree types in coppiced woodland in England are presented
- Values are comparable with other European studies
- Four methods of reconstructing vegetation from pollen were tested on surface pond sediments
- No reconstruction approach performed well consistently across the three ponds used

1. Introduction

Many parts of the world are dominated by cultural landscapes: those where the present day vegetation cover is the product of both natural environmental factors (such as climate, geology and local topography) and human activity, both direct and indirect, over long time scales. Pollen analysis of sediment cores offers evidence of changes in vegetation over time, which can then be translated into reconstructions of land cover and the impact of processes such as human activity assessed. Most translation is still qualitative yet questions related to the dynamics of cultural landscapes, such as the extent of woodland clearance, have driven many recent developments in the interpretation of pollen data, such as the PolLandCal Network's activities (reviewed in Gaillard, et al. 2008). More recently, the LANDCLIM project has demonstrated the potential of using records from large sedimentary sites (>500-750ha) or combining large numbers of small sites to reconstruct the relative abundance of the main plant taxa present in regional landscapes, allowing changes in the extent and distribution of woodland, heathland, pasture and crop land (Marquer, et al. 2014; Trondman, et al. 2015) to be mapped across areas measured in hundreds of square kilometres. Reconstructing cultural landscape processes at smaller, more 'human' scales in quantitative terms remains challenging, although various strategies have been proposed and are being explored (Sugita, 2007a; Bunting and Middleton, 2009; Sugita, et al. 2010a, Tipping, et al. 2009).

All these reconstruction methods depend, implicitly or explicitly, on being able to quantify the amount of pollen contributed to a sedimentary pollen assemblage by different plant taxa. This varies depending on a range of factors concerning both the producing plant (such as reproductive strategy, plant height, vegetation structure) and the receiving sedimentary system (e.g. size, system type). In the vast majority of the literature, pollen productivity is assumed to be a constant, at least for a given taxon in a given region over a given time period. Estimates of pollen production are usually expressed as a ratio to a reference taxon, or Relative Pollen Productivity (RPP), and empirical estimations of abundance of the main taxa recorded in a region's pollen records, has been a fruitful area of recent research in Europe (e.g. Broström, et al. 2008; Mazier, et al. 2012a etc.) and beyond (e.g. Duffin and Bunting, 2008; Bunting, et al. 2013; Li, et al. 2015).

The assumption that a single RPP can be assigned to a taxon is clearly a simplification. At range limits, climate conditions are known to affect pollen production (e.g. Sugita, et al. 2010a; Mazier, et al. 2012b), and many plants vary investment in flowering facultatively in response to environmental stressors such as grazing or light availability. Using an ecological approach, Waller et al. (2012) showed that flowering rates, and therefore pollen production, vary over time as a result of the woodland management practice of coppicing, and used a simulation approach to explore the effect of those variations on the representation of tree taxa in pollen records from landscapes as the management practices changed. Similarly Baker (2012) has shown that heavy grazing can have a suppressive effect on Poaceae pollen production. This may explain some of the differences in pollen productivity estimated in different studies, for example Broström et al. (2004) report results from grazed meadows which show common forb pollen types to have higher productivity than grasses, whereas Hjelle (1998) found the opposite when analysing samples from hay meadows. Grazing suppression of Poaceae has also been used to support arguments that the pre-farming landscapes of north-west Europe included extensive grazed grasslands despite producing tree-dominated pollen records (Vera, 2000; Mitchell, 2005). In this paper, we present estimates of RPP from coppiced woodlands derived from modern pollen assemblages, rather than ecological methods, and consider the implications for reconstruction of past vegetation cover around small ponds in tree-rich habitats.

Coppicing was a common form of sustainable woodland management across northern Europe, with evidence for its practice going back into prehistory. Traditionally a means of controlling and maximising the production of timber, underwood and wood derivatives (e.g. charcoal) from woodlands, coppicing is recognised as a key factor in determining the characteristics of ‘heritage’ woodlands such as the extent of spring ground flora like *Hyacinthoides non-scripta* or provision of nesting sites for *Luscinia megarhynchos*, and is increasingly being reintroduced as a conservation measure. In coppiced woodland, some trees are allowed to grow to maturity with a single trunk (standards), but the majority of trees are cut back periodically, leading to regrowth of multiple stems from a near-ground-level base (the stool). Flowering of these coppiced plants will differ from standards, at least in the early years of regrowth. Differences will arise from a range of factors, including variations in the length of time branches of individual species take to reach sexual maturity, competition between regrowths and changing light conditions in the below-canopy growing environment related to the canopy type and density of the standards.

Waller et al. (2012) explore the pollen signal from three coppiced woodlands with different species compositions, using a range of methods. Direct measurement showed that flowering response to coppicing varied widely by species. For the studied tree species *Tilia cordata* and *Alnus glutinosa*, the overall amount of pollen produced is substantially reduced even when there are long intervals between cutting events. In contrast, *Corylus avellana* regrowths flower within 1-2 years of coppicing. This species therefore produces pollen under the shortest of likely cutting regimes and pollen production during the early stages of regrowth appears to be higher than in later stages due to the reduction of competition for light from nearby stools. Records from the sediments of small ponds within these coppiced woods, sampled contiguously at high (annual to sub-annual thickness) resolution, showed patterns which could be interpreted in terms of known woodland history, but determining unambiguous markers of coppice management which could be used in the interpretation of palaeoecological records was not possible. Zones of sediment inwash associated with local disturbance during winter cutting were probably the strongest single indicator observed. The differences between pollen assemblages collected in pollen traps placed in the middle of areas (compartments) of coppice of different age could not be simply explained as the result of years since cutting, probably due to local variations in vegetation composition and structure. The background pollen component, that sourced from beyond the compartment being studied (and therefore originating from compartments of different ages), appears to have been substantial. Using the information about flower production, estimates of relative pollen productivity from Southern Sweden (Sugita, et al. 1999; Broström, et al. 2008) were adjusted to give multiple values for each of the key coppiced taxa reflecting pollen production at different regrowth stages. These values were then used in simulations to explore the effects of landscape-scale changes in woodland management regime (proportion of landscape under coppicing, duration of coppice cycle) on the pollen assemblages deposited in small and large lakes and in a wooded peatland. These simulations supported inferences of coppicing from oscillations seen in Neolithic pollen records, especially in East Anglia and the northern Alpine Forelands, but the study as a whole suggested that the pollen signal from these complex cultural landscapes was likely to be highly variable and that simple, unambiguous signals of management could not be defined, even for pollen records from small basins with restricted source areas in landscapes which are believed to record woodland dynamics at the stand scale (Bradshaw, 1981a; Calcote, 1995).

The adjusted values used for modelling assumed that the overall RPP for the taxa in the managed woodlands, reflecting the pollen production of both canopy trees and coppice stools of all ages, was comparable to the estimates from southern Sweden presented by Sugita et al. (1999). In this paper we test that assumption by estimating RPP for the main woody taxa based on both percentage and influx pollen data from the Tauber trap records presented by Waller et al. (2012). These RPP values are then used to reconstruct vegetation cover around the small ponds studied by Waller et al. (2012) from the pollen assemblages in the uppermost year of sedimentation, to investigate whether simple (and simplistic) reconstruction approaches improve the interpretation of such assemblages significantly over a narrative interpretation based on the raw pollen assemblage. Comparing the different approaches and their assumptions with the actual vegetation allows us to identify ways forward to develop more realistic reconstructions of complex cultural landscapes with a multi-layered vegetation structure.

2. Field sites

Three woodlands in East Anglia, UK (Figure 1), currently subject to coppice management, were selected for investigation by Waller et al. (2012). At Chalkney Wood (51°54’N 0°43’E; Fig 1b) in central Essex, *Tilia cordata* is the main coppiced species but in some parts of the wood it is co-dominant with *Castanea sativa* and less commonly with *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’ (non-pollarded or coppiced trees) 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.

[INSERT FIGURE 1 HERE]

At Bradfield Woods (52°09’N 0°06’W) in Suffolk (Fig 1c), 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. Tree data from the third site studied by Waller et al. (2012), Hayley Wood, were not included in these analyses because, unlike the other woods, only a small part of Hayley is coppiced.

3. Estimates of relative pollen productivity

3.1. Introduction/background

Estimates of Relative Pollen Productivity (RPP) presented here are based on a widely used model of the pollen-vegetation relationship which assumes that pollen deposited at a point is proportional to the vegetation cover around that point, with a taxon-specific correction factor reflecting the amount of pollen produced per unit contributing to the pollen dispersal by each taxon. The basic approach used in much work within this tradition (Andersen, 1970; Prentice, 1985, 1988; Jackson, 1990, 1994; Sugita, 1993 et seq.) is a simple linear model of the form:

Pollen deposition at point of one type = (amount of pollen produced by those plants) x (proportion transported from plant to point) summed across all the plants within the source area + background transport of pollen of that type from beyond the source area

Which can be expressed algebraically as:

$$y_{ik} = \alpha_i \psi_{ik} + \omega_i \qquad \text{Equation 1}$$

where y_{ik} = pollen influx from type i at site k, ψ_{ik} = the distance-weighted plant abundance of taxon i around site k and α_i and ω_i are constants, the pollen productivity and background pollen component of taxon i in the studied region respectively. Pollen productivity, which can be thought of as the amount of pollen produced per vegetation unit (which can be defined in different ways; most commonly it is conceptualised as the vertical projection coverage of the plant within a vegetation canopy, but other options such as biomass are also possible), is generally treated as a constant for a given taxon in a given region (but see e.g. Mazier, et al. 2012). The background component depends on the abundance of the specific taxon in the sampled region, and can vary in both space and time.

Details of the distance weighting of vegetation models have been discussed in multiple places (e.g. Prentice, 1988; Jackson, 1994; Nielsen, 2005; Bunting, et al. 2013). In this paper, we use the Sutton-Prentice distance-weighting algorithm (Sutton, 1953; Prentice, 1985, 1988; Appendix 1), which varies with plant taxon and involves making the following assumptions:

1) Even wind distribution around the compass during pollen dispersal

2) Majority of pollen transport takes place above the vegetation canopy (C_c from the Tauber model dominates; Tauber 1965, 1967)
3) The vegetation canopy is a single, flat layer
4) Pollen deposition occurs within a gap in said canopy (this is important to remove effects of C_t and C_g).

Assumption 1 is considered to be reasonable. However, assumptions 2-4 are problematic for small ponds, forest hollows or pollen traps, and for coppiced sites. Figure 2a shows the simplified situation underlying the Prentice-Sutton pollen dispersal and deposition algorithm (hereafter, P-S model). In the P-S model, pollen is dispersed in all directions around each source, and the amount of pollen deposited at the sampling point is calculated by working out the contribution from all pollen sources in all directions around the basin, and summing the results.

[INSERT FIGURE 2 HERE]

At relatively coarse scales, these assumptions are reasonable: where a basin is large enough, the variations in pollen deposition associated with the change in height of the vegetation surface and therefore air flow path at the vegetation edge (see e.g. Raynor, 1971; Caseldine, 1981) are not likely to have a significant effect on the pollen signal at the sampling point since such ‘edge effects’ seem to extend only 50-100m at most into the basin (Bunting, et al. 2013). This can be explained using the Tauber model by arguing that pollen dispersal within the canopy (C_t and C_g in the Tauber model; Tauber, 1965, 1967) occurs over relatively short distances and therefore makes little contribution to a bog-centre sample (the ‘edge effect’ is in essence made up of two components: trunk space and gravitic deposition; and turbulence-related deposition/entrainment processes as the air stream changes height and the surface roughness also changes).

The P-S model has been applied with reasonable success to small hollows and ponds (e.g. Calcote, 1995, Sugita, et al., Sugita, et al. 2010b) in woodlands, suggesting that even within the ‘edge effect’ distance, the assumption of above-canopy pollen transport dominance is a reasonable approximation. Coppiced woodlands present an additional challenge to the P-S model assumptions, since the canopy roughness and porosity varies through the coppice cycle. Figure 2b below shows a small hollow in a coppiced woodland. In the mature compartment (left hand side of figure) the regrowths and standards together form a closed canopy with fairly even surface, but in early stages (right hand side of figure) standards emerge from lower-growing stools, creating an uneven canopy layer with greater porosity, suggesting that the boundary layer of turbulent, pollen-carrying air is thicker, and therefore that the pollen transport situation is more complex.

In this study, we will continue to assume a flat vegetation canopy with pollen release and transport occurring at/above the uppermost vegetation, although this assumption is clearly stretched to its limits.

3.2. Pollen data

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. All trap pollen samples were processed following the methodology of Hicks et al. (1996), including the addition of tablets of exotic pollen to allow the calculation of pollen influx (Stockmarr, 1971). A minimum of 1000 total land pollen (TLP) grains were counted from each trap and influx calculated in grains cm^{-2} yr^{-1}.

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. 2010a). Whilst these methods do reduce the effects of climate-related interannual variability in plant flowering (e.g. Autio and Hicks, 2004; Huusko and Hicks, 2009; Jackson and Kearsley, 1998), they would have blurred the signal of the coppice cycle which we seek to study. 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, such as from anthers or pollen-bearing insects falling into the trap. Influx data for a defined taxon from a single trap was removed from analysis if the difference in values between that trap and the other two traps was greater than an order of magnitude, and that difference in influx was greater than the difference explained by calculated counting error (Maher, 1972; 1981).

Tauber trap placement was determined by the goals of the broader study (Waller et al. 2012), therefore the sampling strategy is systematic (trap arrays are in the central area of compartments) rather than random in order to maximise the likelihood of detecting years since cutting related changes in the pollen signal. Randomised sampling strategies are considered the most effective for studies of RPP (Broström et al. 2005) but systematic sampling can still yield meaningful results (Twiddle et al. 2012).

3.3. Vegetation data

Vegetation data from the compartments in which the traps were set were collected within a minimum 20m radius area centred on the trap. The position of all woody plants and, for trees, size (trunk circumference at breast height), was recorded. These data were then translated into percentage canopy cover for each taxon (see appendix 1) and used to calculate vegetation composition for 10m wide rings out to 100m around the trap. These rings were then distance weighted using the P-S model and summed to give cumulative distance weighted plant abundances at different distances, which we hereafter refer to as dwpa(z) where z is the distance between the centre of the trap array and the outer edge of the largest ring included in the summation.

3.4. Data analysis approach

Equation 1 is linear when pollen values for taxon i are independent of each other, for example with pollen influx data, and an algebraic solution for the value of the constants can be found for each taxon separately using empirical data. However, where pollen data for taxon i are expressed as percentages, they become interdependent, and an iterative approach has to be taken to estimate the constants; the Extended R-Value approach has been developed for this situation (Parsons and Prentice, 1981; Prentice and Parsons, 1983).

3.4.1. Regression analysis using independent pollen influx data

The pollen data from Tauber traps can be expressed as pollen influx and therefore taxa can be considered independent. This allows estimates of the relationship between pollen influx (hereafter 'influx') and dwpa(z) separately for each taxon via linear regression analysis. Relative Pollen Productivity can then be calculated by taking the ratio of the slope terms for the taxon of interest and the reference taxon. Each trap within the trap array was treated as a separate estimate of the influx, therefore most sample points had multiple influx values for each vegetation value allowing error estimation. 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 a small number of obvious outliers (values for insect-pollinated taxa lying more than an order of magnitude above the general trend at that distance weighted vegetation value, assumed to represent deposition via insect visit to the trap rather than by aerial transport; see above) were removed from some scatter plots.

A one-tailed null hypothesis of no positive linear relationship between dwpa and influx was tested for each dataset 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) and intercept (background pollen influx of the taxon). This analysis was carried out for all ten vegetation datasets from dwpa(10) to dwpa(100) for each taxon.

Quercus was chosen as the reference taxon, since it was not found as a coppiced species at either site, and was widely present in the vegetation, with pollen present in all samples and plants recorded within 20m of all but five of the trap clusters and within 30m of all trap clusters. *Quercus* also showed statistically significant linear correlation (Pearson product-moment correlation: $p<0.01$) between cumulative dwpa(z) and influx at all distances. Pollen productivity for all taxa relative to *Quercus* – hereafter $\text{RPP}_{Quercus}$ - was calculated by taking the ratio of the relevant 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 at the distance best approximating the taxon-specific source area. Statistical analyses were carried out using SPSS v.19.

3.4.2. Extended R-value analysis using pollen percentage data

Most published studies are based on sediment pollen assemblages rather than Tauber traps, therefore pollen data are only available as percentages, and the Extended R-value approach is used to estimate RPP (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Sugita, 1993; Broström, et al. 2008). For comparison, pollen percentages were calculated for each compartment from the summed influxes of each taxon in all the traps in the array, and ERV analysis was carried out. Only those taxa which were present in both the pollen and the vegetation datasets from at least 4 plots were included in the analysis. Analysis was carried out in PolERV (software written by R. Middleton based on code developed by S. Sugita) using 200 iterations and running the analysis three times to check whether a stable solution had been found for both ERV model 1 and ERV model 2. Again *Quercus* was used as the reference taxon. Likelihood function score plots were created to estimate the relevant source area of pollen (RSAP).

3.5. Results

Scatter plots comparing pollen influx and distance-weighted plant abundance to 100m (dwpa(100)) were created for the eleven palynologically distinct taxa for which multiple datapoints were available: *Acer campestre*-type*, Alnus glutinosa, Betula, Carpinus betulus, Castanea sativa, Corylus avellana*-type*, Fraxinus excelsior, Quercus, Salix, Tilia cordata* and *Ulmus* (Appendix 2). Inspection of the scatters suggested that the taphonomic model assumption of a single abundance-related dominant model of pollen delivery was not valid for all taxa.

Figure 3 shows the pollen influx plotted against dwpa(100) for *Fraxinus excelsior* and *Quercus*. Both plots show some separation of the samples from the two woods, reflecting differences in the abundance of the trees (e.g. Chalkney Wood samples generally have low *Quercus* dwpa(100) whilst Bradfield Woods has a wider range of values) and possibly differences in pollen taphonomy. The points outlined with a solid oval show a positive trend of increasing influx with increasing dwpa(100), the type of pattern the Prentice-Sutton approach aims to model. Both plots also show a small number of points where plants are highly abundant but pollen influx is low (marked with dashed ovals on Figure 3). All points for *Fraxinus excelsior* are derived from Bradfield Woods. For *Quercus*, these points came from both woods, and with the exception of the 1991-felled compartment in

Chalkney Wood, all come from trap arrays where other traps yielded points which fell into the solid oval. These points could reflect locations where management interventions or environmental differences have affected the flowering of specific trees, a counting or sampling artefact, a difference in taphonomy, or in the case of dioecious *Fraxinus excelsior* a dominance of female rather than male trees at Bradfield Woods compared with Chalkney Wood. For some taxa such as *Fraxinus excelsior*, a third group of points could be identified, marked by the dotted oval on Figure 3, with high pollen influx at locations with low tree presence. This is interpreted as either showing the effects of an additional transport mode - one delivering high influx at relatively low tree coverage (gravity or insect-mediated transport) - or for dioecious species differences in the presence of male trees at different sites. For this group of taxa it was not considered appropriate to continue with model fitting assuming a single dominant mode of dispersal and deposition, and on this basis *Fraxinus excelsior*, *Salix* and *Ulmus* were not analysed further. The scatterplots for *Quercus* and the other seven taxa have some unexpectedly low influx points, as discussed above, but most points lie broadly within the solid oval, suggesting that the single dominant mode of transport approach assumed by the Prentice-Sutton model was appropriate for these data. All scatters were somewhat 'messy', probably due to a combination of sampling error and the contribution of other dispersal modes in addition to the single dominant mode.

[INSERT FIGURE 3 HERE]

3.5.1. Regression analysis using independent pollen influx data

Correlation coefficients between pollen influx and cumulative dwpa at different distances are shown in Figure 4 for the remaining 8 taxa, *Acer campestre*-type*, Alnus glutinosa, Betula, Carpinus betulus, Castanea sativa, Corylus avellana*-type*, Quercus,* and *Tilia cordata*. Moderate to strong positive correlations between pollen influx and dwpa were found at all distances. Correlation coefficient values are stable beyond about 30m. Where fit decreases (correlation coefficient falls) over the first three samples (from dwpa(10) to dwpa(30); e.g. *Betula*, *Castanea*), this is interpreted as either showing that the taxon is not effectively recorded in the vegetation beyond the area of direct survey or as showing a strongly local taphonomic relationship. However, the explanatory power of the linear models varies widely, with r^2 values (proportion of variance in the data explained by the model) ranging from 0.55 (*Tilia*) to 0.10 (*Acer*) (see Table 1); explanatory power is good for taxa which only occur as plants in Chalkney Wood (*Tilia*, *Castanea* and *Carpinus*) and for *Corylus*, but weaker for other taxa.

[INSERT FIGURE 4 HERE]

Relative pollen productivity relative to *Quercus* ($RPP_{Quercus}$) is estimated from the slope ratios and summarised in table 1 and Figure 5.

[INSERT FIGURE 5 HERE]

[INSERT TABLE 1 HERE]

3.5.2. Extended R-value analysis using pollen percentage data

ERV-analysis was carried out as described above. Figure 6 shows the likelihood function scores for models 1 and 2 for the data from both woods, showing that the trend in likelihood function values obtained by both models are approaching an asymptote by 100m surveyed area, but have not yet reached a stable point. $RPP_{Quercus}$ and the relevant background terms was estimated from the final two ring values. Although model 1 output produced significantly lower likelihood function scores than model 2, suggesting a better fit to the data, the $RPP_{Quercus}$ values were considered less plausible than for model 2 for *Carpinus, Castanea* and *Tilia*, which are only found in Chalkney Wood (see table

1). RPP$_{Quercus}$ values are summarised in Table 1, and show marked differences from the values estimated from influx data using regression analysis for most taxa, with differences in rank order as well as the actual productivity value. Since some taxa were only recorded in the surveyed compartments at Bradfield Woods (*Alnus*) or at Chalkney Wood (*Castanea, Carpinus, Tilia*), the dataset was then split according to wood of origin and reanalysed, but small sample size led to highly variable output suggesting that the algorithm could not find a single preferred solution.

[INSERT FIGURE 6 HERE]

4. Applications in reconstruction

The purpose of estimation of RPP is to estimate vegetation cover from palaeo-pollen assemblages. The complex multi-layered and managed woodland canopy is clearly not an ideal target, but woodland is hugely important and interesting to end users of pollen records. Waiting until we have a perfect method is, we consider, not a good strategy – refining the method has to go hand in hand with actually applying the imperfect methods we have available in order to test model assumptions and refine the approaches necessary to permit validated reconstructions to be achieved. Pond sediment pollen assemblages are available from three ponds in the woods investigated here, and vegetation surveys were carried out around the ponds when sediments were collected (Waller, et al. 2012). Therefore reconstruction of vegetation can be attempted by comparing the linear regression derived RPP$_{Quercus}$ values on the one-year pollen samples, with the surveyed vegetation to determine whether, at this early stage, one or more of these quantitative reconstruction is a worthwhile aid to interpretation of the pollen assemblages from such ponds.

4.1. The ponds

A pond at the south-east corner of Bradfield Woods (Figure 1) was cored and is referred to informally as “Bradfield Pond”. The pond surface area is about 75m^2, therefore occupies less than a third of the inner 10m radius ring (314m^2) in area. The pond lies in a compartment last coppiced in 1995 and adjacent to one coppiced in 2000, with the main coppiced species *Corylus avellana*. The pond is quite close to the edge of the present-day woodland; all non-woodland land was treated as non-pollen producing for the purposes of extrapolating vegetation data between 20 and 100m radius.

Two ponds were investigated at Chalkney Wood (Figure 1), informally named “Alder Pond” (A on Figure 1) and “Vegetation Pond” (B on figure 1). “Alder Pond” lies close to the boundary between compartments last cut in 1987 and 1984 respectively, and has a surface area of around 180m^2. The name derives from a single large stool of *Alnus glutinosa* on the north-east bank of the pond, the only specimen of that species recorded during vegetation survey in the whole of Chalkney Wood. The surrounding vegetation is dominated by coppice stools and standards of *Tilia cordata* and *Castanea sativa*. “Vegetation Pond” lies close to the boundary of two compartments last cut in 1999 and 2002 respectively, and to the boundary with a coniferized section of the Chalkney Wood located north-east of and directly adjacent to the coppiced section studied; this was treated as non-pollen producing when extrapolating the vegetation data. This pond has an area of about 50m^2 and *Tilia cordata* is the main species present locally as both coppice stools and maidens.

4.2. Distance-weighted plant abundance

The centre of the surveys carried out was positioned within the centre of each pond. Pond surfaces were treated as non-pollen producing areas, which has an equivalent effect to setting the basin radius to a non-zero value in the weighting model, and otherwise the vegetation data to 100m radius around the centre point were processed as described above (in section 3.3) and in Appendix

1. For reconstruction purposes tree species composition was expressed as the percentage of the total dwpa to 100m radius for the eight tree taxa studied – hereafter expressed as %dwpa(100).

4.3. Pollen assemblages

Ponds were cored using a modified Livingston-type corer (Wright, 1967), and a chronology constructed using SCP profiles, ^{210}Pb and ^{137}Cs profiles (see Waller, et al. 2012, Supplementary data 2, for full details). Cores were sampled contiguously, and sample thickness was chosen to be equivalent to or less than annual resolution. Age models were consulted to determine how many samples would be combined to represent the 2007 pollen influx ("Bradfield Pond" 3 samples, "Alder Pond" 2 samples and "Vegetation Pond" 1 sample). Standard pollen preparation methods were used (Moore, et al. 1991) and *Lycopodium* tablets added to enable the concentration of pollen accumulation rates (PARs). A minimum of 1000 TLP grains were counted per sample.

Since each pond represented a small canopy opening, and the pollen traps were considered to be under the vegetation canopy, pollen influx (and hence annual PAR) might be expected to be lower in the ponds, but since nearly all influx values measured in the ponds fell within the range of values obtained from the pollen traps this was ignored.

4.4. Data analysis

Four reconstruction methods were applied to the three pollen assemblages. Firstly, the inverse of each of the methods used to estimate $\text{RPP}_{Quercus}$ was applied, prediction of dwpa(100) from pollen influx using the linear model (converted to % dwpa(100) for comparison purposes), and application of the inverse form of the ERV equations (Prentice and Parsons, 1983). Secondly, two other simple reconstruction techniques were applied; the Modern Analogue Technique (identifying the most similar assemblage from the available pollen traps, e.g. Overpeck, et al. 1985); and Correction for Pollen Productivity using the linear regression estimated RPP values (the approach used by Davis, 1963 and Bradshaw, 1981b, but applied here to dwpa rather than vegetation cover). All methods are explained in more detail in Appendix 3. In the first three cases, since the calibration data sets relate to Tauber traps and the target data sets are from small ponds, there are differences in the pollen source areas and therefore proportion of background pollen loading between the two situations.

In order to determine whether the reconstruction methods gave a better estimate of the vegetation composition than the original pollen proportions, results were compared with the measured vegetation around each pond using the Bray-Curtis Index (Bray and Curtis, 1957; Kindt and Coe, 2006). This metric is widely used in ecology (Clarke, et al. 2006; Kindt and Coe, 2006) and was chosen for this study because it can be used for proportion or non-proportion data, it is sensitive to both abundance and composition, and because the output value is not affected by the numerical size of the input value.

The equation used is:

$$I_B = 1 - \frac{\sum_1^j |x_{ik} - x_{im}|}{\sum_1^j x_{ik} + x_{im}} \qquad \text{(Equation 2)}$$

Where I_B is the Bray-Curtis Index, x_{ik} is the measurement of interest for taxon i in sample k, k and m are the two samples being compared, and there are a total of j taxa in the combined taxon list of the two samples taken together.

4.5. Results

4.5.1. The input data

Figure 7 shows a graphical comparison of vegetation and pollen assemblage data from the three ponds. The vegetation around “Bradfield Pond” is dominated by *C, avellana*, mostly as coppice stools, and since the compartment was last cut 12 years before sampling these stools are expected to be producing pollen less abundantly compared to the early years after coppicing (Waller, et al. 2012). The pollen assemblage contains substantially more *Quercus* pollen and less *A. campestre* and *C. avellana* than the vegetation data.

[INSERT FIGURE 7 HERE]

The vegetation around “Vegetation Pond” is dominated by *Tilia* but much of this is in the form of coppice stools. The compartment was last cut in 1999, and Waller et al. (2012) showed that *T. cordata* flowering is heavily suppressed by coppicing for at least 20 years, so these stools were treated as non-pollen-producing and the vegetation data recalculated accordingly (figure 7). These adjusted vegetation data were used for the calculation of Bray-Curtis Indices shown in Figure 8. Comparing the “Vegetation pond” corrected vegetation with the pollen assemblage, *T. cordata* and *C. betulus* are under-represented and *Betula, Quercus* and to a small extent *C. sativa* are over-represented.

“Alder Pond” has a single large *A. glutinosa* on the north-east bank, the only specimen of that species recorded during vegetation survey in the whole of Chalkney Wood, therefore pollen will be entering the record via gravity input as well as aerial transport. The wider vegetation is dominated by coppice stools and standards of *C. sativa* with some *T. cordata*. In the “Alder Pond” pollen assemblage, *C. sativa* and *T. cordata* are under-represented, and *Quercus* and *A. glutinosa* are over-represented. This might suggest that *C. sativa* flowering is, like *T. cordata*, suppressed after coppicing, although the same effect is not seen at “Vegetation Pond” where regrowths are actually younger.

The apparent under-representation of *C. sativa* in the assemblages from "Alder Pond" and of *C. betulus* in "Vegetation Pond", even though both have estimated overall $\mathrm{RPP}_{Quercus}$ values, comparable to the well- and over-represented *Betula* and *Quercus* (see Table 1), suggests that both may experience suppression of flowering for multiple years after coppicing as observed for *T. cordata*.

4.5.2. Comparison of vegetation data with pollen-based reconstructions

Figure 8 shows the Bray-Curtis indices for comparisons between % dwpa(100) at each pond and the different pollen-derived reconstructions. The horizontal bar shows the value calculated for the comparison shown in Figure 7, of uncorrected pollen percentages against % dwpa(100m), with other symbols showing comparisons with the different correction methods (section 3.4 above; Appendix 3). For "Alder Pond", the uncorrected pollen assemblage was the second-best reconstruction method. This may be explained by the effects of coppicing suppression on flowering of not just *Tilia cordata* (corrected for here) but also *C. betulus* and *C. sativa.* At "Vegetation Pond" the Modern Analogue Technique (MAT) produced the best reconstruction, and for "Bradfield Pond", applying the inverse linear regression model, simple correction and MAT all produced statistically more similar reconstructions of the vegetation than the simple pollen values. The inverse ERV method produced a substantially less similar reconstruction.

[INSERT FIGURE 8 HERE]

4.5.3. Modern analogue technique reconstructions

The modern analogue technique reconstruction was carried out using squared-chord distances to compare the pond assemblages with those from the Tauber traps. A distance of less than c. 0.25 is usually taken as indicating a reasonable reconstruction when considering palaeoecological data, although thresholds as low as 0.05 have been suggested where all samples come from the same biome (Lytle and Wahl, 2005). In this exercise, comparing ponds and traps, the identified best fit trap analogues had distance scores between 0.09 and 0.21.

The “Bradfield Pond” pollen assemblage had closest matches with two traps placed elsewhere in Bradfield Woods; one from a compartment felled in 1983 (distance: 0.09) and one from a compartment felled in 1988 (distance = 0.13). Both compartments abut the edge of Felsham Hall Wood (see Figure 1b), like the compartment where the pond is situated. Although that compartment’s vegetation was surveyed, no pollen trap was placed within it, so an assemblage from the specific compartment was not available as a modern analogue.

The “Vegetation Pond” pollen assemblage’s closest match was with a trap placed in compartment 113 in Chalkney Wood, which was last felled in 1987 (distance: 0.21), ironically the compartment which actually contains “Alder Pond”. The closest analogue for “Alder Pond” was in Bradfield Woods, in a compartment felled in 2006 (Distance: 0.158), reflecting the very local distorting effect of the single stool of *Alnus glutinosa* – this species is an important coppiced taxon in parts of Bradfield Woods, but elsewhere absent in Chalkney Wood.

5. Discussion and further work

5.1 Estimates of relative pollen productivity

Using a linear regression of pollen influx against dwpa produced $RPP_{Quercus}$ values which are comparable with other published European studies (see Figure 5 above: e.g. Sugita, et al. 1999; Broström, 2008; Mazier, et al. 2012). Whilst statistically significant differences in $RPP_{Quercus}$ are seen across studies for some taxa such as *Alnus*, one or more of the known effects of differences in vegetation survey methods (e.g. Bunting and Hjelle, 2010), pollen sampling method (mosses versus one year Tauber traps; Lisitsyna and Hicks, 2014), dominant habitat (Bunting, et al. 2005), climate regions (Mazier, et al. 2012) and other environmental factors are likely to be sufficient to explain these differences, rather than the possible data concerns raised within this study (relatively weak explanatory power of the reference taxon, *Quercus*, sampling in a not entirely random way in order to maximise the range of coppice ages represented in the datasets (trap arrays were located >20m from any compartment edge and not directly beneath a standard, and compartments were selected on the basis of years since last felling) and the conservative approach to data cleaning taken, only excluding the most obvious outliers: see section 3.2). These findings support the approach to modelling the effects of coppicing in the pollen record taken by Waller et al. (2012), where an empirically derived single value for a taxon was modified to reflect the length of the coppice cycle and the species-specific effects of coppicing on floral production.

Extended R-value analysis derived RPP estimates for this study were different by orders of magnitude for some taxa, from both the linear regression estimates and from previous published values (e.g. Sugita, et al. 1999; Broström, 2008; Mazier, et al. 2012). The sample size was small (although in excess of the “2 samples per taxon of interest” threshold suggested by S. Sugita pers. comm.), taxa were not randomly distributed between the woods, sampling location placement was not purely random (see above) and the additional assumption of constant background pollen rain of those taxa at all sites required to apply the ERV model (Parsons and Prentice, 1981) may not be reasonable within and between coppiced woodlands. A larger than usual number of algorithm repeats was needed to obtain stable solutions (200+ rather than the 50 iterations usually used), and repeats of the entire analysis produced slight variations in results, suggesting that the model-fitting process does not have a single best-fit solution. The estimated RPP values obtained using this method are considered unreliable.

For Tauber trap data with limited numbers of years available, we conclude that the linear regression of influx against dwpa(z=estimated RSAP) is a more effective method of estimating RPPs than ERV analysis and, where vegetation data can be collected for multiple traps in the same region, can contribute substantially to the growing database of RPP values used for reconstruction studies (e.g. Broström, et al. 2008; Mazier, et al. 2012).

5.2 Estimates of Pollen Source Area

Estimating RPP requires consideration of pollen source area. The RSAP (Sugita, 1994) is a widely used estimate of the distance within which changes in both the proportion and position of vegetation elements are reflected by changes in the pollen assemblage, and is a measurement dependent on the whole assemblage, affected by vegetation factors such as mosaic patchiness (Bunting, et al. 2004) and evenness (Hellman, et al. 2009a). The likelihood function score plots generated by the ERV approach (Figure 6) suggest that the RSAP is close to but has not been reached by the 100m maximum survey distance since the curves appear to be approaching an asymptote but have not reached it. This is in accord with other published estimates for RSAP in closed canopy woodland which range from 50m -150m (Sugita, 1994; Calcote, 1995; Bunting, et al. 2005). Constrained vegetation survey distance is therefore not considered to be the prime cause of the substantial difference in $\mathrm{RPP}_{Quercus}$ estimated using the two different methods.

The linear regression of influx method, on the other hand, allows us to present estimates of Taxon Specific Source Areas (TSSA) using a similar goodness-of-fit based definition as RSAP (see e.g. Jackson, 1990, 1994) (as contrasted with the Prentice Percentage source area; e.g. Prentice, et al 1987); the TSSA would be defined as the distance z at which the correlation between pollen influx and dwpa(z+e) does not improve over the correlation with dwpa (z), where e is the increment of survey distance (e.g. ring width). These values are expected to vary with taxon, depending on factors such as grain size and plant growth form. Figure 4 shows correlation coefficients for influx against dwpa(z) for this study. All taxa reach a point where the correlation coefficient changes by less than 0.01 with added distance between 10m and 60m radius. For some taxa (*Betula*, *Carpinus* and *Castanea*) the correlation initially gets worse with increasing distance of vegetation survey, contrary to the theory. This may be an effect of differences in flowering through the coppice cycle by stools of these taxa; in the absence of empirical data, these taxa were assumed to produce pollen at all stages in the cycle, when present as cut stools (see 5.3 below), but the evidence from the pond surface samples suggests this is not the case. Coupled with the change in detail of vegetation survey beyond 20m, these factors may explain the pattern seen, rather than a problem with the underlying conceptual model.

5.3 Other coppiced taxa

The detailed ecological study of the effects of coppicing on flowering in *Corylus avellana, Alnus glutinosa* and *Tilia cordata* of Waller et al. (2012) made it possible to calculate dwpa values excluding non-flowering coppice stools. However, these were not the only species subject to coppicing in the woodlands; occasional coppice stools of *Acer campestre*, *Betula*, *Cornus sanguinea*, *Crataegus monogyna* and *Salix* were recorded and in places in Bradfield Woods coppiced stools of *Fraxinus excelsior* were co-dominant with *Corylus* and/or *Alnus,* whilst *Carpinus betulus* and *Castanea sativa* stools were locally co-dominant with *Tilia* and/or *Corylus* in Chalkney Wood. It is not clear if mixed-species would have been the norm in historical and traditional practices, where coppicing was primarily carried out to obtain materials with specific properties, rather than the modern conservation-led approach used in many woodlands, where trees are coppiced to create specific habitat structures. For species which are known to flower early as trees, such as *Betula*, the difference in vegetation data created by allowing for flowering suppression may have not been significant, since only one year of suppression was recorded for *Corylus avellana* by Waller et al. (2012). For other taxa, which take longer to reach sexual maturity, the effect could be substantial. *Tilia cordata* flowering was found to be still increasing in the oldest sites studied by Waller et al.

(2012), and the tree is reported to take 60 years to reach flowering maturity from germination (Pigott, 1991). This could also apply to *Castanea* (flowering age for young trees 25-30 years; Balkan Ecology Project, n.d.) and *Carpinus* (flowering age around 30 years; Matthias, et al. 2012). There is also some support for this interpretation from the comparison of vegetation and pollen assemblages in the pond samples (section 4.5.1 above).

Without correction for the effects of coppicing on flower production, these other species are likely to be over-estimated by the dwpa(z) data used for linear regression estimation of RPP or TSSA (5.2 above), but this over-estimation will also vary widely between sites, since the presence of single standards close to the traps can have a large effect on the pollen influx. Therefore future work to determine stages of flowering behaviour in other coppiced taxa, and to determine if the effects are the same from other management activities such as pollarding, shredding and layering, will enable better incorporation of woodland management into both simulation studies of pollen signals from prehistoric landscapes (Hellman, et al. 2009b) and in reconstructions of past vegetation from pollen assemblages.

5.4 Vegetation survey issues

The vegetation survey methodology, largely dictated by the demands of other parts of the overall research project (see Waller, et al. 2012), differs markedly from other studies aimed primarily at determining RPP (reviewed in Bunting, et al. 2013). Very detailed survey within 20m radius of the trap focused on stem size and position rather than crown coverage, and composition beyond 20m was estimated using the compartment map and simplifying assumptions about compartment composition (see Appendix 1), in addition to vegetation surveys within adjacent compartments. The transformation of the inner area survey into ring cover data involved the simplification of organising the data into 10m wide rings, rather than dividing the inner rings more finely as is sometimes preferred for ERV analysis (see e.g. Broström, et al. 2008; Bunting, et al. 2013). This reduces the relative importance of trees, shrubs and stools closest to the traps in comparison to systems with finer inner ring divisions, and may thus make comparison with other studies problematic. Bunting et al. (2013) explore the effects of variations in ring width on the relative importance of plants in the inner area of the survey, and show quite marked differences, which may contribute to the anomalous results of the ERV analysis. However, translating the data collected in this project into finer-grained rings is not a trivial proposition, and would involve making more assumptions about the shape and extent of both tree and shrub canopies and of the growing stools (see Appendix 1 for description of assumptions made).

All studies of vegetation for comparison with pollen data involve making decisions balancing the time taken to complete each survey and the number of sampling points that can be surveyed, and this remains a major limitation in studies of pollen dispersal and deposition. The ‘pollen’s eye view’ of vegetation which the survey seeks to capture is also not well understood. The collective standardisation process used to develop the ‘Crackles Project methodology’, described by Bunting et al. (2013), had not begun when this project was undertaken. Recording stem diameter and stool density made ecological sense and suited the requirements of the wider research project, but the models used for calibration assume that the ‘pollen’s eye view’ of vegetation are controlled by the canopy so emphasise recording vegetation cover. The data transformation approach used here was time-consuming and involved assumptions, but we believe is capable of supporting the inferences drawn and comparisons made.

Future studies of this type would be improved by

a) using a randomised or stratified-random sample design, coupled with testing the possible effects of sampling strategy on ERV-analysis results using simulations,
b) including direct recording of the canopy in vegetation survey, especially in the inner parts of the survey area, to permit finer ring-width intervals for compatibility with other studies and

for potential assessment using other models of pollen dispersal and deposition (see 5.5 below). Technological advances in remote sensing technologies, such as the development of LiDAR (including ground-based systems such as portable canopy LiDAR) to record high-resolution canopy and sub-canopy layers, and availability of unmanned aerial vehicles (UAV) to take targeted aerial photography linked with ground truthied points and detect the occurrence of flowering at canopy, potentially make this a less time-consuming task than in 2007.

c) extending the survey of canopy using a lower-intensity recording approach such as the Crackles Project Methodology zone B to at least 50m around the pollen trap, and

d) recording an empirical estimate of the upper canopy composition of all the main mapped units in the woodland (compartments not sampled for pollen, larger rides and glades, any distinct marginal communities) to improve the data available for ring extraction. This would permit ring data extraction beyond 100m, which would allow inclusion of the full RSAP, an important means of improving the utility of ERV-analysis in such datasets and therefore particularly important when only pollen percentage data are available, that is, when pollen traps are in the form of mosses or sediments rather than Tauber traps.

5.5 Models of pollen dispersal and deposition

The vegetation distance weighting algorithm used in this paper was originally designed on the assumption that above-canopy aerial transport is the only mode of pollen delivery from plant to sampling point, and includes atmospheric parameters such as turbulence and wind speed which are chosen for that transport context. However, several other modes of pollen transport are also expected to affect the assemblages forming in Tauber traps; trunk space aerial dispersal (where wind speed is lower and other atmospheric conditions may also differ), gravitic dispersal from overhanging plants (since the trap arrays were not placed in large canopy openings) and insect-borne dispersal. Incorporating these elements into a future model requires two components, first the identification of a suitable mathematical expression for the transport process and secondly determining how to combine the different processes. The latter will include some means of determining the relative importance of each process and confirming whether taxon specific parameters can be transferred between models (e.g. should fall speed in trunk space and gravitic components allow for the greater incidence of duads and larger clumps of grains dispersing through these processes?). Additional factors to be considered might include the variable distribution of flowering locations between tree species (some flower mostly at the top of the canopy, others throughout the tree) and the effects of leaf emergence on the trunk space air flow and probability of removal of grains through physical interception rather than deposition to the ground surface.

Whilst it would be relatively simple in theory to create additive models extending equation (1), taking the form given in equation 3 below, careful empirical testing would be needed before such an approach could be formally adopted.

$$y_{ik} = \alpha_i(\psi_{ik} + \phi_{ik} + \chi_{ik}) + \omega_i \qquad \text{Equation 3}$$

Where y_{ik} = pollen influx from type i at site k, ψ_{ik} = the distance-weighted plant abundance of taxon i around site k using an above-canopy pollen dispersal model derived weighting term, ϕ_{ik} = the distance-weighted plant abundance of taxon i around site k using a trunk-space pollen dispersal model derived weighting term, χ_{ik} = the distance-weighted plant abundance of taxon i around site k using a gravity-dominated pollen dispersal model derived weighting term, and α_i and ω_i are constants, the pollen productivity and background pollen component of taxon i in the studied region respectively.

These physical processes are not the only mode of pollen transport. Zoophilous transport is much harder to model, and is expected to have different effects on assemblages forming in traps with open water present (e.g. Tauber traps or ponds) than terrestrial samples such as moss polsters, since open water may actively attract animal vectors in comparatively dry habitats.

5.6 Reconstruction methods

The complex, multi-layered vegetation of managed cultural landscapes such as coppiced woodlands, and the relatively small scale recording properties of Tauber traps and small ponds present considerable challenges to pollen-based quantitative reconstruction approaches. Recent advances in reconstruction approaches at the regional scale (considering vegetation composition in areas with radii 50-100km) show the potential of these methods (Marquer, et al. 2014, Trondman, et al. 2015), but by averaging a large number of small sites or using large (500ha plus) area sedimentary basins the pollen signals considered contain very little of the local vegetation component. Handling the local details recorded by small sedimentary basins is still challenging; the assumption of a single dominant taphonomic relationship between pollen and vegetation underlying the approaches is clearly more problematic as the size of the basin used decreases. Given these concerns, we expected poor results from applying reconstruction approaches to the pond pollen assemblages available, but since such reconstruction is the long-term purpose of this research programme, the results are presented here as an indication of the work yet to do.

Figure 8 shows that no single reconstruction approach performed equally well at the three ponds, and at one of the three ponds the uncorrected pollen proportions were most similar to % dwpa(100), rather than any of the reconstruction methods. Processes likely to be influencing these results include:

- differences in taphonomy between ponds and Tauber traps
- the influence of pond-margin vegetation (e.g. the presence of a single stool of *Alnus glutinosa* at “Alder Pond” in Chalkney Wood)

- the possible influence of greater flowering associated with the increase in light availability along rides and at the woodland edge, and changes in air flow associated with the interruptions in the vegetation canopy at those locations (e.g. “Bradfield Pond” and “Vegetation Pond” both include woodland edges and rides within their estimated RSAP, since pond location is not determined by suitability for pollen work)
- lack of knowledge of the flowering behaviour of coppice stools of some of the tree species present. Our data as suggests that, as with *Tilia cordata* (Waller, et al. 2012), both *Castanea sativa* and *Carpinus betulus* experience suppression of flowering for multiple years after coppicing. This may also be the case for other trees frequently managed in the past such as *Fagus sylvatica*.

Simulation approaches, allowing comparison of pollen signals generated both by woods of different composition and by woods subject to different regimes of coppice management, may offer a better way forward than production of a single numerical representation via quantitative reconstruction. The approach demonstrated by Waller et al. (2012), where a taxon’s estimated RPP was weighted by the coppicing stage to model the variation in flowering within the managed woodland, seems justified by the findings presented here.

The key finding of the reconstruction section of the paper is that we are not yet in a position to apply reconstruction to individual small sites, but we do have usable tools for using simulations to explore possibilities and predict patterns. The prospects for quantitative reconstruction of past vegetation from pollen records from small sites in complex cultural landscapes are not entirely gloomy – there is clearly a vegetation signal in the pollen datasets obtained (see Figure 7 and appendix 2) - but we are still some way from understanding that signal well enough to reconstruct past vegetation composition and management from pollen records.

6. Conclusions and recommendations for future research

This study demonstrates that palaeoecologists are not yet in a position to effectively reconstruct vegetation around individual small sites in managed woodlands, and outline the tools needed and approaches to obtaining them. There is a signal in the pollen data from small sub-canopy traps which reflects the local vegetation, but that the models developed in larger basins are not sufficient to capture its main features. The effects of manipulation of different landscape elements through management, such as the creation of different aged blocks of regrowth within a coppiced woodland, create variations in the pollen production which are averaged out in sites with large RSAPs. For small sites, these variations probably need to be explicitly identified and incorporated in reconstruction approaches, and reconstructions which are probabilistic and multi-scenario are more realistic than achieving robust single quantifications of past vegetation.

In this paper, we show that linear regression of pollen influx from Tauber traps against distance weighted plant abundance generates $\mathrm{RPP}_{Quercus}$ values for eight tree taxa which are comparable with previous European studies (e.g. Sugita, et al. 1999; Mazier, et al. 2012), whilst ERV analysis results were unreliable. For Tauber trap data with limited numbers of years available, we conclude that the linear regression of influx against dwpa(z=estimated RSAP) is a more effective method of estimating RPPs than ERV analysis and, where vegetation data can be collected for multiple traps in the same region, can contribute substantially to the growing database of RPP values used for reconstruction studies (e.g. Broström, et al. 2008; Mazier, et al. 2012). This could be of particular use in locations where natural pollen traps such as moss polsters and small ponds are not readily available, such as semi-arid Mediterranean and grassland communities.

Incorporating the differences in flowering with coppice stage for the three taxa studied by Waller et al. (2012), *Corylus avellana*, *Alnus glutinosa* and *Tilia cordata*, improved the relationship between vegetation and pollen signal. An important next step towards the reconstruction of coppiced woodlands is to determine the effects of coppicing on flowering in other important taxa such as *Betula, Castanea* and *Carpinus*, and to extend investigation to other types of management such as pollarding, shredding and layering. Similar effects are likely to affect the dominant taxa of other habitats subjected to management, such as grazed grassland (Baker, 2012) or moorland subject to grazing and burning and also merit empirical study. The length of time each species takes to reach first flowering when growing as a new tree may provide a useful indication of the likely flowering response (i.e. enhancement or suppression of pollen production) in response to coppicing. The palynological visibility of some taxa (e.g. *Tilia*) can be changed substantially by widespread management, and this has the potential to transform our understanding of Holocene biogeography.

The complexity of pollen-vegetation relationships recorded by Tauber trap for some taxa, such as *Fraxinus excelsior* (see Figure 3), clearly does not conform to the assumption of a single dominant pollen dispersal and deposition mechanism which underlies most model-based reconstruction approaches. Other taphonomic models can be proposed and tested using empirical approaches, and are probably needed to achieve robust reconstruction of past vegetation from small sites.

The findings presented here show that applying quantitative reconstruction methods based on the assumption that above-canopy pollen transport is the dominant taphonomic mode to individual small sites in the coppiced woodlands studied here (and likely in other complex cultural landscapes) is not currently a useful activity. Validation of methods using statistical comparisons of surveyed and reconstructed vegetation data offers a useful check on the effectiveness of reconstruction strategies, and could be used more widely, especially for sites where the underlying assumptions are only weakly met such as small canopy openings or non-circular lakes and ponds. At present, there are too many gaps in our understanding of the effects of management on pollen production of key taxa and of the pollen taphonomy in sub-canopy settings, especially for taxa with complex flowering and pollination strategies such as *Fraxinus excelsior*. This project has taken bold steps in attempting to resolve some of these knowledge gaps and has helped to identify methodological considerations that could be adopted in future studies to test and shed light on understanding pollen-vegetation relationships within such complex managed landscapes. Given the interaction of factors creating the pollen signal in such systems, we also argue that a probabilistic, multiple scenario type reconstruction approach is likely to be more meaningful and appropriate in these systems than single quantitative representations of past vegetation.

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Glossary

PAR: Pollen Accumulation Rate

RPP: Relative Pollen Productivity

RSAP: Relevant Source Area of Pollen

TLP: Total Land Pollen

TSSA: Taxon Specific Source Areas

UAV: Unmanned aerial vehicle

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List of Figures

Figure 1: Location map showing a) location of study woods within southern Britain, b) compartment map of Chalkney Wood and c) compartment map of Bradfield Woods.

Figure 2a: The Prentice-Sutton pollen dispersal and deposition model. The double basal line defines the sampled sedimentary deposit, with the solid dot representing the sample point. The solid line abutting it denotes the vegetated land surface. The grey box shows a single pollen-producing unit, and the upwards arrow shows pollen release. The narrow line shows the movement of air (and pollen) above the vegetation canopy, and the downward arrows show deposition from that air stream. The graph below shows the proportion of pollen from the grey source deposited at each point across the landscape through gravitic settling from the moving air.

Figure 2b: schematic representation of a small hollow (double line, with solid circle indicating pollen sample point) with some overhanging vegetation in a coppiced woodland. Pale grey points on trees indicate a concentration of flowering structures in parts of the main canopy exposed to most light. The pale grey lines above the vegetation represent the above-canopy air flow, which is assumed to be the dominant mode of pollen transport by the Prentice-Sugita model (see text for details). Spirals indicate turbulent eddies in the air flow, generated by the roughness of the vegetation surface over which it passes. On the left of the sample point, the compartment is in a relatively early stage after felling, with coppice stools shorter than standards; the canopy is rough, and turbulent air can penetrate easily into the trunk-space, creating a complex flow for pollen transport. The blue line denotes the position of the canopy. To the right of the sample point, the compartment is quite late in the coppice cycle, regrowths are forming a continuous canopy with the standards, and the pollen transporting air stream is largely kept above the canopy.

Figure 3: pollen influx against dwpa to 100m: left: *Fraxinus*, right: *Quercus*. Open circles show samples from Bradfield Woods, closed circles from Chalkney Woods. The solid oval outlines data points which seem to conform to a linear model with a positive relationship with distance and low slope angle, as predicted by the simple aerial transport model outlined in the text. The dashed oval outlines points where abundant plants are associated with minimal low pollen influx. The dotted oval on the *Fraxinus excelsior* plot outlines data points which show a wide range of pollen influx values for locations where the tree is relatively uncommon

Figure 4: Pearson Product Moment Correlation Coefficients between pollen influx and cumulated dwpa at increasing distances around the pollen traps. All values except *Acer* at dwpa(10) are statistically significant at the 0.01 level (two-tailed).

Figure 5: comparing the $RPP_{Quercus}$ values for the eight tree taxa for this study with published estimates derived from ERV methods, recalculated to $RPP_{Quercus}$ where necessary.

Figure 6: likelihood function scores for ERV analysis of the eight tree taxa, as described in the text. Solid lines show ERV model 1 runs and dashed lines show ERV model 2 runs. Results shown for three iterations of each model, showing that the results of runs similar but not identical (see text).

Figure 7: graphical comparison of proportions of the 8 tree taxa in terms of %dwpa(100) around pond centres (black bars) and pollen proportions in 2007 samples (grey bars) (see text for details). The white bars on the Vegetation Pond plot show %dwpa(100) with all *Tilia* stools in the survey area assumed to be non-pollen producing (see text for details).

Figure 8: Bray-Curtis Indices from a comparison of vegetation reconstruction against measured % dwpa to 100m radius around the pond centre for the eight tree taxa studied in this paper. The

horizontal bar denotes the value for a simple comparison of pollen proportion and dwpa proportion with no reconstruction, and other symbols show the results for different reconstruction methods (see text for details).

Table 1: summary of pollen productivity values relative to *Quercus* estimated using various methods. For comparison, means for Europe (using method PPE.st2 Mazier et al. 2012) and from Southern Sweden (Sugita et al. 1999) are also given. These results were presented in the publications as $\mathrm{RPP}_{\mathrm{Poaceae}}$ but are converted to $\mathrm{RPP}_{\mathrm{Quercus}}$ for ease of comparison. Standard errors for the new values were calculated using propagation of errors formulae.

Appendix 1: Distance weighting of plant abundance

For the distance-weighting model, vegetation data needed to be converted into the form of percentage canopy cover of taxa within 10m wide rings centred on each of the pollen traps. This was achieved via the following steps (see figure A1.1):

[INSERT FIGURE A1.1 HERE]

1) Canopy cover was estimated from the diameter at breast height for all trees and shrubs with trunks within 20m of each survey centre point using relationships given in Savill (1991).
2) Canopy cover was summed for each of two concentric rings, 0-10m and 10.1-20m, assuming that the canopy of a tree fell entirely within the ring where the trunk was positioned. This value was generally much less than 100%, since standards are dispersed amongst the coppice stools.
3) Coppice stools were assumed to form the canopy in every other part of the ring (in the early stages of regrowth, this will not be accurate, but information was not collected on the rate with which stools formed closed cover). The species composition for the coppice component was estimated from the proportion of stools of each type recorded within the 0-10m ring (where all coppice stools were recorded at all sites).
4) Pre flowering age stools of *Corylus avellana* (younger than 2 years), *Alnus glutinosa* (those younger than 7 years) and *Tilia cordata* (those younger than 11 years) were treated as non-pollen-producing surfaces.
5) Data for canopy vegetation in rings beyond 20m radius around each trap were extracted from the compartment maps using HUMPOL software (R. Middleton unpublished). Figure A1.2 shows an example. The vegetation composition of each compartment was defined as the mean of the composition of the surveyed area or, where traps were not present and

therefore survey data not available but the 100m ring around a pollen trap included that compartment, by assuming that the composition was the same as that in the nearest recorded plot which had been cut within 3 years of the felling date for the unrecorded compartment.

[INSERT FIGURE A1.2 HERE]

The vegetation data for each ring were then distance-weighted using the taxon-specific Sutton distance-weighting term (Sutton 1953; Prentice 1985; Sugita 1993) for stable atmospheric conditions (but see Jackson & Lyford 1999):

$$g_i(z) = b_i \gamma z^{\gamma-1} e^{-b_i z^{\gamma}} \qquad \text{(equation A1.1)}$$

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

$$b_i = 75.2 \frac{v_{si}}{u} \qquad \text{(equation A1.2)}$$

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 speeds are taken from Sugita et al. 1999 or 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).

Cumulative distance-weighted plant abundance from the trap was then calculated for each ring, and used as input to the data analysis methods described below.

Figure captions

Figure A1.1. Schematic of the survey area around a single trap. The long dashed lines mark circles at radius 10m and 20m around the trap. The central black dot shows the location of the pollen trap. Hatched circles show the position and size (at breast height) of trunks of trees and saplings. Coppice stool positions are marked with ‘x’. Grey circles around the hatched circles show the estimated canopy cover (calculated using equations from Savill 1991) of each tree.

Figure A1.2: schematic of method for extracting ring canopy data for the area 20m-100m around each trap. The lettered areas are compartments cut at different points in time, with date of last felling shown in brackets. The red crosses show the location of pollen traps and the centre of the 20m radius surveys carried out at each site, which are shaded darker grey. These are surrounded by concentric 10m width rings out to 100m. Compartment composition is determined as described above: for compartment G, for example, the ring sequence overlaps into compartments H and I. Compartment G composition beyond 20m is estimated by the area-weighted mean of the inner survey area, and compartments H and I are assumed to have the same composition as compartment F (the nearest compartment with data felled within ±3 years).

APPENDIX 2: scatter plots of pollen influx (grains cm^{-2} $year^{-1}$) against dwpa(100) for all tree taxa considered. Note that axis scales vary between graphs.

[INSERT FIGURE A2.1 HERE]

Appendix 3: Reconstruction methods used

1. Influx-based regression equations to reconstruct dwpa (taxa are independent)

This approach estimates vegetation in terms of dwpa from the pollen influx by inverting the linear regression equation used to estimate RPP_{ref} and background pollen influx using the equation:

$$\widehat{\chi_\iota} = \frac{c_i - \omega_i}{\alpha} \qquad \text{(equation A3.1)}$$

Where χ_i is the dwpa of taxon i around the sample point of interest, c_i is the concentration of pollen of taxon i in the sample of interest, α_i is the pollen productivity of taxon i, and ω_i is the estimated background pollen contribution from taxon i.

2. Inverse ERV (percentages: taxa are not independent)

The Inverse Extended-R value approach inverts the ERV-model equations to reconstruct the vegetation composition from a given pollen assemblage (Prentice & Parsons 1983).

Model 2:

$$\hat{v}_{ik} = \frac{p_{ik}/\widehat{\alpha}_i}{\sum_{j=1}^{m} p_{ik}/\widehat{\alpha}_i} \left\{1 + \sum_{j=1}^{m} \left(\frac{\hat{z}_j}{\widehat{\alpha}_j}\right)\right\} - \left(\frac{\hat{z}_i}{\widehat{\alpha}_i}\right) \qquad \text{(Equation A3.2)}$$

Where i and j denote pollen taxa taken from a list of m taxa in total, k denotes the site of the pollen sample around which the vegetation is to be reconstructed, $\hat{v}_{ik}$ is the estimated vegetation proportion of taxon i around site k, p_{ik} is the proportion of taxon i recorded in the pollen assemblage at site k, $\hat{\alpha}_i$ is the estimated relative pollen productivity of taxon i and $\hat{z}_i$ is the estimated background pollen term for taxon i (defined for model 2 as ${}^{\omega_i}\!/_{x_{\cdot k}}$ where ω_i is the background pollen influx of taxon i, that is, the influx from the distance beyond the area surveyed or the source area, and $x_{\cdot k}$ is the absolute abundance of all m plant taxa around site k)

3. Modern analogue technique

Each trapped compartment is represented by the mean of the pollen assemblage from the 'screened' pollen trap data (described above), expressed as a percentage of the relevant base sum of the taxon list. Similarities are calculated using squared-chord distance (Lytle & Wahl 2004).

$$d = \sum_{i=1}^{m}\left(\sqrt{s_i} - \sqrt{t_i}\right)^2 \qquad \text{(equation A3.3)}$$

Where d = squared-chord distance, s_i is the proportion of taxon i in the possible analogue sample and t_i is the proportion of taxon i in the reconstruction target sample. There are m taxa in the datasets being compared.

4. Simple correction using RPPs

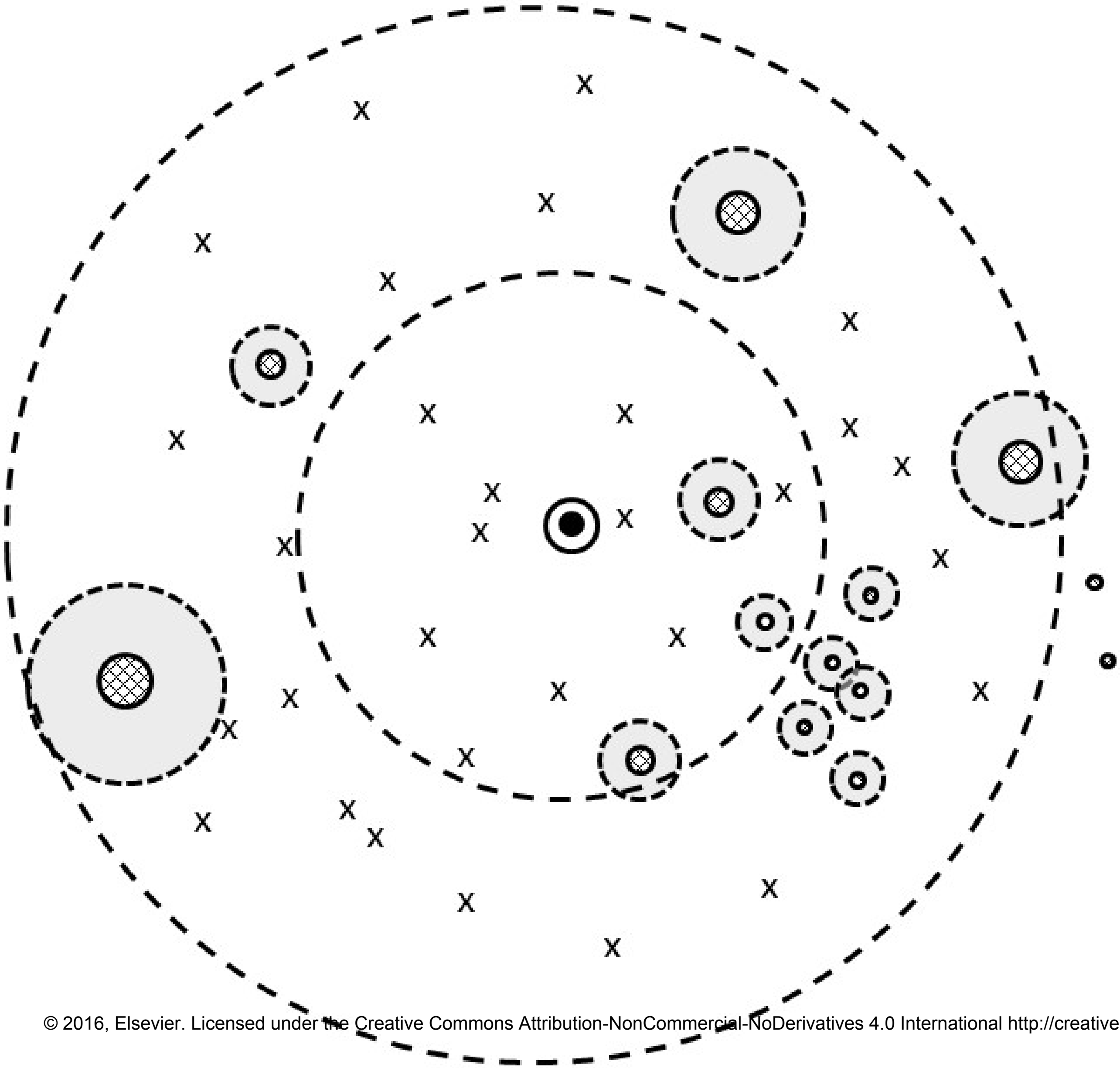
The simple correction approach follows Davis (1963) in assuming that the background pollen influx is negligible. Vegetation proportions are estimated using the following:

$$\widehat{v_i} = \frac{p_i}{r_i \sum_1^m (\frac{p_i}{r_i})} \qquad \text{(equation A3.4)}$$

Where p_i is the proportion of pollen of taxon i in the sample of interest, r_i is the $\mathrm{RPP}_{\mathrm{ref}}$ of taxon i, and there are m taxa in the sample of interest.

Table 1

	r^2 of linear regression model for dwpa(100)	$\mathrm{RPP}_{Quercus}$ regression method	$\mathrm{RPP}_{Quercus}$ (regr) rounded values for ‘simple reconstruction’	$\mathrm{RPP}_{Quercus}$ Mazier et al. (2012) PPE.st2	$\mathrm{RPP}_{Quercus}$ Sugita et al (1999) South Sweden	RPP_{Q} ERV model 1	RPP_{Q} ERV model 2
Acer	0.104	0.185±0.078	0.2	0.137±0.040	0.169±0.060	0.008	0.005
Alnus	0.295	0.377±0.111	0.4	1.556±0.044	0.558±0.019	0.119	0.668
Betula	0.348	0.793±0.226	0.8	0.530±0.048	1.178±0.018	0.036	1.930
Carpinus	0.487	0.857±0.226	0.9	0.609±0.075	0.336±0.009	278.3	5.353
Castanea	0.476	3.511±0.926	3.5	-	-	2261.4	15.910
Corylus	0.543	0.142±0.037	0.1	0.341±0.035	0.186±0.005	0.041	0.335
Quercus	0.216	1	1	1	1	1	1
Tilia	0.552	0.305±0.078	0.3	0.137±0.006	0.106±0.004	284.8	2.294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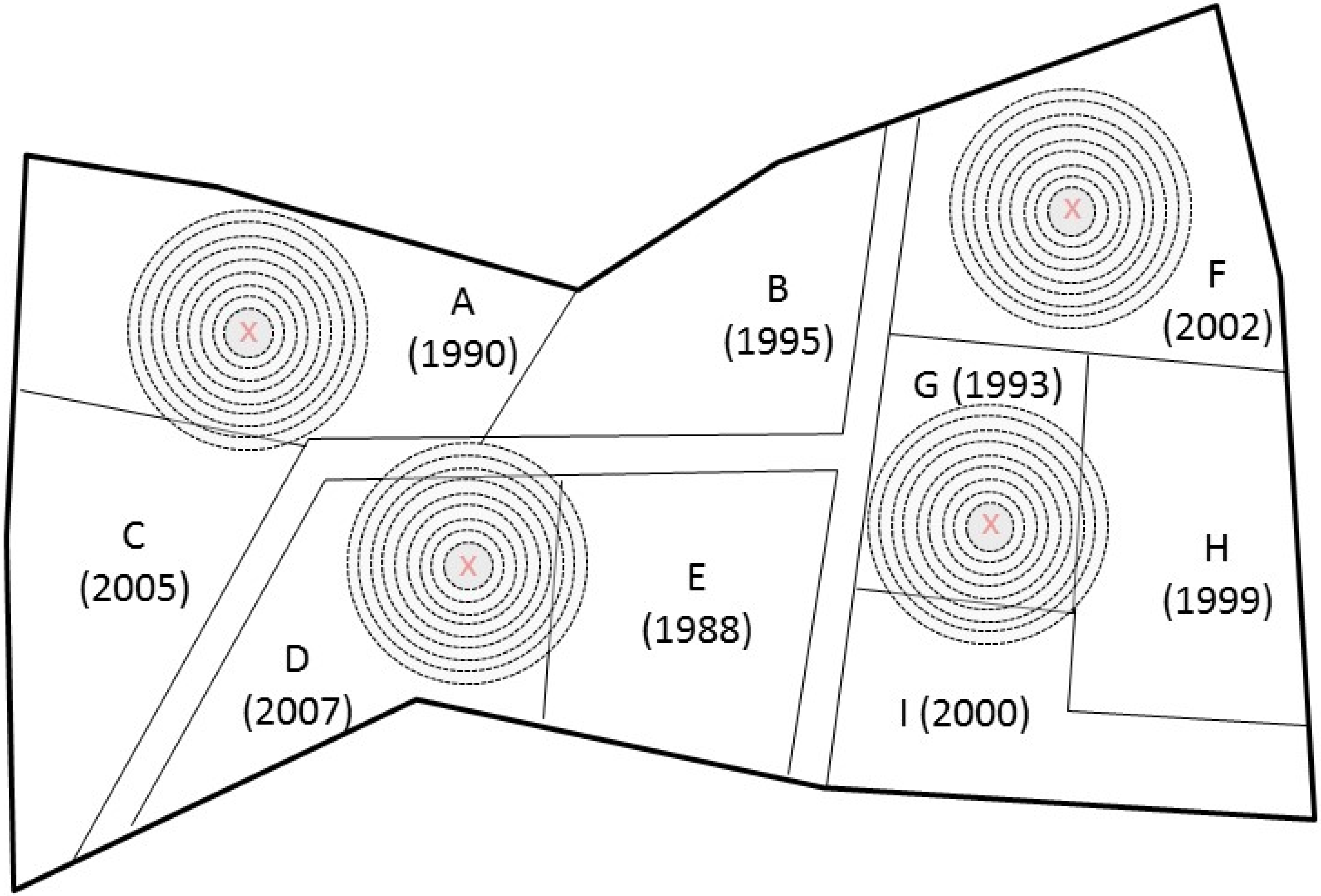
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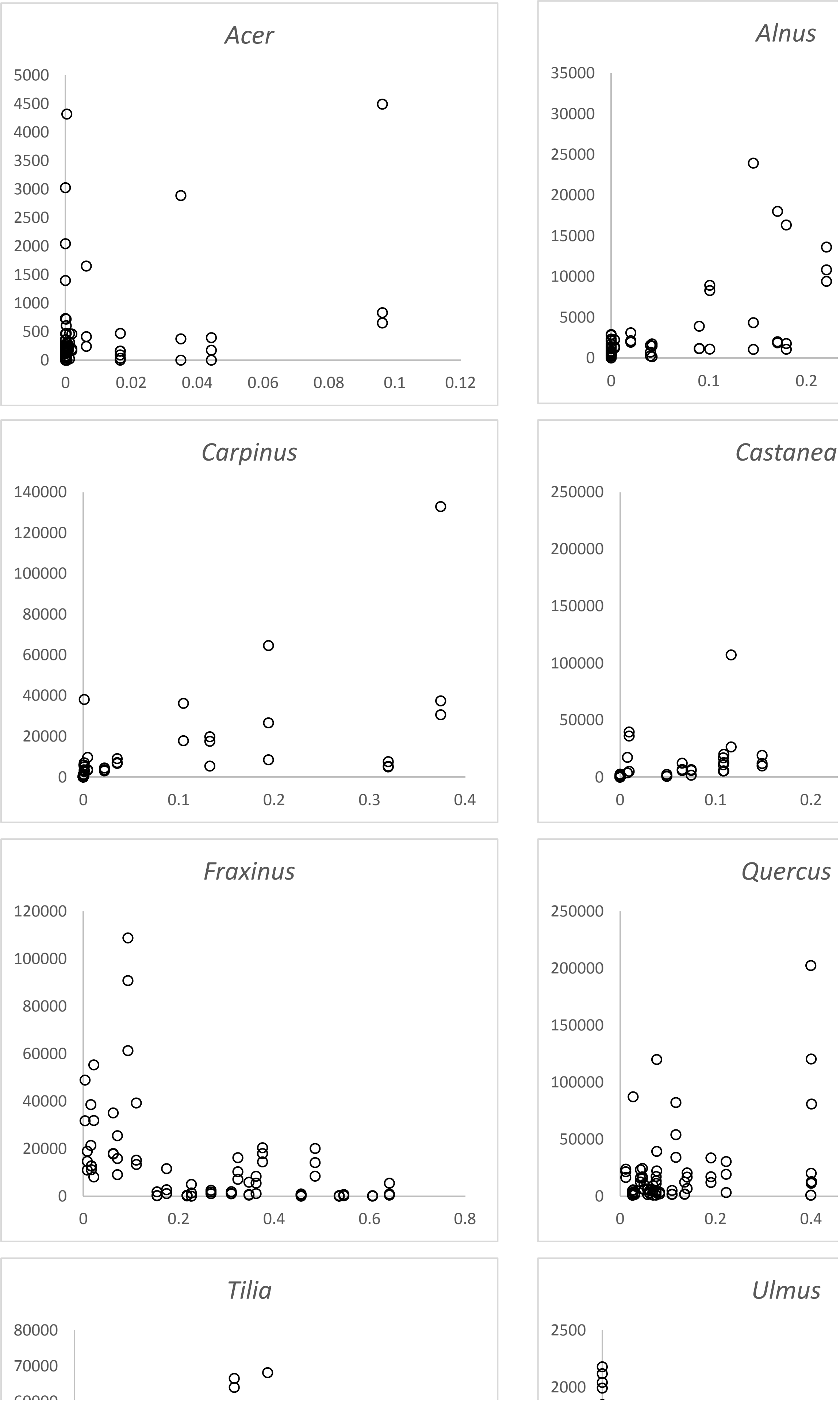
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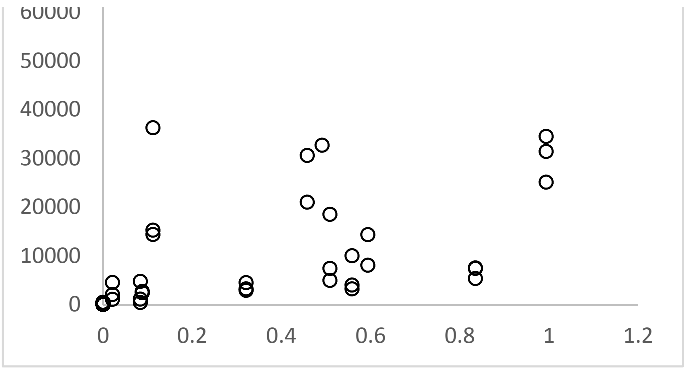
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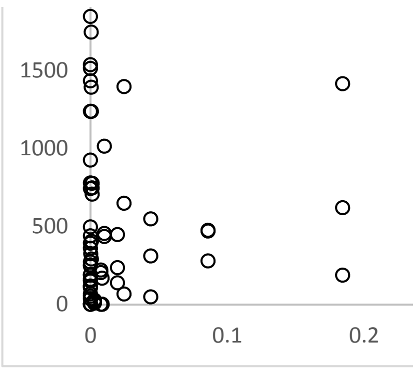
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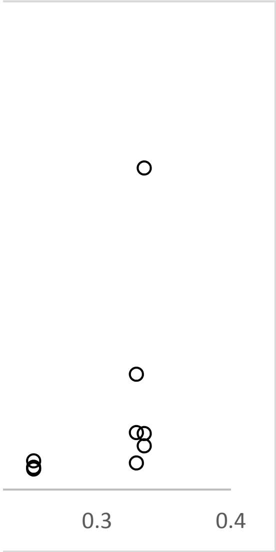
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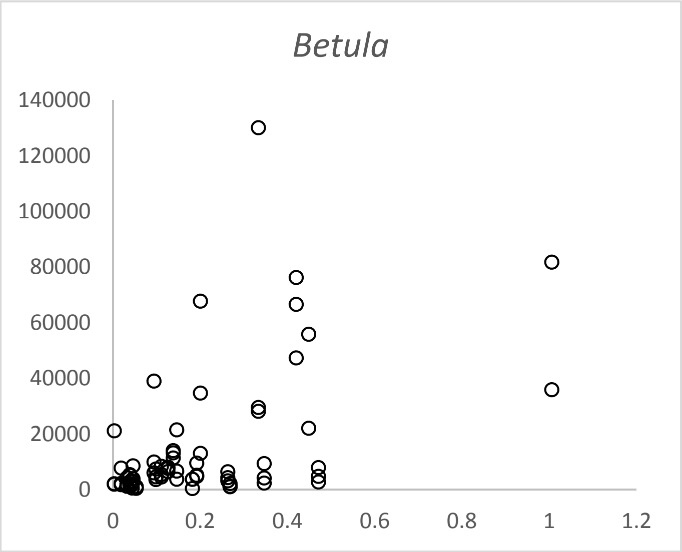
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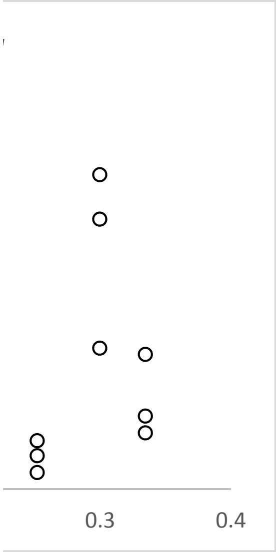
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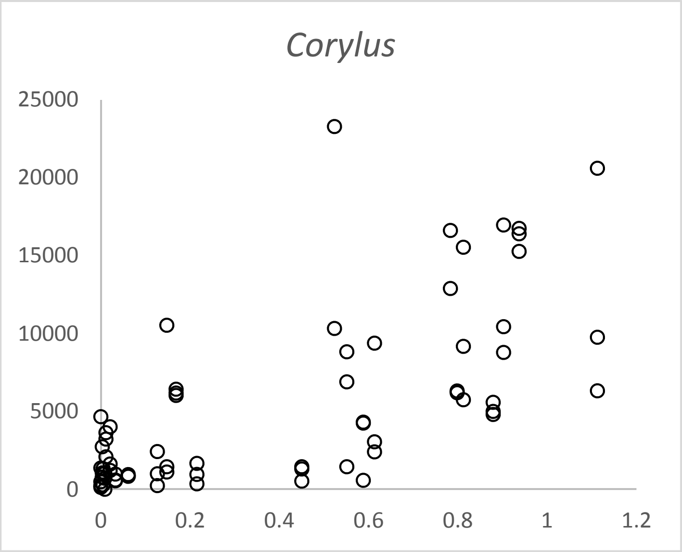
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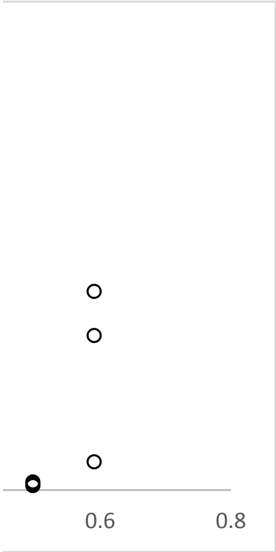
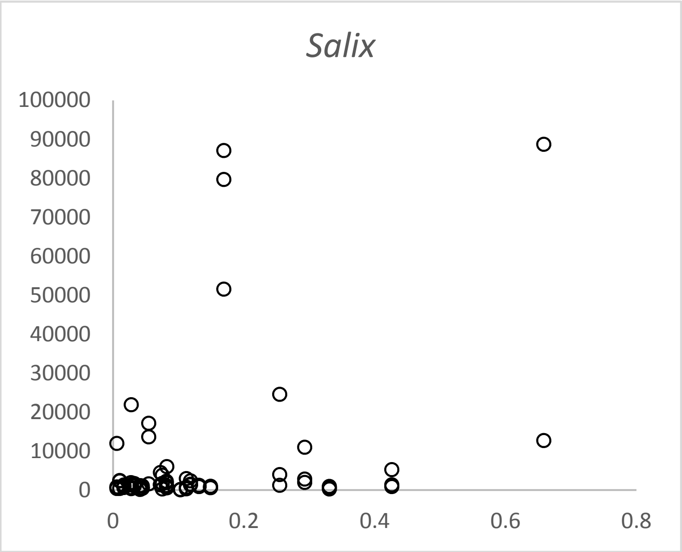
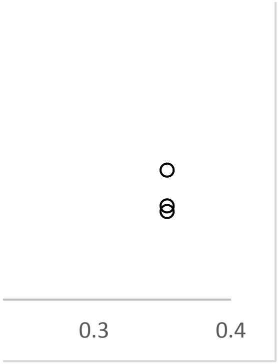
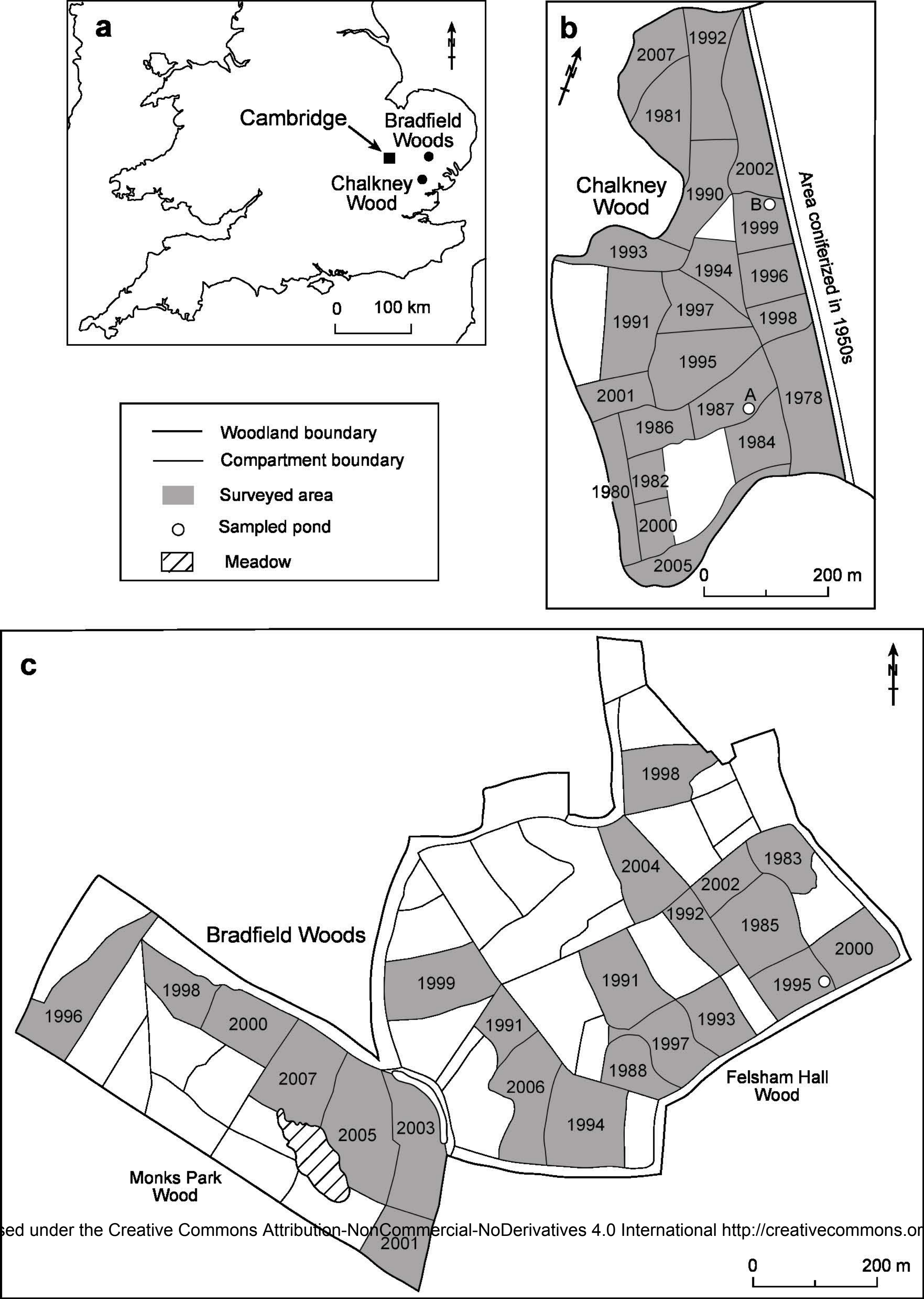
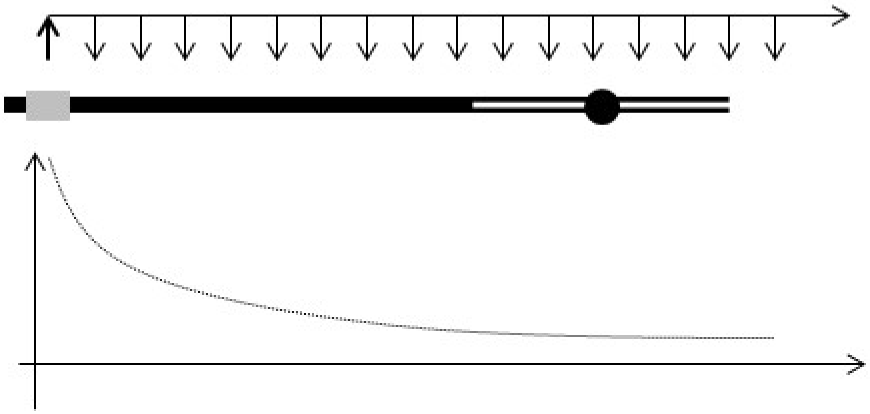
1
1.2

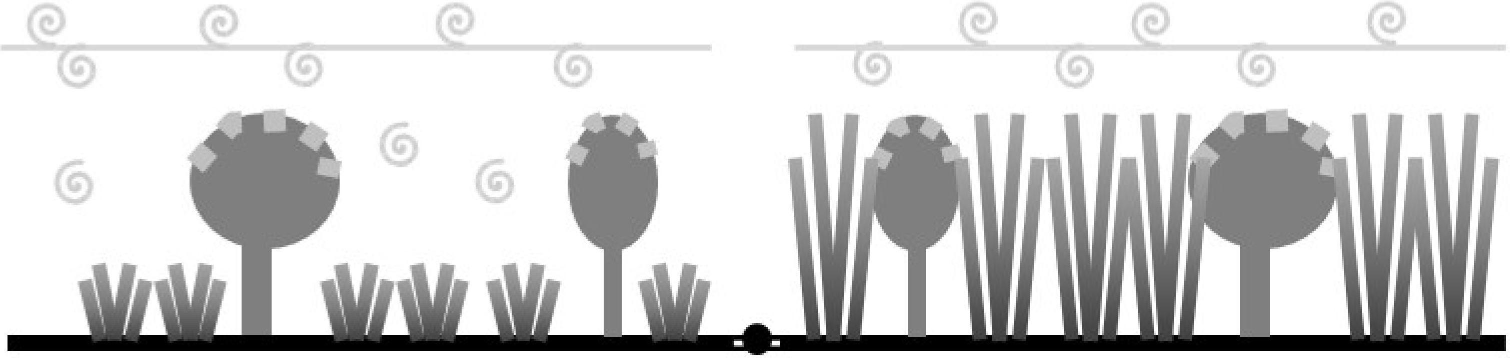

0.6
0.8

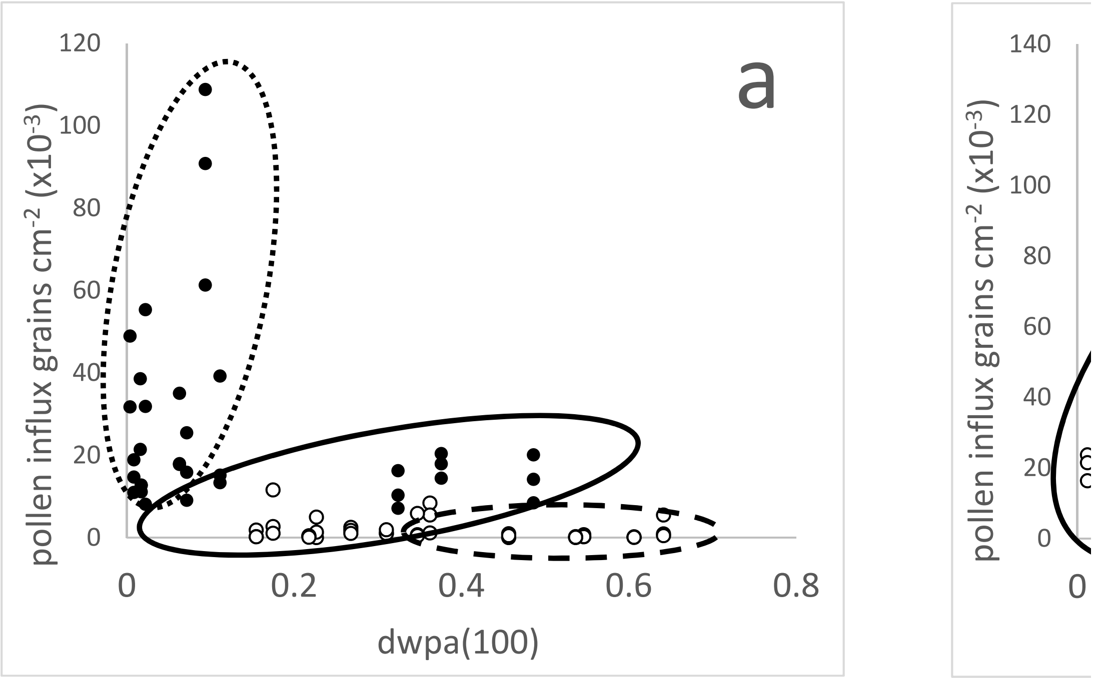

Salix
100000
90000
80000
70000
60000
50000
40000
30000
20000
10000
0
0
0.2
0.4
0.6
0.8

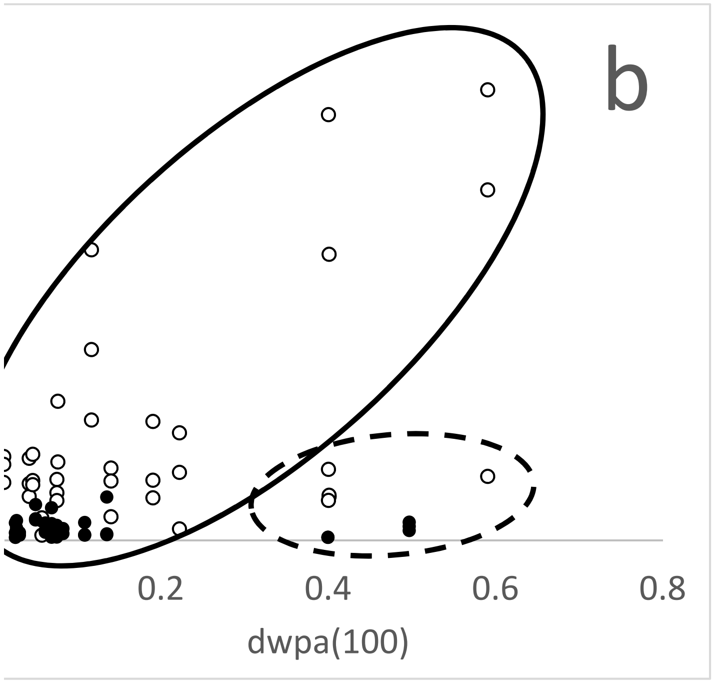

0.3
0.4

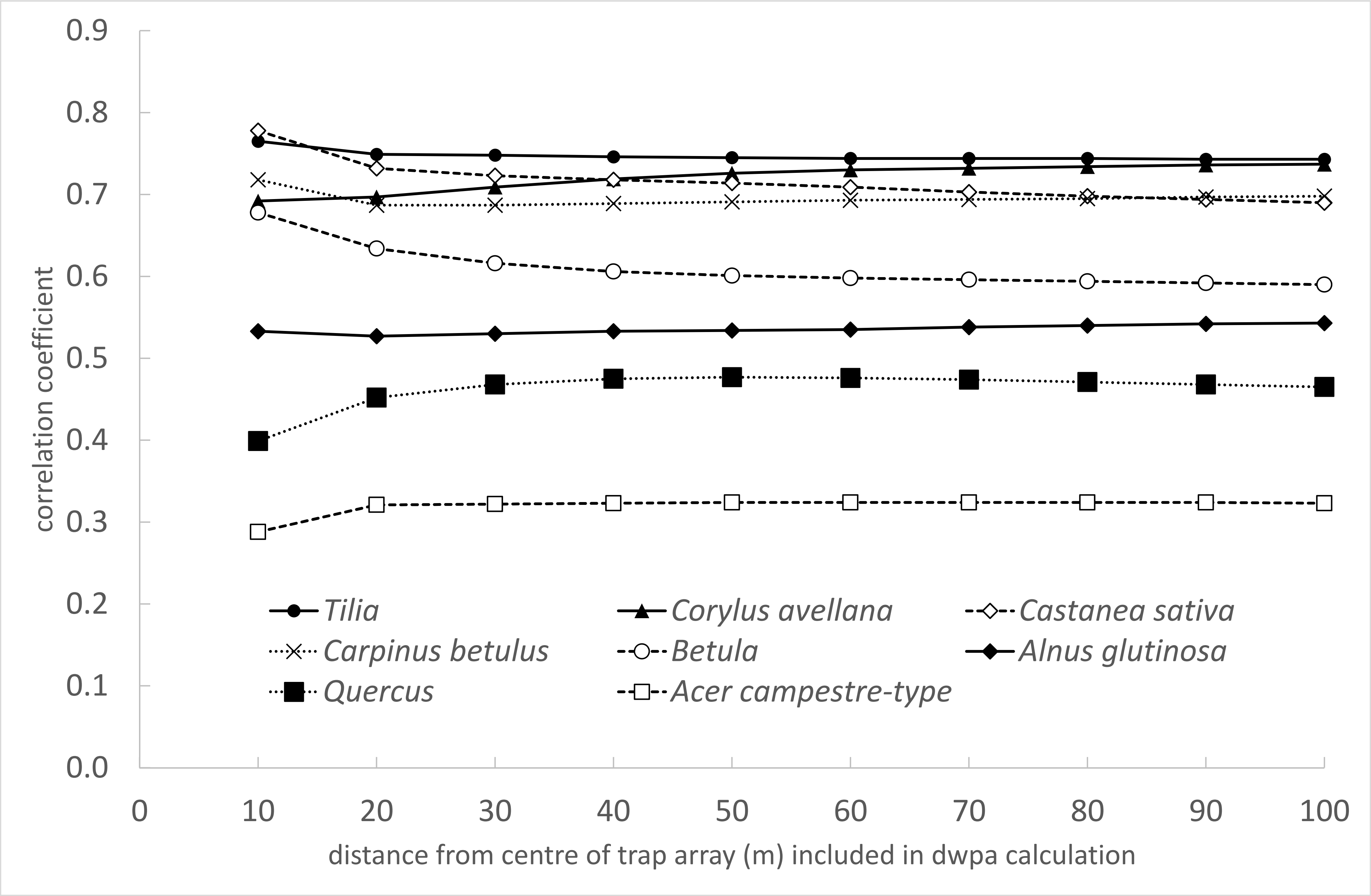

a
N
Cambridge
Bradfield Woods
Chalkney Wood
0
100 km
Woodland boundary
Compartment boundary
Surveyed area
Sampled pond
Meadow
b
N
2007
1992
1981
2002
Chalkney Wood
1990
B
1999
Area coniferized in 1950s
1993
1994
1996
1997
1991
1998
1995
2001
A
1987
1978
1986
1984
1980
1982
2000
2005
0
200 m
c
N
1998
2004
1983
2002
1992
1985
2000
Bradfield Woods
1999
1991
1995
1996
1998
2000
1991
1993
1997
2007
1988
Felsham Hall Wood
2006
1994
2005
2003
Monks Park Wood
2001
0
200 m

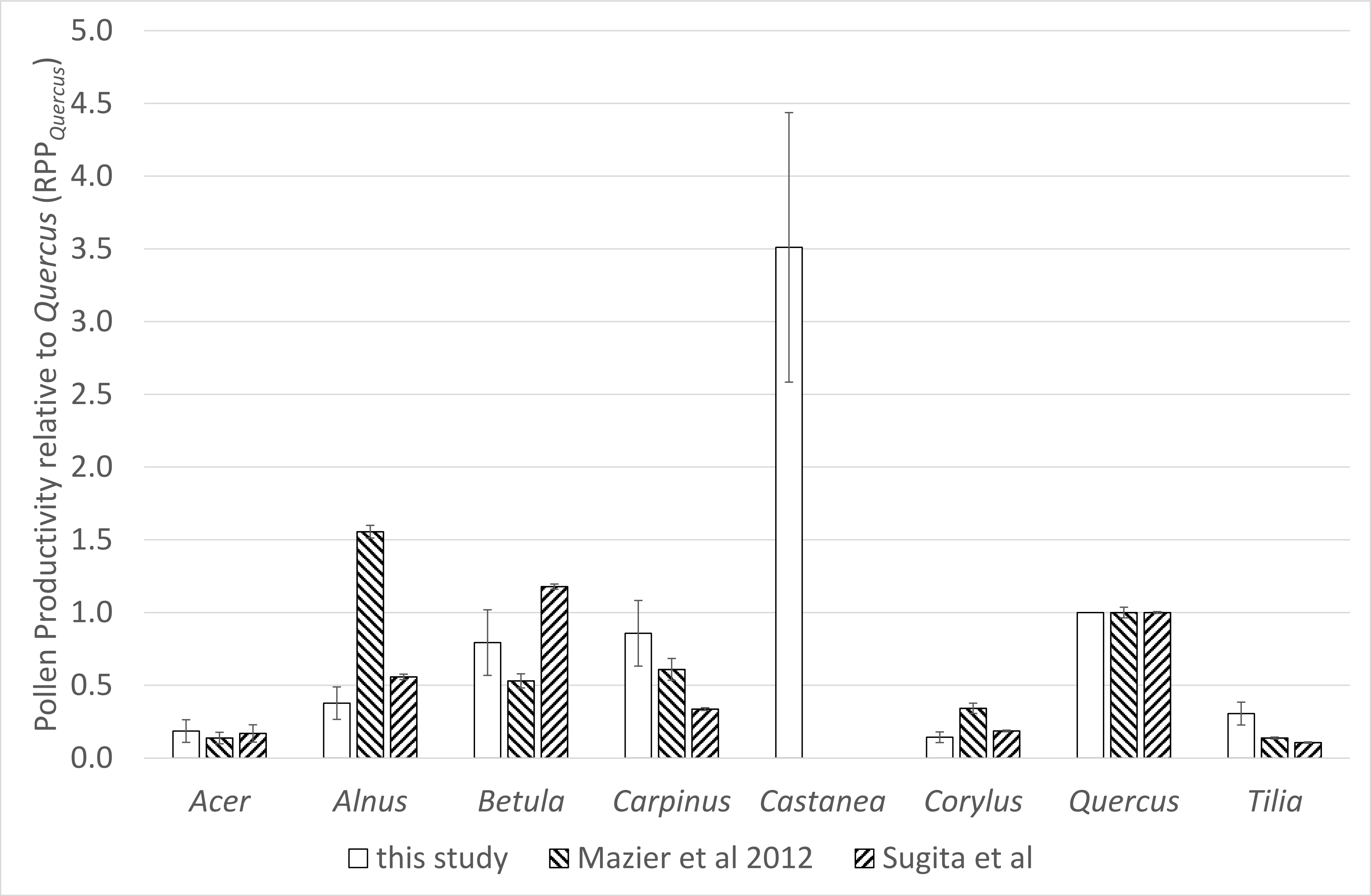


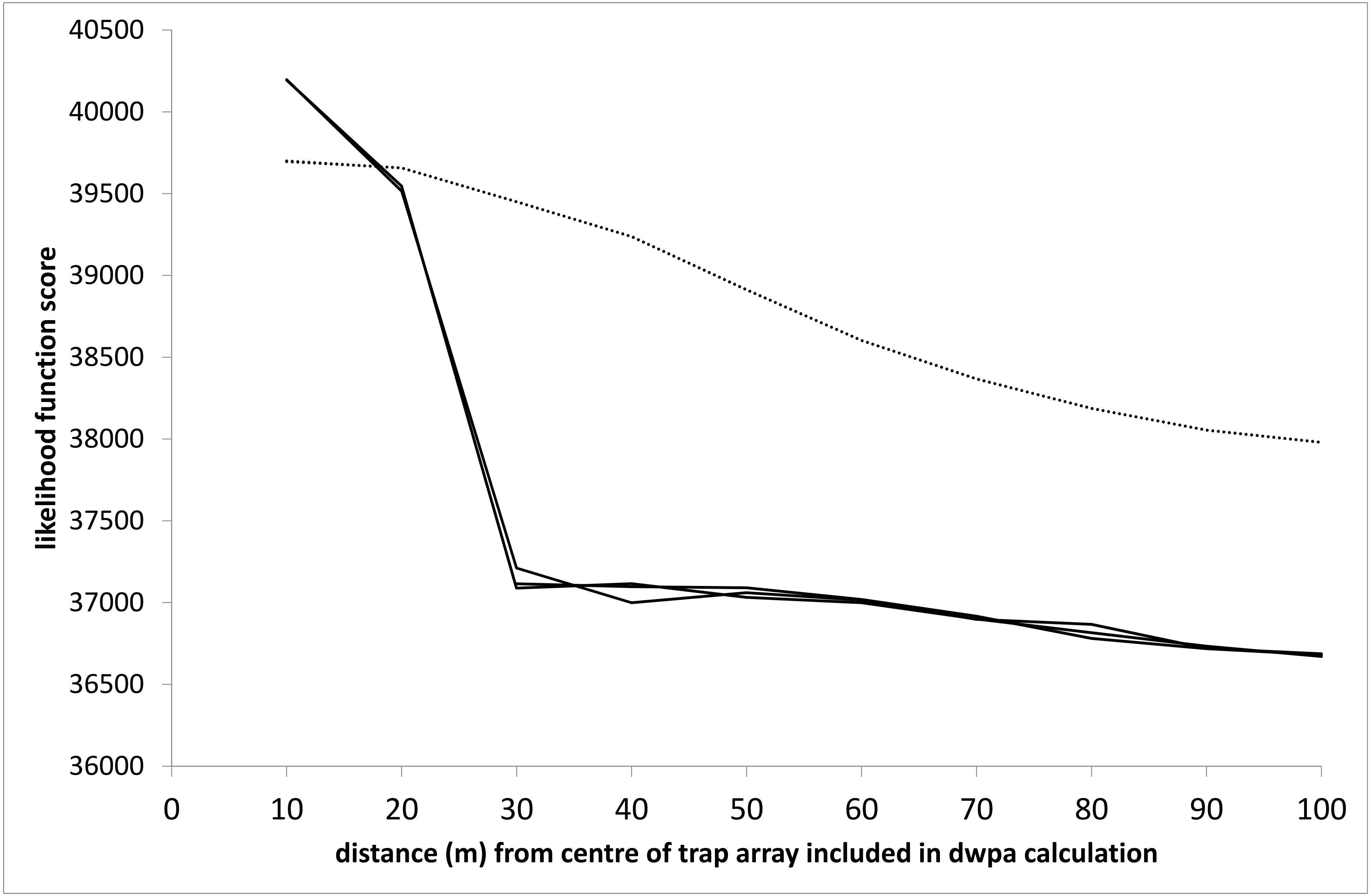


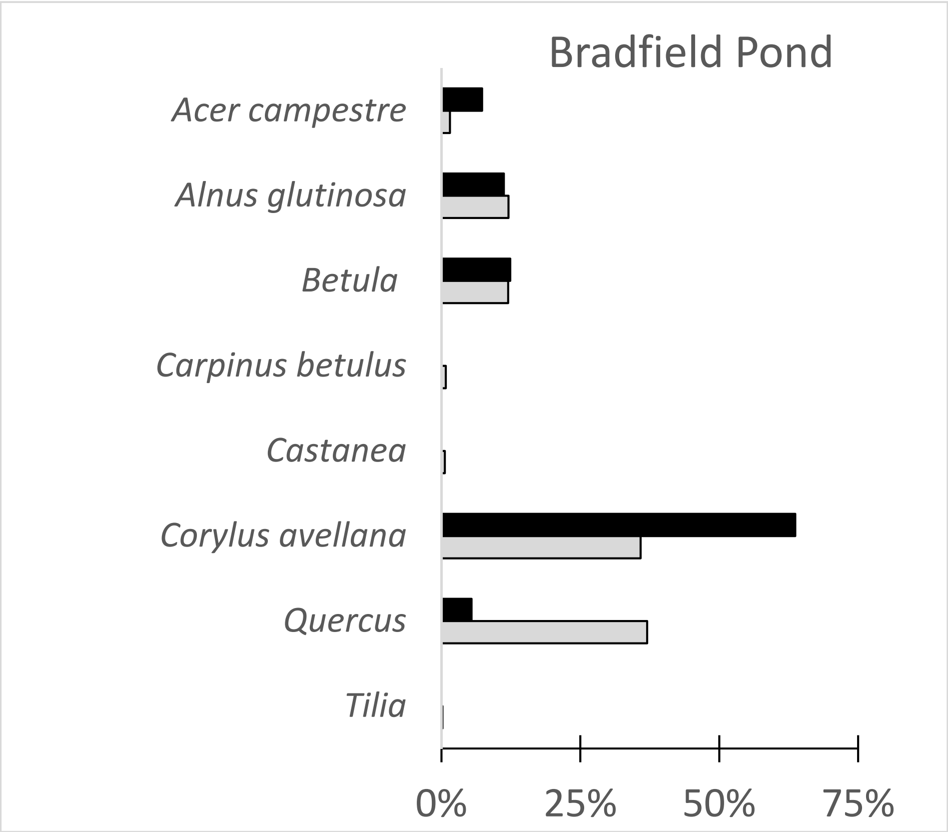

a
pollen influx grains cm^{-2} (x10^{-3})
120
100
80
60
40
20
0
0
0.2
0.4
0.6
0.8
dwpa(100)
pollen influx grains cm^{-2} (x10^{-3})
140
120
100
80
60
40
20
0
0

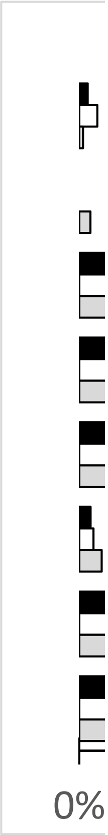

b
0.2
0.4
0.6
0.8
dwpa(100)

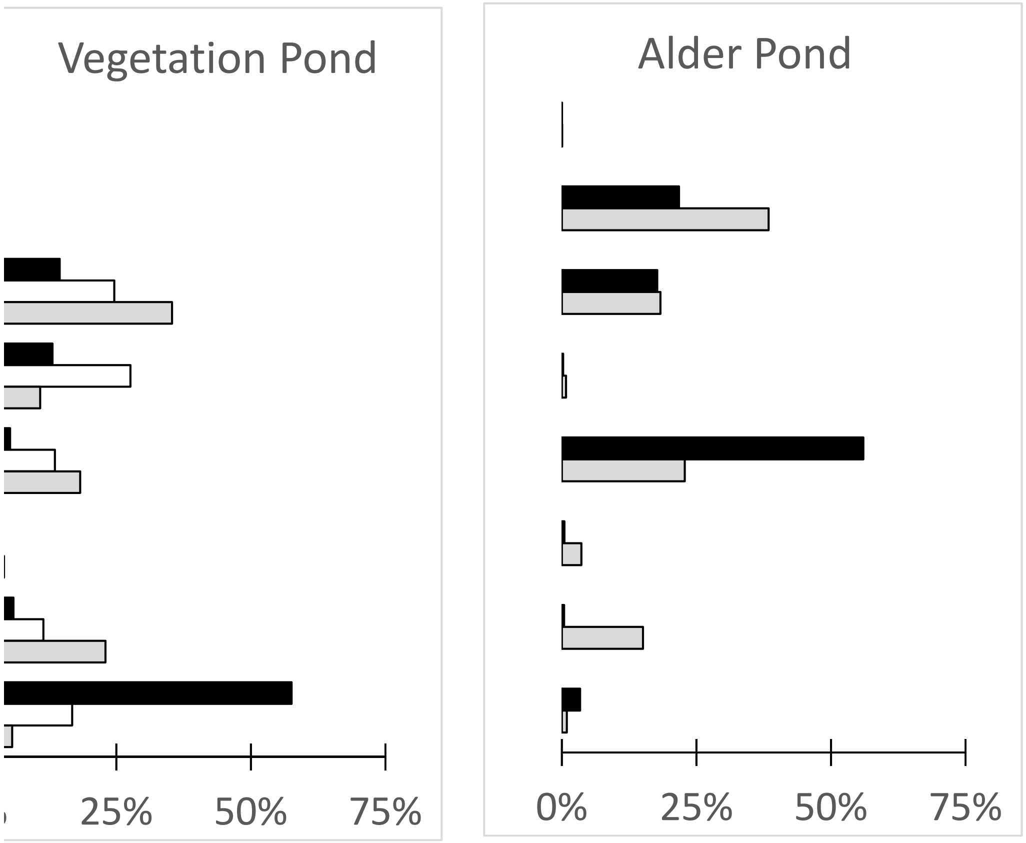

0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
correlation coefficient
0
10
20
30
40
50
60
70
80
90
100
distance from centre of trap array (m) included in dwpa calculation
Tilia
Corylus avellana
Castanea sativa
Carpinus betulus
Betula
Alnus glutinosa
Quercus
Acer campestre-type

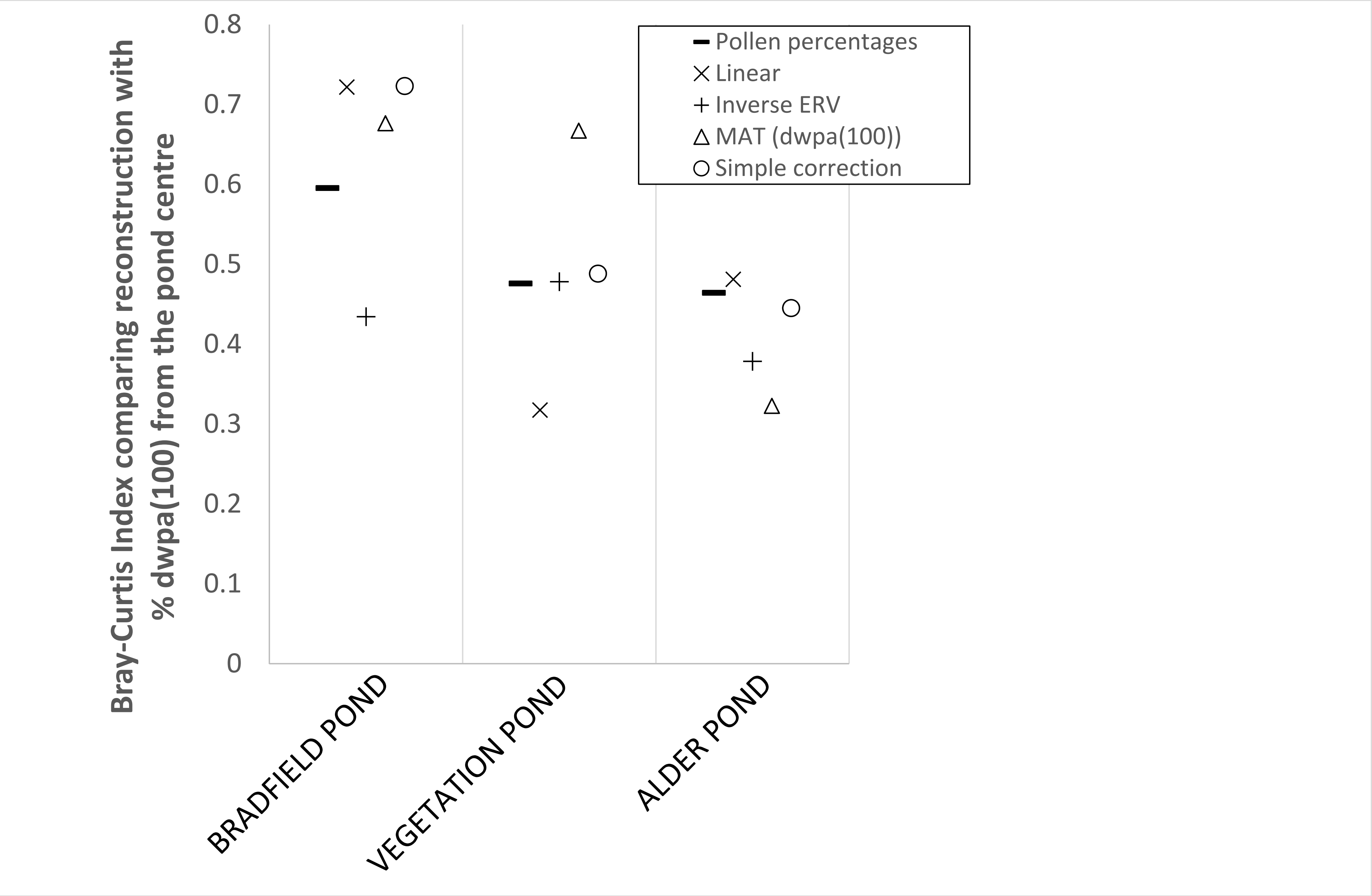

Pollen Productivity relative to *Quercus* (RPP$_{Quercus}$)
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Acer
Alnus
Betula
Carpinus
Castanea
Corylus
Quercus
Tilia
☐ this study
▧ Mazier et al 2012
▨ Sugita et al


40500
40000
39500
39000
38500
38000
37500
37000
36500
36000
likelihood function score
0
10
20
30
40
50
60
70
80
90
100
distance (m) from centre of trap array included in dwpa calculation


Bradfield Pond
Acer campestre
Alnus glutinosa
Betula
Carpinus betulus
Castanea
Corylus avellana
Quercus
Tilia
0%
25%
50%
75%


0%


Vegetation Pond
25%
50%
75%
Alder Pond
0%
25%
50%
75%


Bray-Curtis Index comparing reconstruction with % dwpa(100) from the pond centre
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
BRADFIELD POND
VEGETATION POND
ALDER POND
Pollen percentages
Linear
Inverse ERV
MAT (dwpa(100))
Simple correction