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**Webb, Julia C ORCID logoORCID: <https://orcid.org/0000-0002-1652-965X>, Bunting, M Jane and Farrell, Michelle (2026)  
Pollen in the courtroom: Enhancing forensic palynology with  
quantitative modelling. Forensic Sciences Research, 11 (2).  
doi:10.3788/tfsr20250012**

Official URL: <https://www.researching.cn/articles/OJfa49d2a95b493d60>  
DOI: <http://dx.doi.org/10.3788/tfsr20250012>  
EPrint URI: <https://eprints.glos.ac.uk/id/eprint/15916>

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# Pollen in the courtroom: enhancing forensic palynology with quantitative modelling

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## Abstract

Pollen grains are tiny and widely dispersed and can be recovered in large numbers from small samples of a variety of contexts from soils to human hair and clothing. Forensic palynology, the use of pollen assemblages recovered from samples associated with criminal investigations as a line of evidence, has been used since the 1950s, and largely uses the methods and interpretive frameworks developed by ecological and archaeological palynologists working mostly with samples taken from sediments accumulating in lakes or mires. In this paper, we explore whether recent methodological developments in those allied fields can contribute to improving the robustness and objectivity of assemblage interpretation in forensic palynology. We demonstrate that models of pollen dispersal and deposition can improve the interpretation of assemblages from some sample contexts and provide additional supporting evidence. We also propose an approach to incorporating quantitative estimates of post-depositional changes in assemblages into interpretations, since some forensic samples are taken from contexts which are not ideal for pollen preservation. Both methods are only appropriate for a subset of forensic palynological samples, and we present a workflow to identify suitable situations in which to apply these interpretive tools, if investigative budgets allow. We demonstrate the potential of these approaches and set out a research programme to both better define when these methods should be used and strengthen the underlying evidence base. Thoughtful incorporation of methodological developments in allied fields has the potential to improve interpretation of forensic palynology samples and strengthen the evidence presented as well as arguments made in court.

## Key Points

- Methods in ecological and archaeological palynology can improve the robustness and objectivity of forensic pollen analysis.
- Models of pollen dispersal and post-depositional changes can help enhance the accuracy of interpretations, particularly in challenging sample contexts.
- A proposed workflow and future research agenda aim to better define when these new methods should be applied to strengthen forensic palynology evidence.

**Keywords:** forensic sciences; pollen dispersal and deposition; pollen preservation; taphonomy; crime scene reconstruction; criminal investigation

## Introduction

Microscopic pollen grains (and spores) preserved in sediments have traditionally been used by palaeo-palynologists (palaeo = ancient; palynologist = expert in pollen analysis) to reconstruct past vegetation cover which can be interpreted in terms of former landscapes and environmental conditions [1–6]. However, the utility of palynology is not restricted to investigation of past environments. Forensic palynology, just like in palaeo-palynological studies, can be used to reveal a landscape (or botanical location) of interest. As such, it has been used as a law enforcement tool since the 1950s; its use was limited at first but increased through the latter part of the 20th century and into the 21st century [7–13]. Forensic palynology has been used in a range of cases extending from assault and robbery, murder and terrorism, to wildlife crimes (such as illegal fishing or badger baiting) [12]. However, unlike palaeo-palynology where pollen is extracted from sequentially accumulating sediments, pollen in forensic studies often needs to be extracted from pertinent objects and matched to crime scene materials. Extraction of pollen from fabrics such as clothes and shoes

by standard laboratory washing techniques [14] is commonplace for cases where mapping of a journey or visit to pertinent places is key to resolving criminal cases.

To date, pollen recovered during forensic cases has been used to relate suspects to a pertinent place, object or drugs; prove or disprove alibis; locate missing items or bodies; and determine the routes items or people have taken [12, 15, 16]. An example of the use of forensic palynology is provided by a case from the USA. Pollen from blankets wrapped around a body washed up in Boston Harbour, Massachusetts was analysed. The lack of pollen from rural plants and presence of non-native *Cedrus* (cedar) pollen in the samples led police to an urban arboretum in Boston. The palynological evidence was key in securing arrests and conviction for murder and accessory to murder [17].

Palynology is not a “silver bullet” in botanically led forensic investigations. Fundamental to presenting unbiased interpretations of pollen data in court is the ability to account for taphonomic variables in pollen production and dispersal.

“Taphonomy” refers to the set of processes acting between the release of the pollen grain or spore from the source plant

Received: January 16, 2025. Accepted: February 27, 2026

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and its recovery from a depositional setting. These include the production of pollen by the source plant (production); movement of the pollen from the flower to the location where the assemblage will form (dispersal); and modification of the pollen grain following initial deposition (preservation). Generally, pollen production in entomophilous (insect pollinated) taxa is relatively low as the life strategy of the plant is to channel resources into features that attract insects (flower structure/nectar sources), so that pollen can “hitch a ride” and be delivered directly to other flowers by those insects. Conversely, anemophilous (wind pollinated) taxa produce large quantities of pollen as they cannot rely on targeted transport to the recipient flower by an insect vector in order to reproduce. Instead, pollen from anemophilous species needs to be carried on the wind in sufficient numbers to reach the intended recipient by chance. However, the effects of this on pollen production are not as straightforward as simply entomophilous taxa = low pollen producers and anemophilous taxa = high pollen producers; variations in production within both groups add to the complexity. A case reported by Wiltshire [18] exemplifies the importance of differences in pollen production in a forensic context. During the investigation of an alleged rape, soil and exhibits from the crime scene revealed a surprisingly high proportion of *Pinus* (pine) pollen while vegetation at the location was actually dominated by *Acer* trees (sycamore). Pine is a prolific producer of pollen (even in the context of other anemophilous taxa) and at this crime scene there was no pine growing in the immediate vicinity. Palynologists concluded that the pine pollen was being blown in downslope from a lone pine tree and was entering the woodland beneath the canopy. Sycamore is an insect dispersed taxon, and there were very few sycamore pollen grains present in the exhibit washes and soil. Understanding the relative production of pollen was important in this case, which provides a reminder of the disconnect that is often present between pollen assemblages and vegetation surveys.

In addition to the variable relative pollen production from differing species, the amount of pollen produced by a parent plant also varies by plant age. Immature plants (those not having reached full sexual maturity) will produce little to no pollen. Wiltshire [18] also reports a case exemplifying this, where a body was discovered in a plantation of *Picea sitchensis* (Sitka spruce) but the pollen profile recovered from the victim contained less than 1% spruce pollen owing to the immaturity of the plantation.

Once pollen is produced and released, multiple factors affect its dispersal. Its size and shape reflect how easily it remains airborne, and landscape features like topography, prevailing air currents, obstructions (such as buildings or dense stands of vegetation), and weather conditions all have an influence on the movement of pollen [19] and need to be considered when examining pollen assemblages from forensic contexts. For example, large grains (e.g., *Cerealia*—cereal grasses such as wheat) will settle rapidly, close to the parent plant, but grains which have evolved flotation devices such as air bladders (common on Pinaceae (pine family)) can be carried for vast distances. Given warm air currents providing uplift, no obstructions and clear skies, *Pinus* (pine) pollen has been known to travel across continents in some cases [20–23].

Regardless of obstructions and meteorological conditions, vast quantities of pollen will still be deposited onto soil, sediment, human-made surfaces and clothes. From there, further processes take place that can impact the probability

of finding well-preserved (and morphologically unaltered) pollen grains allowing ease of identification. Although pollen has been recovered from 150-million-year-old sediments [24], it is more likely that pollen will deteriorate and identifying features become lost long before then. Microbial activity, oxidation and physical abrasion are the primary actions that degrade pollen, and different taxa will degrade at differing rates, adding further to the complexity of analysing a pollen assemblage [25]. This alteration, also known as post-depositional biasing, has been particularly noted and studied in archaeological contexts [26, 27] and various “tests” have been proposed to help identify situations where a pollen assemblage may have been altered and therefore should be interpreted with caution or removed from further analysis [28]. This aspect potentially has importance for forensic samples from soil contexts since soils can be a challenging environment for pollen preservation. This is exemplified in a case whereby a tenant farmer was wrongfully convicted of growing cannabis on the basis of pollen evidence. The sentence was revoked when an appeal suggested the pollen had persisted since previous occupants of the farm [12]. In this example, the persistence of pollen, rather than its loss through degradation, was key to the investigation, but it does illustrate the potential for differential degradation of pollen taxa to lead to incorrect conclusions.

Forensic palynologists take all these factors into account, drawing on their personal experience and expert knowledge of taphonomic processes to develop broadly narrative interpretations of pollen assemblages recovered from samples. In the allied fields of archaeological and palaeoecological palynology, recent research advances have provided methods for quantitative reconstructions of vegetation and land cover from pollen records by developing mathematical descriptions of the production and dispersal components of pollen taphonomy. In the early days of these disciplines, narrative interpretations took little account of the complexity of pollen taphonomy beyond dividing locally sourced pollen types from those originating in the wider landscape and those potentially travelling over long distances (providing a background “signal”). Estimates of difference in pollen production between plant types were sought to enable pollen assemblages to be “corrected” and give a better estimate of plant abundance. The first models assumed that areal coverage of plants in the landscape around the sampling location was directly correlated with the amount of pollen produced [29], then developed to take account of the spatial arrangement of vegetation as well as the abundance of different taxa [30–32]. Today these models overtly incorporate the spatial arrangement of plants and the properties of the sediment system where deposition occurs and have been built into software packages enabling reconstruction of land cover from pollen assemblages [33–35].

The “Landscape Reconstruction Algorithm” (LRA) [34, 35] combines pollen count data with relative pollen productivity estimates (RPPEs) and fall speed (a measure of dispersal ability) of taxa and average atmospheric conditions to generate quantitative land cover reconstructions using the Prentice-Sugita model [32, 36, 37]. The LRA has been evaluated using modern pollen samples and vegetation data from several locations worldwide [38–41] and adds value and replicability to vegetation reconstructions by removing some of the variability of analyst interpretations. In palaeo-palynology, often working at much larger scales than that of criminal

cases, these models can be interpolated to generate land cover maps [42]. The mapped outputs are easily readable and readily understood by colleagues from related disciplines (archaeologists, climate scientists, conservation managers or forensic investigators, for example).

Whilst the LRA is an algebraic approach, the multiple scenario approach (MSA) [33] is an iterative approach using computer processing capacity to identify possible land cover arrangements which could produce the pollen signals found in the analysed samples. The MSA uses environmental parameters such as topography and geology and the main taxa present to simulate a large number of possible land cover scenarios, then simulates the pollen assemblages using the Prentice-Sugita model [43] (which has required inputs of RPPEs, pollen fall speed and atmospheric conditions, as for the LRA). These simulated assemblages are then compared statistically with actual assemblages recovered from the target locations to identify possible past land cover arrangements. One of the strengths of the MSA is that, since it tests a wide range of possible scenarios, it is able to identify when multiple ecologically distinct land cover arrangements, or multiple locations within a landscape, can produce near-identical pollen assemblages (equifinality). So far, published examples of the MSA reconstruct aspects of past land cover relevant to archaeological questions [44]. Such interpretations have only previously been available from narrative-based interpretations of pollen data and did not include regional scale land cover maps. The full MSA approach can involve testing tens of thousands of possible scenarios, which with present processing power of desktop computers is time-consuming.

A related method to support interpretation of pollen data using a lighter touch is the “thought experiment”, where a limited number of often simplified land cover maps can be created, pollen assemblages simulated, and the different scenarios compared. Published examples of this approach include exploration of the effect on the pollen record of woodland management [45] and comparison of several hypothetical land cover arrangements to reconcile apparently contradictory pollen records from different contexts [46]. In situations where limited locational information is available, this approach can be a valuable check on the ability of the pollen signal to discriminate between contrasting land cover arrangements, and to explore its limitations [47].

While narrative-based interpretations have been the mainstay for the palaeo-palynological community over the greater part of the last century, the utility of modelling for removing operator bias is an exciting development for all groups who use palynological data. Models taking pollen production and dispersal into account are now readily available for use on a desktop computer, but so far, although there are methods for identifying which samples have experienced post-depositional modification due to degradation [28, 48], there is no quantitative tool available to account for these effects and support interpretation. Given the importance of correctly attesting results presented from forensic palynology in courts of law, it is incredibly important that natural variables are considered appropriately, and that variability or bias is minimised between interpretations from different experts. Therefore, in this paper, we will explore: 1) whether current advances in pollen dispersal and deposition modelling used in palaeo-palynological research can strengthen the interpretations and arguments made by forensic palynologists in forensic interpretations; and 2) whether a similar model can be developed to reduce the effects of post-depositional taphonomic alteration on pollen assemblages. We propose an approach for a quantified and visual output of forensic palynological data that is simpler for non-experts to comprehend. Finally, we set out a programme of work for further developing quantitative methods to support forensic palynology.

## Methods

### *Objective 1– Testing pollen dispersal and deposition models in forensic settings*

#### *Approach 1*

Two approaches were employed to address this objective. Approach 1 was to compare expert narrative interpretation of individual pollen assemblages from unknown locations with a partial quantification approach. One author X identified three pollen assemblages that they had sourced from locations known to them, counted, and developed accompanying hypothetical forensic “stories” (referred to as case studies A–C; Table 1). The pollen assemblage data were then shared with author Y who provided an expert narrative

**Table 1.** Background information for four hypothetical criminal cases used in this paper.

| Case study | Objective                                                                           | Background information (hypothetical forensic “story”)                                                                                                                                                                                                                                                                                                                                                                                                                                               |
|------------|-------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| A          | Compare narrative and RPPE-adjusted interpretations (Objective 1, Approach 1)       | A rape victim does not remember the location where the offense took place. Police are keen to identify the geolocation to be able to consult nearby CCTV. The victim’s hair is washed and the residue subjected to palynological investigation.                                                                                                                                                                                                                                                      |
| B          | Same as above                                                                       | A person with a past record of wildlife crimes is pulled over for speeding. Police search their car and suspect that badger baiting has taken place. They seize a spade from the boot of the car, the soil of which is subject to palynological investigation to identify the location of the badger sett to aid in prosecution.                                                                                                                                                                     |
| C          | Same as above                                                                       | Police seize a bag of counterfeit coins during a raid in Yorkshire. They suspect there are others buried or stashed in a pit (the bag is muddy). Forensic palynologists are charged with geolocating the hideaway using pollen retrieved from the mud on the bag.                                                                                                                                                                                                                                    |
| D          | Apply a thought experiment approach to geolocate a sample (Objective 1, Approach 2) | Missing body; police have a suspect who has admitted to having been for a walk in a large area of woodland with the missing person. Police suspect that the missing body is buried in the woodland, but walked transect searches have been fruitless. Dog searches cannot be used as the amount of turnover of soil from wild boar populations would confuse the scent. Police request palynologists to narrow down the search area by analysing the pollen from the suspect’s sediment-laden boots. |

RPPE: relative pollen productivity estimate; CCTV: closed-circuit television.

interpretation and with author Z who used a partial quantification approach to “correct” the pollen assemblages for differential pollen productivity, before providing an interpretation of the likely context.

Narrative interpretation, where a palynologist draws on implicit knowledge derived from experience with both their own analyses and from reading the wider literature to generate a story about the likely environmental setting which produced the pollen assemblage, is widely used in many applications of pollen analysis. Whilst there is clear agreement across experts about parts of this body of knowledge (for example, that pine (*Pinus* sp.) pollen is produced in much larger amounts per tree than lime (*Tilia* sp.) pollen), in other aspects the particular experience of the individual analyst can lead to different interpretations. For example, an analyst who has worked mainly in lowland England is likely to interpret a grass-rich assemblage differently than an analyst whose experience is mainly from the uplands of Scotland, due to the very different ecologies and land management strategies which generate grass-rich habitats in those areas. Analysts are also likely to disagree about the interpretability of an assemblage; for example, it is possible to interpret a few grains of pollen from the Rosaceae family as originating from understorey shrubs and hedgerow elements, or as garden ornamental roses. Such differing interpretations could have huge consequences in forensic settings.

For the partial quantification approach, knowledge of RPPE of different taxa was applied to “correct” the raw pollen counts (that is, to weight them to give a better representation of the abundance of different vegetation types around the sampled location). Numerous estimates of relative pollen productivity for taxa commonly found in northwest Europe are available, and estimates for the same taxa vary both between and within regions [49–51]. The RPPEs used in this study are those calculated by Githumbi et al. [52] as a set of mean values derived from synthesis of published empirical studies combining present-day vegetation data and pollen assemblages from natural pollen traps (e.g., mosses, soils) to estimate relative pollen productivity for a specific region within Europe. The earlier version of this RPPE dataset [53] has been validated through application to reconstruction of present-day land cover from modern pollen samples in several regions of Europe [39, 54–57]. Pollen percentages for each taxon were divided by RPPE to weight the results and show which taxa are affected by over- or under-representation in the pollen assemblage. This approach only considers the production part of the pollen assemblage formation process.

Interpretations of assemblages A–C were created independently by author Y and author Z, written down, and sent to author X who compared the two interpretations with the known landscape context to determine whether the use of partial quantification altered or improved confidence in the interpretations.

## Approach 2

In this section, we considered a scenario where a forensic sample was suspected to have come from within a specific landscape, and the analyst wished to provide a more precise location (Table 1: Case D). Here expert narrative interpretation was compared with the use of a “thought experiment” simulation.

Author Y created a hypothetical woodland scenario (named “Crow Wood”, see [Supplementary Information](#) for details) covering an area of 5 km × 5 km and simulated three pollen counts at each of two locations. The count data and woodland map were sent to author X, who carried out a narrative interpretation of the likely location. Count data plus information about the woodland scenario were sent to author Z, who carried out a thought experiment by using LandPolFlow [47] and [Supplementary Information](#) to simulate “surface sample” pollen assemblages from a grid of points across the site and then compared these assemblages with the counts provided using a squared-chord distance (SCD) similarity measure to identify the best match with the actual counts and therefore identify the most likely locations. Firstly, the counts provided by author Y were converted to percentages to facilitate comparison with the pollen loadings generated by LandPolFlow. The three samples from each location were then averaged to provide a single assemblage from each of the two locations. Simulated pollen assemblages were generated in two stages due to limitations of computer processing power. First, assemblages were simulated for each 50 m grid cell across the whole 5 km × 5 km area and compared to the two assemblages provided by author Y by calculating SCD. The results of these first simulations were used to determine two smaller areas (1 350 m × 850 m for location 1, and 1 500 m × 700 m for location 2) for more detailed simulation. In each of these two smaller areas, pollen assemblages were simulated for each 5 m grid cell. SCD was used to compare simulated with actual assemblages as before, and the results were used to recommend focused areas in which to conduct detailed searches. Inferred locations from authors X and Z were then compared with the actual locations provided by author Y as for Approach 1.

## Objective 2 – Developing models of post-depositional taphonomic processes

So far, current models of pollen taphonomy do not make any allowance for post-depositional preservation changes, assuming that once incorporated into a context such as soil or sediment the assemblage remains largely unchanged until it is recovered and analysed. Whilst this assumption is robust for very recent pollen utilised in forensic cases (less than 1 year old, for example), it is not true of pollen assemblages from all types of exhibits, for example, soils from burial sites will have been exposed to strong post-depositional processes, such as microbial activity or repeated wetting and drying. Where post-depositional processes are active, pollen assemblages are progressively altered as grains become unidentifiable at different rates depending on their resistance to decay [27, 58–61].

Palaeo-palynologists have proposed methods for identifying samples which have probably been altered by post-depositional processes [28, 48], and generated rankings for the resilience of some key taxa largely through the experiments of Havinga [25]. In this paper, Havinga’s [25] data will be used to create a relative pollen degradation (RPD) index for some common taxa, which could be applied to a sample identified as having experienced post-depositional biasing to “correct” pollen percentages and aid interpretation.

Havinga’s [25] study began with a known mixture of 19 pollen types, including highly resistant and identifiable *Lycopodium* spores as a reference point, and explored the

deterioration rate of the 19 taxa when buried in *Sphagnum* peat, *Carex* peat, podzol soil, river clay sediment and leaf litter. Data presented showed the percentages of grains of each type which could still be identified after a period of time in different environmental settings, and the proportion of surviving grains of a given type which showed evidence of damage. Since post-depositional biasing effects develop over time, and Havinga's [25] published values reflect a relatively limited span of 5–20 years of natural processes, our RPDs may not be universally applicable across all forensic contexts. While some forensic cases may involve soils with different depositional histories, the RPDs derived from Havinga's study offer a useful benchmark—particularly in cases where soils have developed over comparable timeframes, such as in cold cases or in contexts involving reworked or older soils.

Where the RPDs are based on the proportion of damaged grains, it is assumed that this is correlated with the rate of disappearance of grains of that type from the pollen assemblage altogether, i.e., with how quickly a grain becomes unidentifiable or undetectable. Identifiability varies between grains depending on their diagnostic features. For example, a monoporate psilate grain (like Poaceae) can be rendered unidentifiable by a small amount of damage whereas a poly-porate verrucate grain with thicker walls (e.g., *Plantago*) can often be identified even when only part of the grain can be seen or is less damaged, therefore the latter disappear from the record more slowly than the former. Since the more identifiable grains are typically those with thicker walls and more complex surface structures (e.g., *Plantago*, Asteraceae), the

assumption that they are both damaged more slowly and lost from the identifiable assemblage more slowly seems reasonable without evidence to the contrary.

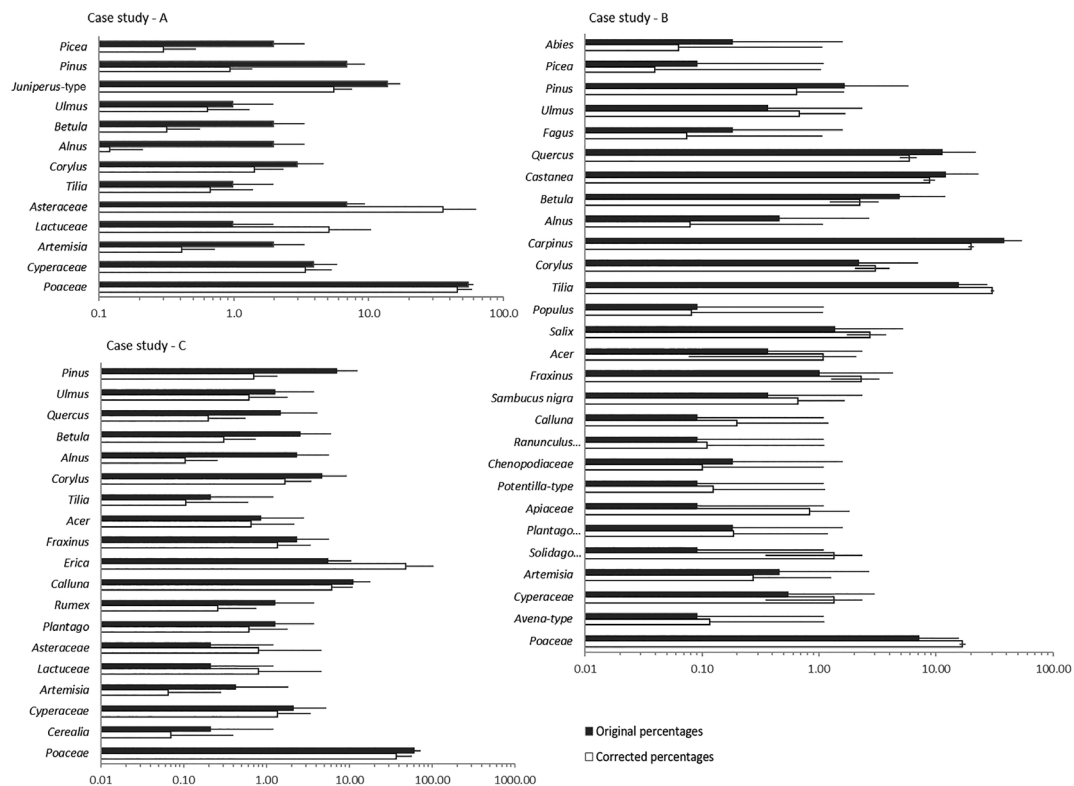
As an initial test of the RPD approach, data were taken from a study by Holloway [62]. He reports a study where a pollen sample was subjected to multiple experimental wetting and drying cycles, and the effect on the proportion of different pollen types that could be recovered and identified was assessed. The sample included pollen from 13 different plants, of which four species are from taxa represented in the RPDs derived from Havinga [25]: *Juniperus monosperma*, *Pinus edulis*, *Quercus virginiana* and *Salix nigra*. These are not the European species studied by Havinga, but they produce the same pollen type as their European relatives (*Juniperus*-type, *Pinus*, *Quercus* and *Salix*). Data from Holloway's Table 2 [62] was extracted for these four taxa, and RPDs applied. Statistical comparison between the original assemblage and the assemblage after treatment, and between the original and the treated assemblage corrected using RPDs, was made using the SCD metric.

## Results

### Objective 1 – Testing pollen dispersal and deposition models in forensic settings

#### Approach 1

Pollen data from three hypothetical cases (reported in Table 1) are shown in Figure 1. When the raw percentage data



**Figure 1** Original and relative pollen productivity estimate (RPPE)-corrected pollen percentages for three test case studies from Table 1. Note the log<sub>10</sub> scale on the x-axis. Whilst the use of log scales is not standard palynological practice, they are used here as an effective method of displaying data with a wide range of values. Error bars shown are positive errors calculated from standard deviations of pollen counts and RPPEs [52] using propagation of errors (see Supplementary Information for more details).

are corrected by RPPE, all taxa show altered values, but not consistently in the same direction—some taxa are over-represented in the pollen assemblages, and others are under-represented. In case study A, 11 out of 13 taxa (85%) report higher percentages after RPPE corrections are applied, whereas case studies B and C report 43% and 84% higher percentages, respectively. The largest differences between the corrected and uncorrected values are seen in the trees (for example, *Pinus*), shrubs (*Erica*) and grasses (Poaceae). These data were used by author Z to produce RPPE-corrected interpretations of each of the case studies, which were compared with the narrative interpretations developed by author Y (Box 1).

Box 1 demonstrates that in all three cases, both palynological experts were able to provide accurate descriptions of the locations that pollen samples were extracted from. Both experts provide details of the local vegetation that the police can then use in establishing a geolocation (perhaps in collaboration with a local botanist for biogeographic information) to focus their searches. In two of the three examples, using the RPPE-corrected approach to interpret palynological data provided more detailed information to the police to aid their investigations, potentially saving resources by providing greater detail and identifying a smaller search area.

**Box 1.** Interpretations of assemblages A–C, created independently by author Y and author Z, compared with the known landscape context.

#### Case study A:

The uncorrected narrative-based interpretations suggest that the closed-circuit television footage should be reviewed around an ornamental park, cemetery or plantation that contains the plant taxa *Taxus*, *Juniperus* and *Tsuga*. While this provides detail for police forces to focus their operations, it has not narrowed down the search area significantly. Our RPPE-corrected pollen assemblage suggests more open ground with plantation nearby. The actual location was Dowdeswell, Gloucestershire (UK): a woodland plantation on the banks of a flood relief reservoir. The primary vegetation comprises *Carex* sp., *Betula*, *Cupressus*, *Pinus sylvestris*, *Quercus* sp., *Larix decidua*, *Rubus*, *Hedera*, *Sorbus*, *Polypodium*, and *Alnus*. In this example, the RPPE-corrected data return a more accurate location than that of the palynologist providing a traditional narrative interpretation.

#### Case study B:

In the search for the badger sett, the narrative-based interpretation suggests an undisturbed woodland area dominated by *Tilia*. The RPPE-corrected interpretation also has the badger sett located in a *Tilia* dominated woodland, but also (and perhaps key in finding the exact location) that the sett is likely to be near a grassy clearing in the wood. The actual location was Chalkney Wood in central Essex (UK), where *Tilia cordata* is the main species and in some places is co-dominant with *Castanea sativa*. In this case, both approaches identified woodland and the main tree taxa; the sample in question was taken from a location which is close to the edge of the wood which had been coppiced 7 years before sampling, which therefore still had a rich understorey. Using the management map of the site, which shows the date each area was last coppiced, would help prioritise locations to search. In this example, the RPPE-corrected interpretation gives a stronger steer than the narrative approach as to where within the wood the sett might be found.

#### Case study C:

Seeking the hidden counterfeit coins, both our expert palynologists providing narrative-based and RPPE-corrected interpretations consider the landscape to be an open, grazed heathland environment, with either scattered trees, or a plantation nearby. The area the pollen profile originated from was indeed a heathland environment in Yorkshire (UK)—Arkengarthdale Moor.

#### Approach 2

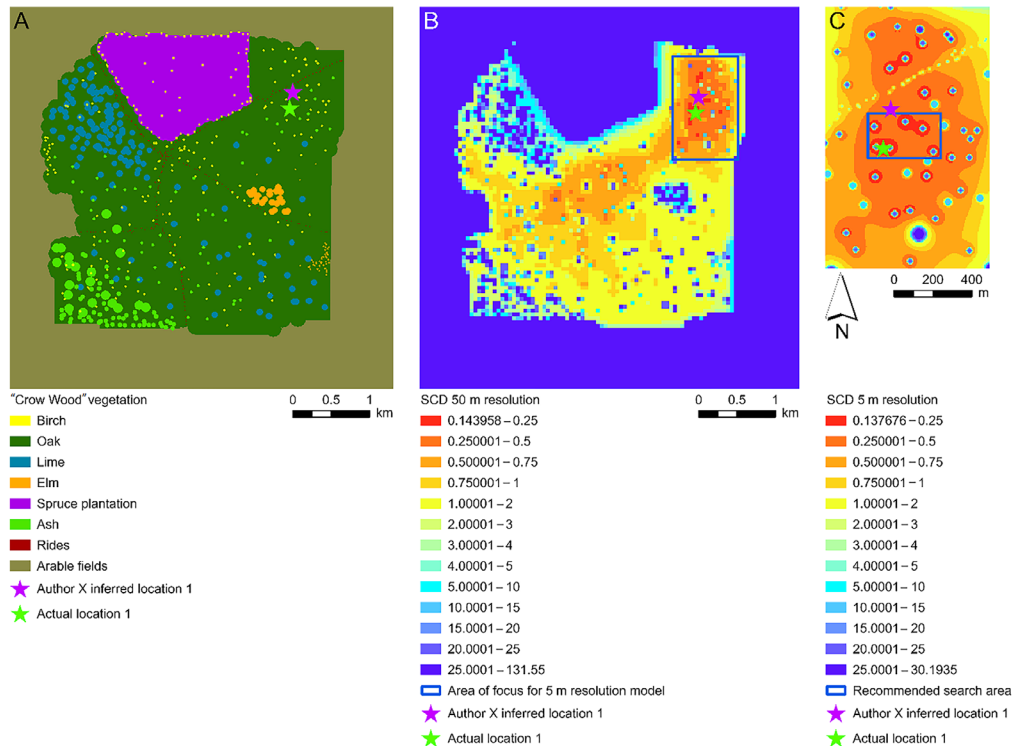
Pollen data from two locations within the hypothetical “Crow Wood” were analysed by both an expert palynologist using a narrative interpretation, and by an expert palynologist using LandPolFlow to implement the Prentice-Sugita model (see [Supplementary Information](#)), to recommend search areas for the local police force. Results for the two locations are shown in [Figures 2](#) and [3](#) (see [Supplementary Information](#) for details of vegetation communities and further discussion of the modelling choices).

The narrative-based interpretation for location 1 suggests that the search for the missing body should focus on the northeast corner of the hypothetical woodland, close to the ride ([Figure 2B](#)). The lack of *Tilia* pollen indicates that the location is either in the northeast or southwest corner of the woodland, and *Fraxinus* is present in lower quantities than would be expected for a southwest location. The presence of some Cerealia grains suggests the location is close to the edge of the woodland due to known low pollen production and limited dispersal of this taxon, and *Plantago lanceolata* is known to thrive in disturbed environments, so it supports the location either being close to the edge of the woodland, or near a ride. The low proportion of *Picea* pollen is perhaps surprising given proximity to the plantation but could be explained if the trees are too immature to produce pollen, or conversely if they are very mature and tall enough to release pollen above the canopy of the woodland.

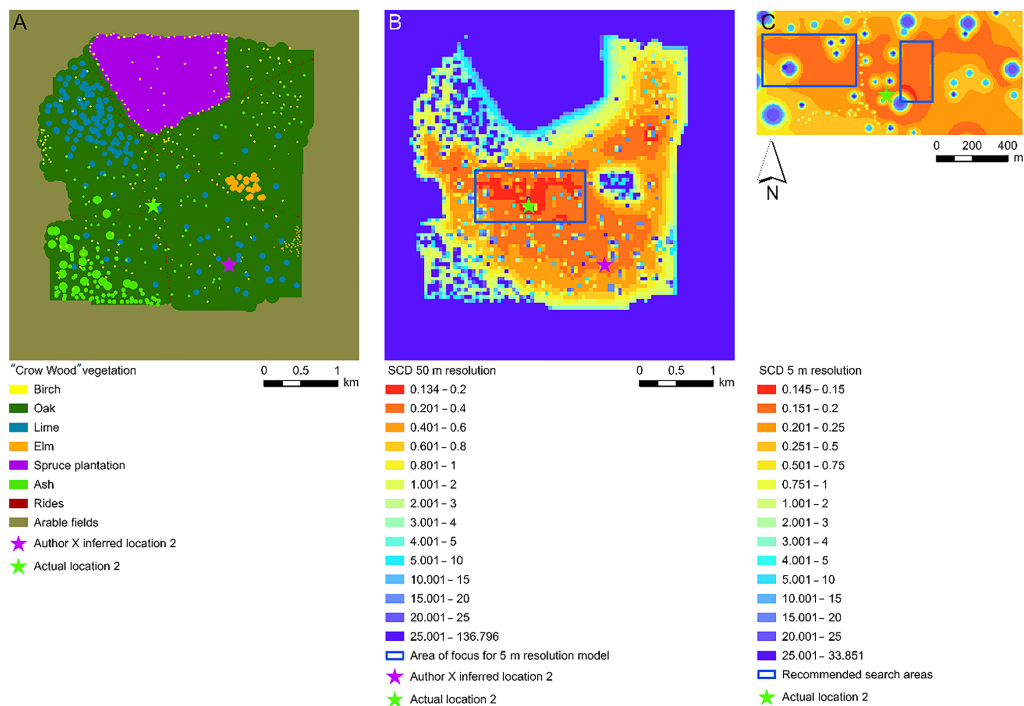
The SCD fit scores generated by application of the Prentice-Sugita model of pollen dispersal and deposition within LandPolFlow suggest that the search should focus on a 375 m × 230 m area in the northeast corner of the wood, very close to the location suggested by the narrative-based interpretation ([Figure 2](#)). The actual location of the pollen sample is within the southeast corner of this suggested search area, again shown on [Figure 2](#).

For location 2, the narrative-based interpretation suggests that the pollen sample comes from the southeast corner of the hypothetical woodland. A location close to the edge is again supported by low quantities of Cerealia pollen. The lower proportions of *Plantago lanceolata* suggest lower disturbance and therefore a location away from rides. *Fraxinus* pollen proportions are again lower than would be expected from an ash-dominated area, and *Picea* proportions are lower than in sample 1, suggesting a location further from the plantation. The presence of *Tilia* pollen, even in small quantities, indicates the local presence of lime trees, since this taxon has low pollen productivity and limited dispersal. Taken together, the evidence points to the southeast corner of the woodland, as shown in [Figure 3](#).

The SCD fit scores generated by LandPolFlow provide two recommended search areas, one of 530 m × 290 m and the other of 180 m × 340 m, both located roughly in the centre of the hypothetical Crow Wood ([Figure 3](#)). The two search areas



**Figure 2** Location 1: (A) Hypothetical woodland scenario ("Crow Wood") used to demonstrate the utility of the modelling approach in narrowing down a search area; (B) Fit scores calculated using squared-chord distance (SCD) for every 50 m grid square in "Crow Wood", with outline of area C shown in blue; (C) Fit scores calculated using SCD for every 5 m grid square within the area outlined in blue on (B), with the outline of the recommended search area from the modelling approach shown in blue. The recommended search location from the narrative interpretation by author X is indicated by a purple star, and the actual location by a green star.



**Figure 3** Location 2: (A) Hypothetical woodland scenario ("Crow Wood") used to demonstrate the utility of the modelling approach in narrowing down a search area; (B) Fit scores calculated using squared-chord distance (SCD) for every 50 m grid square in "Crow Wood", with outline of area C shown in blue, the recommended search location from the narrative interpretation by author X indicated by a purple star, and the actual location indicated by a green star; (C) Fit scores calculated using SCD for every 5 m grid square within the area outlined in blue on (B), with the outline of the recommended search areas from the modelling approach shown in blue, and the actual location indicated by a green star (the location derived from the narrative interpretation by author X is not within area C so is not shown here).

are only 250 m apart, but a cluster of lower fit scores suggests that searching the area in between would be less productive. The actual location is just outside of the southwest corner of the second search area (Figure 3), in between that and the first search area, indicating that pockets of lower fit scores within an area of generally high scores should in fact be searched as well.

In summary, for location 1, the narrative- and model-based approaches performed equally well, both providing a recommended search area that was very close to the true location of the pollen sample. For location 2, where the pollen sample characteristics were more ambiguous and could feasibly have come from several areas within the woodland, the model-based approach provided a more accurate recommendation of where to focus the search. Whilst it was less accurate here than at location 1, it did perform much better than the narrative-based approach and could therefore be used to enable police forces to focus their resources more effectively.

### Objective 2 – Developing models of post-depositional taphonomic processes

Experimental pollen preservation data from Havinga [25] is reported in Table 2. The data have been used to develop an RPD index for specific sediment matrices over differing time periods as well as average values for general use. This index can be applied to a sample believed to have experienced post-depositional biasing to adjust values and aid interpretation. To do so, user-generated pollen data should first be converted to percentages, then divided by the RPD value provided. Users can choose to use values from specific soil types and years since seasonal deposition, or use the average value. Using the average value is at the cost of accuracy but enables the tool to be applied in unknown settings.

This generation of RPD values is, to our knowledge, the first attempt to develop degradation correction factors to improve quantitative palynological interpretations.

Figure 4 shows the results of application of the RPDs in Table 2 to data from Holloway [62]. The SCD between

the control and the RPD-corrected degraded assemblage (16.7) was slightly lower than that for the control and the uncorrected sample (19.2), with about a 15% improvement in similarity. Given the differences between the experimental treatments of Holloway [62] and the range of environmental conditions experienced by the samples reported in Table 2, these results are encouraging and suggest that the approach is worth pursuing.

The RPD approach is undoubtedly simplistic, and like the early steps in the development of production and dispersal modelling, does not provide a full correction but represents a first step towards developing a new tool. RPDs should only be applied to forensic soil/sediment samples for which we know or have good reason to believe the pollen will have deteriorated. As post-depositional deterioration is largely a time-transgressive process, RPD corrections will only be relevant in cases where there are aged samples, for example in burials where the soil is representative of many years' development. Even if the burial is recent, soil development is very slow—perhaps only a centimetre of soil is produced in a century [63].

## Discussion

### Objective 1 – Testing pollen dispersal and deposition models in forensic settings

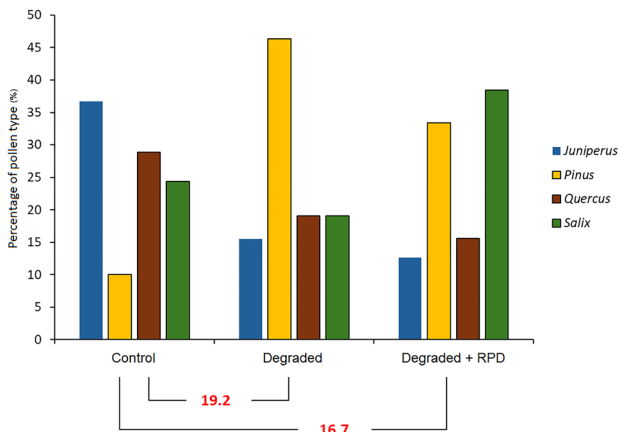
In this paper we have highlighted the discrepancy between a frequently used narrative-based approach and our proposed modelling techniques in interpreting pollen data in forensic cases. We presented two approaches to refine interpretations of pollen data based on methods used in other palynological disciplines.

The first approach adjusted the pollen assemblage crudely by weighting the pollen counts according to taxon-specific RPPEs. An expert forensic palynologist already makes a similar correction, whether overtly in argument or indirectly in appeal to expert knowledge, when they interpret some plants

**Table 2.** Relative pollen degradation (RPD) values for 19 major northern hemispheric plant taxa generated from Havinga's [25] Tables 1A, 1B and 2.

| Taxon             | River clay<br>(5 years) | River clay<br>(10 years) | Leaf mould<br>(5 years) | Leaf mould<br>(15 years) | <i>Sphagnum</i> peat<br>(20 years) | <i>Carex</i> peat<br>(20 years) | Podzol<br>(20 years) | Mean (± SD) |
|-------------------|-------------------------|--------------------------|-------------------------|--------------------------|------------------------------------|---------------------------------|----------------------|-------------|
| <i>Lycopodium</i> | 1.00                    | 1.00                     | 1.00                    | 1.00                     | 0.98                               | 0.91                            | 0.73                 | 0.95 ± 0.10 |
| <i>Taraxacum</i>  | 0.60                    | 0.65                     | 0.72                    | 0.56                     | 0.92                               | 0.83                            | 0.64                 | 0.70 ± 0.13 |
| <i>Polypodium</i> | 0.98                    | 0.40                     | 0.98                    | 0.61                     | 0.53                               | 0.43                            | 0.24                 | 0.59 ± 0.29 |
| <i>Fagus</i>      | 0.42                    | 0.28                     | 0.45                    | 0.37                     | 0.77                               | 0.70                            | 0.46                 | 0.49 ± 0.18 |
| <i>Tilia</i>      | 0.18                    | 0.18                     | 0.25                    | 0.27                     | 0.91                               | 0.82                            | 0.64                 | 0.46 ± 0.32 |
| <i>Pinus</i>      | 0.17                    | 0.05                     | 0.16                    | 0.15                     | 0.93                               | 0.85                            | 0.64                 | 0.42 ± 0.37 |
| <i>Juniperus</i>  | 0.28                    | 0.20                     | 0.29                    | 0.21                     | 0.70                               | 0.55                            | 0.37                 | 0.37 ± 0.19 |
| <i>Quercus</i>    | 0.23                    | 0.17                     | 0.43                    | 0.30                     | 0.75                               | 0.50                            | 0.20                 | 0.37 ± 0.21 |
| <i>Betula</i>     | 0.06                    | 0.10                     | 0.43                    | 0.21                     | 0.76                               | 0.68                            | 0.27                 | 0.36 ± 0.28 |
| <i>Carpinus</i>   | 0.05                    | 0.02                     | 0.11                    | 0.06                     | 0.85                               | 0.75                            | 0.63                 | 0.35 ± 0.37 |
| <i>Alnus</i>      | 0.01                    | 0.01                     | 0.02                    | 0.10                     | 0.86                               | 0.76                            | 0.60                 | 0.34 ± 0.38 |
| <i>Acer</i>       | 0.04                    | 0.05                     | 0.15                    | 0.02                     | 0.76                               | 0.75                            | 0.40                 | 0.31 ± 0.33 |
| <i>Myrica</i>     | 0.00                    | 0.01                     | 0.01                    | 0.01                     | 0.83                               | 0.74                            | 0.50                 | 0.30 ± 0.38 |
| <i>Corylus</i>    | 0.01                    | 0.01                     | 0.02                    | 0.03                     | 0.80                               | 0.72                            | 0.44                 | 0.29 ± 0.36 |
| <i>Fraxinus</i>   | 0.03                    | 0.02                     | 0.19                    | 0.08                     | 0.69                               | 0.69                            | 0.26                 | 0.28 ± 0.29 |
| <i>Ulmus</i>      | 0.02                    | 0.02                     | 0.08                    | 0.05                     | 0.75                               | 0.53                            | 0.35                 | 0.26 ± 0.29 |
| <i>Populus</i>    | 0.05                    | 0.05                     | 0.09                    | 0.04                     | 0.57                               | 0.55                            | 0.26                 | 0.23 ± 0.24 |
| <i>Salix</i>      | 0.05                    | 0.02                     | 0.15                    | 0.06                     | 0.67                               | 0.45                            | 0.08                 | 0.21 ± 0.25 |
| <i>Taxus</i>      | 0.09                    | 0.03                     | 0.08                    | 0.21                     | 0.62                               | 0.14                            | 0.03                 | 0.17 ± 0.21 |

SD: standard deviation.



**Figure 4** Application of relative pollen degradation (RPD) correction coefficients to data from Holloway [62]. Bar charts show the percentages of four pollen taxa for the Control (original experimental mixture of pollen grains), Degraded (pollen grain mixture recovered after multiple cycles of wetting and drying) and Degraded + RPD (the degraded sample after correction using the RPD values in Table 2). The red numbers show the squared-chord distance (SCD) between pairs of samples, with a lower value indicating greater similarity.

as being over-represented in the pollen record and others as under-represented. Using specific, empirically derived values to substantiate that terminology may add weight to the argument, and in the case studies here slight differences in the confidence and detail of interpretation were seen with more detailed interpretations derived from the RPPE-corrected data in two cases. Since our example used only one expert for each method, these differences may partially reflect differences in style of narrative interpretation between analysts. However, we believe there is potential for use of modelling in forensic palynology to improve confidence in interpretations, which should be explored further.

The second approach used a more complex pollen dispersal and deposition model to demonstrate how simulation could be used to support expert interpretation in a case where a general area is defined, and the forensic palynologist seeks to narrow down the precise location that samples originated from. The example presented here showed the potential for effective visual communication of statistical findings; continuing to empirical testing of the approach has the potential to improve evidence for the subset of cases where pollen samples are used to target the precise location of an object or activity within a defined area.

Both examples show how using elements of the modelling approach can provide additional support for expert opinion. We caveat though that existing models are developed for a specific subset of pollen-rich samples, those where pollen accumulates over multiple years within a sedimentary system, whilst forensic pollen samples are derived from a far wider range of assemblage formation processes. The decision of whether one or another of these approaches can be applied to a particular sample depends on the analyst's understanding of how that sample was formed, and therefore whether existing models can be usefully applied. In some cases, these models have clear utility and demonstrate the potential of quantitative approaches in forensic palynology. Their applicability may also vary across climatic zones—for example, arid or tropical environments may present different taphonomic

processes that affect pollen preservation and accumulation. This highlights the value of empirical testing to determine when models are appropriate and where adaptations may be needed. Developing similar approaches for a wider range of environmental and depositional contexts will increase the range of situations where the modelling approach can be part of the forensic palynologist's toolkit. We discuss possible ways forward below.

## Objective 2 – Developing models of post-depositional taphonomic processes

Although pollen grains are designed to protect cells and genetic material during transport through a hostile environment, the identifiable outer casings do break down over time in soil [25, 27, 59, 60]. Each pollen grain type deteriorates at a different rate and becomes visually unidentifiable at a different point in the decay process; therefore, an assemblage made of a mixture of pollen types is altered over time.

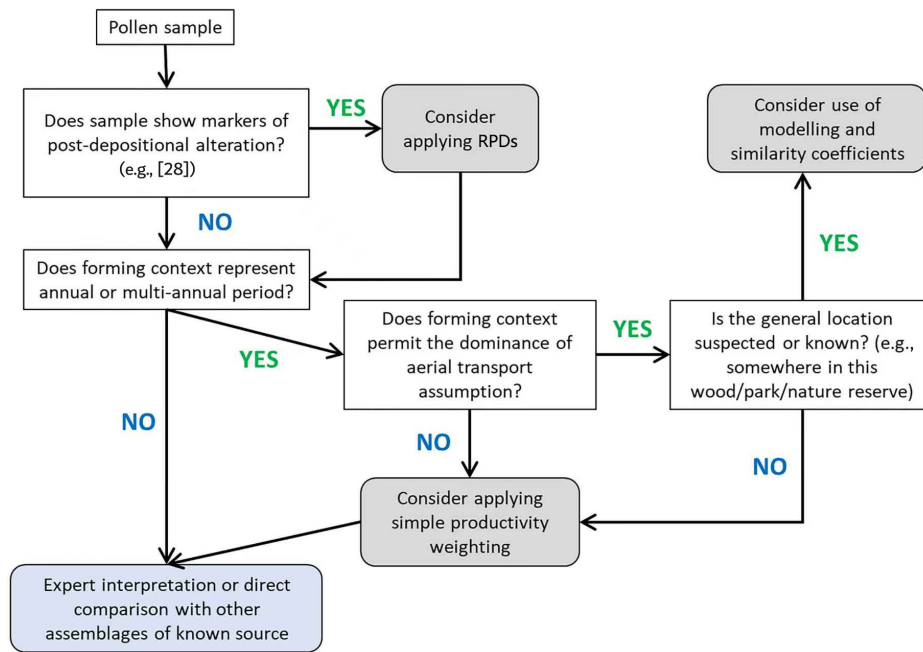
In this paper we proposed a simple weighting approach for “correcting” an assemblage, designed to remove the effects of post-depositional changes resulting from different rates of modification of grains of different types. We presented an exploratory study using published data to estimate weighting terms and carried out a test which suggests that applying these terms could potentially “undo” some of the effects of time. These results suggest that the problem of post-depositional assemblage alteration can be reduced by a relatively simple quantitative empirical correction, and that systematic development and validation of our RPD approach will improve the scope and evidential basis of forensic palynological interpretation for soil samples where the main question being asked is the possible land cover setting of the location of the original soil, and potentially be widely useful for palaeo-palynology and other applications where samples are collected from less than ideal preserving environments. The next section considers what such an approach might look like.

## The future of modelling in forensic palynology

This paper focuses on two ways of bringing increased quantification into the interpretation of forensic pollen samples, and both are found to have promise, although neither has the potential to be universally applicable. A decision flow chart is shown below (Figure 5) to help identify which types of samples might be suitable for which of the methods considered here; organic soil samples are most likely to be suitable for the full range of methods, and the methods are least likely to be appropriate for samples which form rapidly on human-made or human substrates such as fabric (clothing, bags, etc.) or hair washings.

The first area of priority identified for future research is to improve our understanding of when to consider using taphonomic models. Determining which samples, contexts or questions can benefit from quantification approaches is very important to ensure that they are applied appropriately and improve the quality of the evidence. We suggest the following as a programme of research aimed at addressing this question:

- Define groups of samples which may be targeted in forensic investigations, e.g., soils, muds, other surfaces and contexts.



**Figure 5** Decision flow chart for determining when to consider applying the methods discussed in this paper to forensic palynology samples. RPD: relative pollen degradation.

- Carry out empirical studies to collect modern data on context alongside appropriate pollen samples and apply a taphonomic correction or location selection approach in a situation where actual and inferred findings can be compared. What we are proposing here is essentially a more systematic and thorough version of case studies A–C in this paper.
- Test a range of alternative pollen dispersal and deposition models to determine which is most effective for contexts which are commonly encountered in forensic investigations where the assumptions of the standard model used here (mainly that the pollen assemblage is dominated by aerial deposition of pollen onto a receiving surface in a canopy opening) are not met, e.g., samples from riverine muds, salt marshes, where water-borne transport of pollen is also likely to be important.

The second area of priority for future research is the development and testing of RPDs using experimental and observational approaches, and of the screening tools used to identify when application of RPDs is appropriate. This also has wider applicability to palaeo-palynology.

Other recent developments in palaeoecology may also be worth exploring as potential additions to the tool kit. For example:

- Environmental DNA (eDNA) has the potential to enhance forensic palynology by allowing for more precise identification of plant species (palynology alone is limited to identification to family or genus level in most instances) [64], and offer insights on dispersal [65].
- Fourier transform infrared spectroscopy (FTIR) analysis of pollen exines for taxonomic identification has the potential to refine identification of some taxa which cannot be distinguished using light microscopy. The use of FTIR may also allow preservation metrics to be improved [66, 67].

- Adoption and improvement of automated pollen identification and counting to speed up analysis of samples—at present the technology does not match the accuracy of experienced human analysts in all cases. Continuous improvements in technology and methodologies are helping to enhance its reliability, although thorough testing is still needed [68, 69].
- For rapidly formed samples, such as those collected in dynamic environments or during specific meteorological events, comparing the results with contemporary aeropalynological data can provide valuable context and validation. Additionally, employing aeropalynological modelling may help to improve the accuracy of conclusions drawn from rapidly formed samples [70].

## Conclusion

Models of pollen dispersal and deposition are not a universal panacea, and not appropriate for use in all contexts. In this paper, we explore contexts where they could be a useful addition to the forensic palynologist's toolkit and clearly demonstrate potential applications. The interpretation of pollen assemblages from forensic samples requires a high degree of expertise and mostly falls within the “narrative” type of scientific explanation. Narrative explanations rely on the expert knowledge and experience-informed intuition of an individual, are always constrained by that individual's range of prior experience and reading, and their effectiveness in court can depend on the credibility and effect of the presenter (and the unconscious bias of the audience) [71, 72]. By incorporating additional quantitative methods where appropriate, and where financial resources are available, interpretations can be more “analytical” in character.

Our analysis shows that, for appropriate types of forensic sample, current advances in taphonomic modelling used in

palaeo-palynological research may strengthen the interpretations and arguments made by forensic palynologists, and that further development of quantitative methods to support forensic palynology is both possible and desirable.

### Authors' contributions

All authors contributed equally to the conception and design of the study, data interpretation, drafting and critical revision of the manuscript, and approval of the final version.

### Compliance with ethical standards

The author declares that this article complies with ethical standards. The research was conducted in accordance with institutional and international guidelines.

### Disclosure statement

No disclosure statement needed.

### Funding

No funding to declare.

### References

- Marden M, Holt K, Ryan M, et al. Stratigraphy and vegetation signals from an upland, landslide-dammed, paleolake during the last glacial-interglacial transition, Waipaoa sedimentary system, Hikurangi margin, eastern North Island, New Zealand. *N Z J Geol Geophys.* 2022;65:220–241.
- Tzedakis PC. Vegetation change through glacial—interglacial cycles: a long pollen sequence perspective. *Philos Trans R Soc Lond B Biol Sci.* 1994;345:403–432.
- Langgut D, Almogi-Labin A, Bar-Matthews M, et al. Vegetation and climate changes in the south eastern Mediterranean during the last glacial-interglacial cycle (86 ka): new marine pollen record. *Quat Sci Rev.* 2011;30:3960–3972.
- Camuera J, Jiménez-Moreno G, Ramos-Román MJ, et al. Vegetation and climate changes during the last two glacial-interglacial cycles in the western Mediterranean: a new long pollen record from Padul (southern Iberian Peninsula). *Quat Sci Rev.* 2019;205:86–105.
- Miyoshi N, Fujiki T, Morita Y. Palynology of a 250-m core from Lake Biwa: a 430,000-year record of glacial—interglacial vegetation change in Japan. *Rev Palaeobot Palynol.* 1999;104:267–283.
- Webb J, McCarroll J, Morrow D. Palynological contributions towards the Archaeology of Skokholm Island, south west Wales. *Archaeology in Wales.* 2022;60:45–48.
- Bryant VM, Jones JG, Mildenhall DC. Forensic palynology in the United States of America. *Palynology.* 1990;14:193–208.
- Mildenhall DC. Forensic palynology in New Zealand. *Rev Palaeobot Palynol.* 1990;64:227–234.
- Mildenhall DC. Hypericum pollen determines the presence of burglars at the scene of a crime: an example of forensic palynology. *Forensic Sci Int.* 2006;163:231–235.
- Szibor R, Schubert C, Schöning R, et al. Pollen analysis reveals murder season. *Nature.* 1998;395:449–450.
- Horrocks M, Walsh KAJ. Pollen on grass clippings: putting the suspect at the scene of the crime. *J Forensic Sci.* 2001;46:947–949.
- Mildenhall DC, Wiltshire PEJ, Bryant VM. Forensic palynology: why do it and how it works. *Forensic Sci Int.* 2006;163:163–172.
- Riding JB, Rawlins BG, Coley KH. Changes in soil pollen assemblages on footwear worn at different sites. *Palynology.* 2007;31:135–151.
- Webb JC, Brown HA, Toms H, et al. Differential retention of pollen grains on clothing and the effectiveness of laboratory retrieval methods in forensic settings. *Forensic Sci Int.* 2018;288:36–45.
- Monckton-Smith J, Adams T, Hart AG, et al. *Introducing forensic and criminal investigation.* London (UK): SAGE; 2013.
- Wiltshire PEJ. *Protocols for forensic palynology.* *Palynology.* 2016;40:4–24.
- Laurence AR, Bryant VM. Forensic palynology and the search for geolocation: factors for analysis and the Baby Doe case. *Forensic Sci Int.* 2019;302:109903.
- Wiltshire PEJ. Consideration of some taphonomic variables of relevance to forensic palynological investigation in the United Kingdom. *Forensic Sci Int.* 2006;163:173–182.
- Theuerkauf M, Kuparinen A, Joosten H. Pollen productivity estimates strongly depend on assumed pollen dispersal. *Holocene.* 2013;23:14–24.
- Campbell ID, McDonald K, Flannigan MD, et al. Long-distance transport of pollen into the Arctic. *Nature.* 1999;399:29–30.
- Tipping RM. Long-distance transported *Pinus* pollen as a possible chronostratigraphic marker in the Scottish early postglacial. *Boreas.* 2008;18:333–341.
- Hjelmroos M, Franzén LG. Implications of recent long-distance pollen transport events for the interpretation of fossil pollen records in Fennoscandia. *Rev Palaeobot Palynol.* 1994;82:175–189.
- Bajpai R, Kar R. Modern pollen deposition in glacial settings in the Himalaya (India): abundance of *Pinus* pollen and its significance. *Palynology.* 2018;42:475–482.
- Batten DJ, Dutta RJ. Ultrastructure of exine of gymnospermous pollen grains from Jurassic and basal Cretaceous deposits in Northwest Europe and implications for botanical relationships. *Rev Palaeobot Palynol.* 1997;99:25–54.
- Havinga AJ. A 20-year experimental investigation into the differential corrosion susceptibility of pollen and spores in various soil types. *Pollen Spores.* 1984;26:541–558.
- Bryant VM, Holloway RG. The role of palynology in archaeology. In: Schiffer MB, editor. *Advances in archaeological method and theory*, Vol. 6. London (UK): Academic Press; 1983. p.191–224.
- Campbell ID. Quaternary pollen taphonomy: examples of differential redeposition and differential preservation. *Palaeogeogr Palaeoclimatol Palaeoecol.* 1999;149:245–256.
- Bunting MJ, Tipping R. Sorting dross from data: possible indicators of post-depositional assemblage biasing in archaeological palynology. In: Bailey G, Charles R, Winder N, editors. *Human ecodynamics.* Oxford (UK): Oxbow Books; 2000. p.63–69.
- Davis MB. On the theory of pollen analysis. *Am J Sci.* 1963; 261:897–912.
- Andersen ST. The relative pollen productivity and pollen representation of North European trees, and correction factors for tree pollen spectra: determined by surface pollen analyses from forests. *Danmarks Geologiske Undersøgelse II. Række.* 1970;96:1–99.
- Andersen ST. The differential pollen productivity of trees and its significance for the interpretation of a pollen diagram from a forested region. In: Birks HJB, West RG, editors. *Quaternary plant ecology.* Oxford (UK): Blackwell; 1973. p.109–115.
- Prentice IC. Pollen representation, source area, and basin size: toward a unified theory of pollen analysis. *Quat Res.* 1985;23:76–86.
- Bunting MJ, Middleton R. Equifinality and uncertainty in the interpretation of pollen data: the multiple scenario approach to reconstruction of past vegetation mosaics. *Holocene.* 2009; 19:799–803.

34. Sugita S. Theory of quantitative reconstruction of vegetation I: pollen from large sites REVEALS regional vegetation composition. *Holocene*. 2007;17:229–241.
35. Sugita S. Theory of quantitative reconstruction of vegetation II: all you need is LOVE. *Holocene*. 2007;17:243–257.
36. Prentice IC. Records of vegetation in time and space: the principles of pollen analysis. In: Huntley B, Webb T, editors. *Vegetation history*. Dordrecht (the Netherlands): Springer; 1988. p.17–42.
37. Sugita S. A model of pollen source area for an entire lake surface. *Quat Res*. 1993;39:239–244.
38. Poska A, Saarse L, Koppel K, et al. The Verijärv area, south Estonia over the last millennium: a high-resolution quantitative land-cover reconstruction based on pollen and historical data. *Rev Palaeobot Palynol*. 2014;207:5–17.
39. Hjelle KL, Mehl IK, Sugita S, et al. From pollen percentage to vegetation cover: evaluation of the Landscape Reconstruction Algorithm in western Norway. *J Quat Sci*. 2015;30:312–324.
40. Hellman S, Gaillard MJ, Broström A, et al. The REVEALS model, a new tool to estimate past regional plant abundance from pollen data in large lakes: validation in southern Sweden. *J Quat Sci*. 2008;23:21–42.
41. Sugita S, Parshall T, Calcote R, et al. Testing the Landscape Reconstruction Algorithm for spatially explicit reconstruction of vegetation in northern Michigan and Wisconsin. *Quat Res*. 2010;74:289–300.
42. Marquer L, Gaillard M-J, Sugita S, et al. Quantifying the effects of land use and climate on Holocene vegetation in Europe. *Quat Sci Rev*. 2017;171:20–37.
43. Sugita S. Pollen representation of vegetation in quaternary sediments: theory and method in patchy vegetation. *J Ecol*. 1994; 82:881.
44. Farrell M, Bunting MJ, Sturt F, et al. Opening the woods: towards a quantification of neolithic clearance around the Somerset Levels and Moors. *J Archaeol Method Theory*. 2020;27:271–301.
45. Waller M, Grant MJ, Bunting MJ. Modern pollen studies from coppiced woodlands and their implications for the detection of woodland management in Holocene pollen records. *Rev Palaeobot Palynol*. 2012;187:11–28.
46. Tipping R, Bunting MJ, Davies AL, et al. Modelling land use around an early neolithic timber ‘hall’ in northeast Scotland from high spatial resolution pollen analyses. *J Archaeol Sci*. 2009;36:140–149.
47. Bunting MJ, Farrell M. Seeing the wood for the trees: recent advances in the reconstruction of woodland in archaeological landscapes using pollen data. *Environ Archaeol*. 2018;23:228–239.
48. Jones J, Tinsley H, Brunning R. Methodologies for assessment of the state of preservation of pollen and plant macrofossil remains in waterlogged deposits. *Environ Archaeol*. 2007;12:71–86.
49. Broström A, Nielsen AB, Gaillard MJ, et al. Pollen productivity estimates of key European plant taxa for quantitative reconstruction of past vegetation: a review. *Veget Hist Archaeobot*. 2008;17:461–478.
50. Bunting MJ, Farrell M, Broström A, et al. Palynological perspectives on vegetation survey: a critical step for model-based reconstruction of quaternary land cover. *Quat Sci Rev*. 2013;82: 41–55.
51. Bunting MJ, Farrell M. Do local habitat conditions affect estimates of relative pollen productivity and source area in heathlands? *Front Ecol Evol*. 2022;10:787345.
52. Githumbi E, Pirzamanbein B, Lindström J, et al. Pollen-based maps of past regional vegetation cover in Europe over 12 millennia—evaluation and potential. *Front Ecol Evol*. 2022;10:795794.
53. Mazier F, Gaillard M-J, Kuneš P, et al. Testing the effect of site selection and parameter setting on REVEALS-model estimates of plant abundance using the Czech Quaternary Palynological Database. *Rev Palaeobot Palynol*. 2012;187:38–49.
54. Marquer L, Mazier F, Sugita S, et al. Pollen-based reconstruction of Holocene land-cover in mountain regions: evaluation of the Landscape Reconstruction Algorithm in the Vicdessos Valley, northern Pyrenees, France. *Quat Sci Rev*. 2020;228:106049.
55. Mazier F, Broström A, Bragée P, et al. Two hundred years of land-use change in the South Swedish Uplands: comparison of historical map-based estimates with a pollen-based reconstruction using the landscape reconstruction algorithm. *Veget Hist Archaeobot*. 2015;24:555–570.
56. Trondman AK, Gaillard MJ, Sugita S, et al. Are pollen records from small sites appropriate for REVEALS model-based quantitative reconstructions of past regional vegetation? An empirical test in southern Sweden. *Veget Hist Archaeobot*. 2016;25:131–151.
57. Serge MA, Mazier F, Fyfe R, et al. Testing the effect of relative pollen productivity on the REVEALS model: a validated reconstruction of Europe-wide holocene vegetation. *Land*. 2023;12: 986.
58. Sangster AG, Dale HM. Pollen grain preservation of underrepresented species in fossil spectra. *Can J Bot*. 1964;42:437–449.
59. Sangster AG, Dale HM. A preliminary study of differential pollen grain preservation. *Can J Bot*. 1961;39:35–43.
60. Campbell ID, Campbell C. Pollen preservation: experimental wet-dry cycles in saline and desalinated sediments. *Palynology*. 1994;18:5–10.
61. Twiddle CL, Bunting MJ. Experimental investigations into the preservation of pollen grains: a pilot study of four pollen types. *Rev Palaeobot Palynol*. 2010;162:621–630.
62. Holloway RG. Experimental mechanical pollen degradation and its application to quaternary age deposits. *Tex J Sci*. 1989;41:131–145.
63. Stockmann U, Minasny B, McBratney AB. How fast does soil grow? *Geoderma*. 2014;216:48–61.
64. Bell KL, Turo KJ, Lowe A, et al. Plants, pollinators and their interactions under global ecological change: the role of pollen DNA metabarcoding. *Mol Ecol*. 2023;32:6345–6362.
65. Johnson MD, Freeland JR, Parducci L, et al. Environmental DNA as an emerging tool in botanical research. *Am J Bot*. 2023;110:e16120.
66. Berdahl MH. Pollen analysis by FTIR spectroscopy: a feasibility study for an automated method [master’s thesis]. Ås (Norway): Norwegian University of Life Sciences; 2015.
67. Diehn S, Zimmermann B, Tafintseva V, et al. Discrimination of grass pollen of different species by FTIR spectroscopy of individual pollen grains. *Anal Bioanal Chem*. 2020;412:6459–6474.
68. Schaefer J, Milling M, Schuller BW, et al. Towards automatic airborne pollen monitoring: from commercial devices to operational by mitigating class-imbalance in a deep learning approach. *Sci Total Environ*. 2021;796:148932.
69. Sevillano V, Holt K, Aznarte JL. Precise automatic classification of 46 different pollen types with convolutional neural networks. *PLoS One*. 2020;15:e0229751.
70. Scheifinger H, Belmonte J, Buters J, et al. Monitoring, modelling and forecasting of the pollen season. In: Sofiev M, Bergmann K-C, editors. *Allergenic pollen*. Dordrecht (the Netherlands): Springer Netherlands; 2013. p.71–126.
71. Cramer RJ, Brodsky SL, DeCoster J. Expert witness confidence and juror personality: their impact on credibility and persuasion in the courtroom. *J Am Acad Psychiatry Law*. 2009;37:63–74.
72. Jiang X, Pell MD. The sound of confidence and doubt. *Speech Commun*. 2017;88:106–126.