Are modern pollen assemblages from soils and mosses the same? A comparison of natural pollen traps from subtropical China

Yiman Fang [a,b*], M. Jane Bunting [b], Chunmei Ma [c], Xiaoping Yang [a]

a. Key Laboratory of Geoscience Big Data and Deep Resource of Zhejiang Province, School of Earth Sciences, Zhejiang University, Hangzhou 310027, China

b. Department of Geography, Geology and Environment, Cohen Building, University of Hull, Cottingham Road, Hull, HU6 7RX, UK

c. School of Geography and Ocean Science, Nanjing University, Nanjing 210023, China

* Corresponding author: Yiman Fang (yimanfang@zju.edu.cn)

Abstract

This study investigated the pollen spectra from 46 pairs of soil and moss samples (pairs collected within a $1m^2$ squared area). The samples were collected from six common subtropical vegetation communities in the Meiling Mountains, southeast China, with the vegetation proportions recorded at the collection point. Principal Component Analysis (PCA) was used to investigate the separation of the paired assemblages and to determine whether different plant communities produced distinctive pollen spectra. Paired soil and moss samples captured similar levels of variability in the pollen assemblages retained, but there are systematic differences in the mean values of key groups of taxa. Montecarlo sampling shows that, in most cases, intra-pair differences are greater than could be explained by counting uncertainty alone.

In this study, discriminant analysis of surface soil and moss found that 91.3% of the soil samples and 87% of the moss samples were correctly classified into their vegetation communities. However, the detailed pollen assemblages suggest that mosses provide a more accurate representation of the contemporary vegetation composition than soils.

Pollen assemblages from moss samples seem to record local vegetation more accurately than those from soil samples. Higher vegetation diversity within an arboreal forest community leads to greater differences between moss-soil pairs. In bamboo forests, pollen assemblages in soils and moss show strong influence from the surrounding communities, which makes it hard to identify bamboo forest via surface sample pollen assemblages alone.

Keywords

pollen-vegetation calibration, soil and moss, southeast China, subtropical, surface pollen samples, vegetation diversity

INTRODUCTION

The use of surface samples as natural pollen traps to investigate the pollen signal produced by extant vegetation has become a standard tool for improving interpretation of palaeopollen assemblages (Erdtman, 1969; Adam & Mehringer, 1975; Faegri et al., 1989; Moore et al., 1991). Pollen assemblages can be recovered from a wide variety of contexts (e.g. forensic studies (Wiltshire, 2004; Mildenhall, 2006)), but caution is needed when interpreting palaeosamples, as the pollen assemblages is determined by the taphonomic and preservation conditions of the specific context (Potter, 1967; Felde et al., 2016; Xu et al., 2016). Pollen taphonomy is defined as the whole process leading to the creation of pollen assemblages from living vegetation (West, 1973), which is usually divided into pollen production, pollen transport, sedimentation and post-depositional processes (Coles et al., 1989; Campbell, 1999). Surface pollen samples only reflect part of this process, since post-depositional processes have only acted for a period of months to years, whereas palaeosamples experience much longer periods of post-deposition (Figure 1). It is generally assumed that post-depositional processes have negligible effects on pollen assemblages, although this is highly context-dependent (e.g. Havinga, 1984; Holmes, 1994; Twiddle & Bunting, 2010).

For comparison with the assemblages preserved in the sedimentary deposits, surface pollen spectra have been collected in a variety of ways using both artificial traps (e.g. Tauber traps (Tauber, 1974); Cundill traps (Cundill, 1986)) and ‘natural traps’ where taphonomy and preservation are believed to be comparable with the sediment-forming system (mainly from waterlogged sediments (e.g. Faegri et al., 1989; Wilmshurst & McGlone, 2005; Pandey et al., 2021), moss polsters (e.g. Caseldine, 1981; Hjelle, 1998; Pardoe et al., 2010) and soil samples (e.g. Riding et al., 2007)).

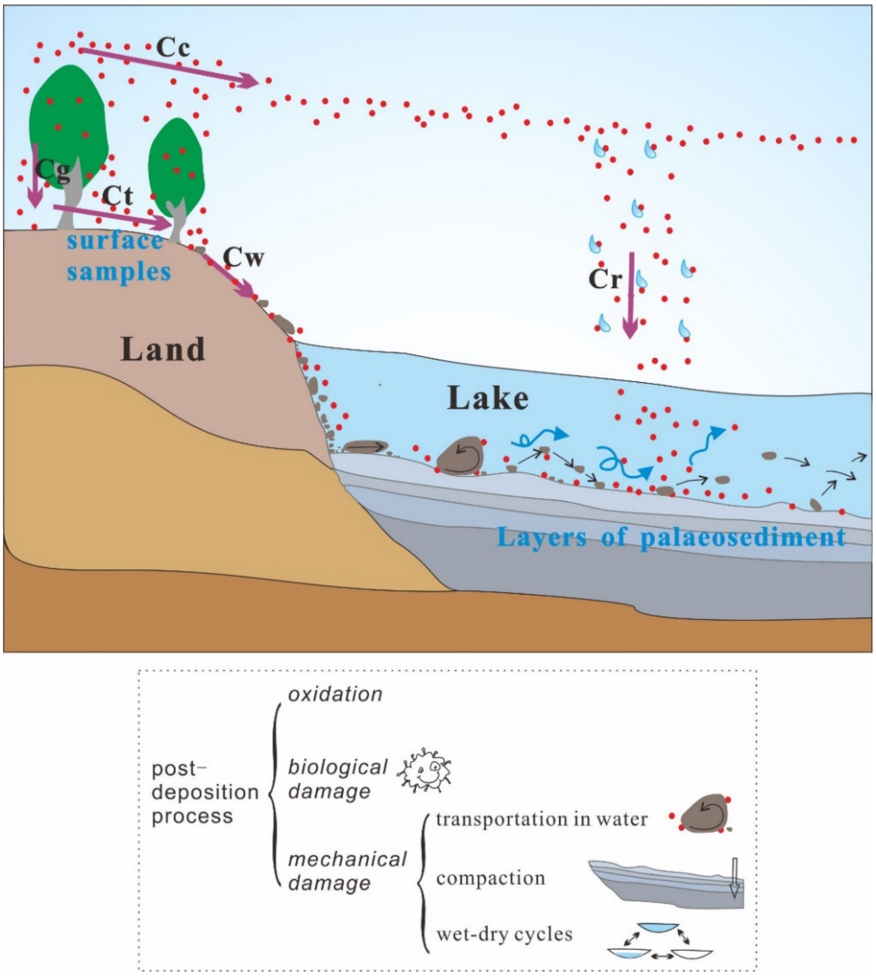

FIGURE 1 Schematic diagram showing Tauber model of pollen taphonomy for surface sample in lakes. Red dot: pollen grain, Cc: canopy component, Ct: trunk space component, Cr: long-distance component by precipitation, Cw: runoff component, Cg: gravity component (after Tauber, 1965, 1967; Jacobson & Bradshaw, 1981; redrawn from Bunting et al., 2013). Post-depositional damage to pollen grains is likely to be context-specific, which is assumed to have more effects on fluvial sediment samples.

Pollen assemblages from mosses and soils have been widely used to inform the interpretation of past land cover from pollen records. For instance, pollen representation studies using moss or surface soil from different vegetation communities aim to see if open and forest communities can (or cannot) be differentiated through modern pollen data (e.g. Tarasov et al., 19 98; Djamali et al., 2009; Connor et al., 2004; Salonen et al., 2011).

Poaceae presents a particular challenge, since the pollen type is widely found in Quaternary sediments, but in subtropical regions it can originate from two functionally different groups, herbaceous and arboreal (bamboo) grasses. Soil and moss samples can also be used to calibrate models of pollen dispersal and deposition (e.g. Mazier et al., 2012). These calibration exercises produce estimates of the Relative Pollen Productivity (RPP) of plant taxa (e.g. Mazier et al., 2008; Broström et al., 2008; Li et al., 2018) and Relevant Source Area of Pollen (RSAP), which for soils or mosses under tree canopies are typically a few hundred meters. Studies in different locations yield varying estimates of RPP for the same taxa, which could reflect real differences between geographic regions due to climate differences and species mixture, or it could be an artefact caused by the use of different pollen traps between studies.

Moss polsters are widely used in terrestrial surface sampling (e.g. Moore et al., 1991; Bunting & Hjelle, 2010; Farrell et al., 2016). Different species of moss may differ in their growth form and surface texture. The growth form, namely the shape, density and height of moss, plays an important role in filtering and retention of different pollen grains (Crowder & Cuddy, 1973; Boyd, 1986). Most investigators do not specify the species of moss collected for their studies although Boyd (1986) indicated that *Brachyiheciitrti rittabuktrn* has the best trapping efficiency among eight moss types studied in Scotland. In general, polster-forming mosses are always a better choice to ensure the efficiency of trapping pollen.

In order to get a reliable pollen assemblage, it is important to have an average of several years of pollen deposition, since annual differences in flowering occur. Unlike artificial pollen traps, the time period over which pollen has been deposited is not easily known for moss polsters. Crowder & Cuddy (1973) suggested that mosses may reflect the pollen deposition from 5-15 years, whilst Bradshaw (1981) proposed that the green parts of the moss represent the last 5 years of growth. Cundill (1985) suggested that the period of pollen deposition represented by moss polsters varied depending on when they were collected. A direct comparison study between modified Tauber traps and moss samples in Finland found that moss samples represented only 1-2 years of pollen deposition (Räsänen et al., 2004). For some mosses, it is possible to identify annual growth markers and therefore determine the age of the sampled material (e.g. *Sphagnum* and *Polytrichum*) (Räsänen et al., 2004).

Surface soil samples are quite widely used to obtain modern pollen assemblages due to their easy accessibility, especially in semi-arid and arid areas where moss polsters are not readily available (e.g. Maher, 1963; Hevly et al., 1965; Hill, 1996; Carrión, 2002; Zhao et al., 2009; Li et al., 2011). However, the pollen assemblages from soils need to be interpreted with caution (Adam & Mehringer, 1975; Hill, 1996). There are potential risks of incorporation of older pollen by mixing, of selective pollen decay and long-term pollen accumulation (Moore et al., 1991). Preservation of pollen in soil can be influenced by factors such as pH level and temperature. Soil fauna, such as earthworms, are also responsible for producing vertical movements of pollen in soils (Walch et al., 1970).

In this paper we present a comparison of soil and moss pollen assemblages in a subtropical forest area where moss and soil were both available. Multiple sites were selected in each of the dominant plant communities, and at each site paired moss and soil samples were collected within a 1m^2 quadrat. We assumed that the initial pollen deposition across the quadrat was even and consistent, and that any observed differences between the paired samples is largely due to differences in the trap type (i.e. soil or moss). The aims of this study are to investigate:

1. whether the pollen assemblages are different between the two types of ‘natural traps’ in a subtropical environment,
2. whether the cause of any detected difference can be identified (e.g. sampling

effects, differences in effective pollen source area, differences in short-term preservation of pollen, etc.),

3. whether pollen assemblages from natural traps are able to discriminate between different sub-tropical vegetation communities, especially between the ecologically distinct Poaceae dominated grassland and bamboo forest.

MATERIALS AND METHODS

Study area and sampling

This study was conducted in the sub-tropical forest in the Meiling National Scenic Area in southeast China (28°31′N - 28°54′N, 115°34′E - 115°53′E; Figures 2a and 2b). The mountain range is approximately 39 kilometers long and oriented in a northeast-southwest direction. The climate is mainly controlled by the southeast subtropical monsoon, with an annual average temperature of 18.8 ℃ and annual mean precipitation of 1760 mm (China Meteorological Administration Data Service Center, 1981-2010).

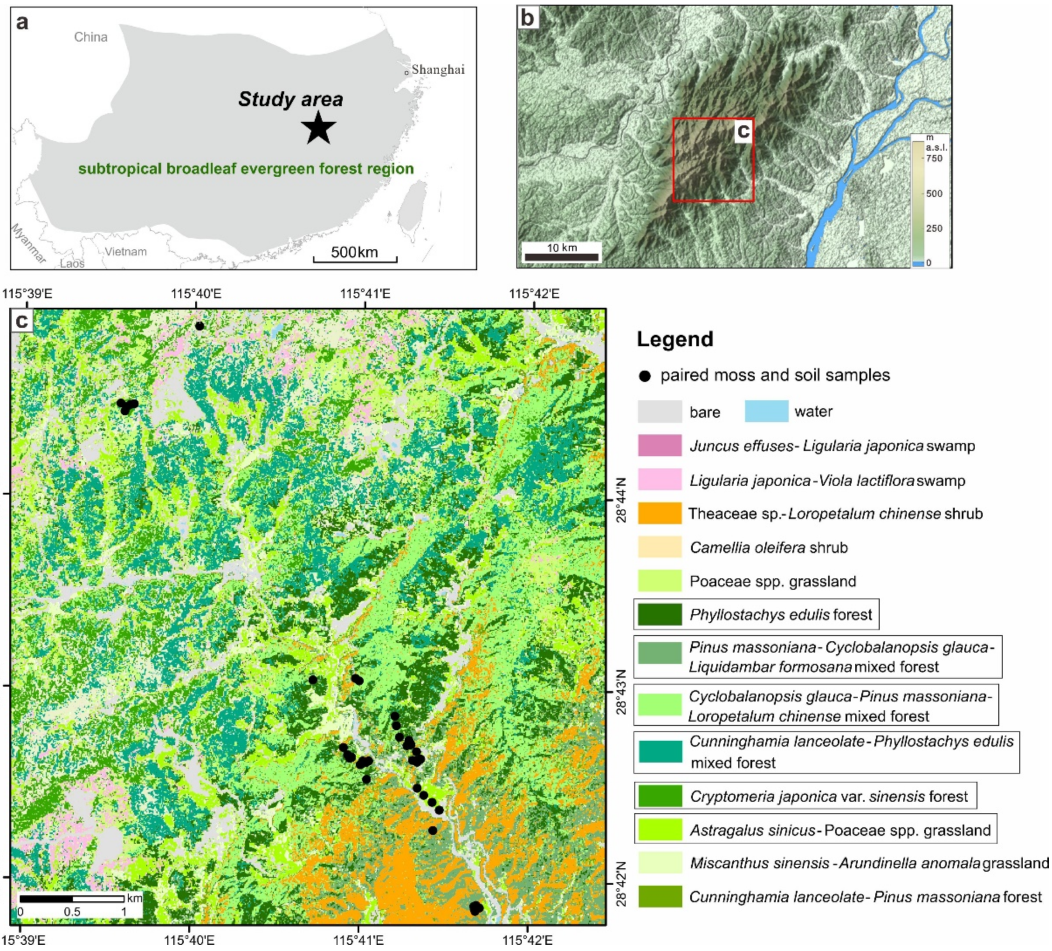

FIGURE 2 Locations of the 46 paired sampling sites in Meiling Mountains, southeast China (a. location of the study area, b. DEM map showing the Meiling Mountains, c. vegetation map showing distribution of 13 biogeographic groups and locations of the 46 paired samples). The paired samples are located in the six main communities, which are highlighted with boxes in the legend.

Forest coverage within the Scenic Area is around 89% (Ding et al., 1965). The vegetation communities are mainly subtropical needleleaf forest (dominated by *Pinus massoniana* and *Cunninghamia lanceolata*), subtropical broadleaf deciduous forest (characterized by *Castanea sequinii*, *Quercus serrata* var. *breviptiolata* and *Platycarya strobilacea*), subtropical broadleaf evergreen forest (dominated by *Castanopsis sclerophylla* and *Cyclobalanopsis glauca*), subtropical bamboo forest (dominated by *Phyllostachys edulis*) and scrub. The bamboo forest is managed by the villagers living nearby. Scattered fields used for growing rice and vegetables occur in the valleys and foothills, which sometimes become grassland when the farmlands are abandoned.

During field excursions in March and April 2016, 46 sample points were selected in the six main communities (five forest and one grassland; Figure 2c; Table 1). In order to avoid different size openings, sampling sites in the forest are chosen to be under forest canopy. The paired sites are spaced at least 50m apart, a distance chosen on the assumption that the pollen source area for ground cover plants under the forest canopy would be short. Samples came from sites not visibly altered by recent human disturbance. The coordinates and altitude of each site were measured with hand-held GPS.

TABLE 1 Number of sample points located in each community

Abbreviation	Vegetation communities	Main species	No. of sample points in each community
Phy. F	*Phyllostachys edulis* forest	*Phyllostachys edulis*, *Theaceae* sp.	10
Cun.-Pin. F	*Cunninghamia lanceolate - Pinus massoniana* forest	*Pinus massoniana*, *Cunninghamia lanceolate*	7
Cyc.-Pin.-Lor. F	*Cyclobalanopsis glauca - Pinus massoniana- Loropetalum chinense* mixed forest	*Pinus massoniana*, *Loropetalum chinense*, *Cyclobalanopsis glauca*, *Liquidambar formosana*	10
Pin.-Cyc.-Liq. F	*Pinus massoniana - Cyclobalanopsis glauca - Liquidambar formosana* mixed forest	*Cyclobalanopsis glauca*, *Liquidambar formosana*, *Pinus massoniana*, *Platycarya strobilacea*, *Castanea* sp., *Cunninghamia lanceolate*	9
Cry. F	*Cryptomeria japonica* var. *sinensis* forest	*Cryptomeria japonica* var. *sinensis*	6
Mis.-Aru. G	*Miscanthus sinensis - Arundinella anomala* grassland	*Miscanthus sinensis*, *Arundinella anomala*	4

At each sample point, a 1m^2 quadrat was placed over a suitable moss polster, and both the moss polster and adjacent soil were sampled. Pollen assemblages from these two sources are referred to as a pair. In order to keep sample volume consistent, samples were collected using inverted sample containers measuring 7.5 cm * 7.5 cm * 1 cm in size, and only the green parts of the moss polster were collected. Vegetation cover (percentage of canopy species present) was recorded using the Crackles Bequest Project methodology (Bunting et al., 2013). The regional vegetation map was derived from interpretation of the Sentinel-2 image coupled with detail ground-based vegetation surveys to define the boundaries of the communities.

Pollen extraction from surface samples followed standard preparation techniques (Faegri et al., 1989; Moore et al., 1991). One *Lycopodium* tablet (27560 spores/tablet) was added to each sample as a tracer. The chemical treatment procedures used include HCl (10%), KOH (10%), HF (40%), and samples were then acetolyzed with acetic anhydride and sulfuric acid (9:1), sieved and mounted in glycerine jelly. A minimum of 400 terrestrial pollen grains were counted for each sample. Pollen were identified with reference to Wang et al. (1995) and Tang et al. (2016) and counted under an optical microscope at magnification of 400×.

Data analysis methods

Pollen data

In order to reduce the bias caused by abundantly produced but poorly dispersed spores (Wilmshurst & McGlone, 2005), pollen percentages of the terrestrial taxa were calculated based on all terrestrial pollen grains. Percentages of aquatic herbs' pollen and ferns' spores were calculated based on a sum of all pollen and spores. The pollen percentage diagram was plotted using Tilia 2.0.4 (Grimm, 1991 and updated versions).

For numerical analysis of pollen assemblages, principal component analysis (PCA) is performed with CANOCO (CANOnical Community Ordination) 4.5 (ter Braak & Verdonschot, 1995; ter Braak & Smilauer, 1997, 2002). The PCA was carried out on a dataset including 49 pollen and spore types, all those with a value of over 2% in at least two samples. A definition of ordination is that it arranges sample points in such a way that distance between points corresponds as well as possible with the dissimilarity between sites (ter Braak, 1994); points which are close together in the diagram are similar in species composition. Therefore, we calculated the Pythagorean distance between each paired sample in the ordination plot as a measure of similarity and compared vectors of difference to determine whether there was a systematic pattern to the differences seen.

We also grouped paired samples according to their community of origin and averaged the distance for each vegetation community, then plotted the centroids of each sample type in the six communities. The coordinates (X_i, Y_i) of centroids were calculated based on the formula below:

$$X_i = \frac{1}{k}\left(\sum_1^k x_k\right)$$

$$Y_i = \frac{1}{k}\left(\sum_1^k y_k\right)$$

Where X_i is the x coordinate of the centroid for community i, and Y_i is the y coordinate of the centroid for community i,

x_k is the axis 1 value of sample core from PCA, y_k is the axis 2 value of sample core from PCA,

i is the number of the vegetation community; in this study, n=1,2,3,4,5,6,

k is the number of the samples in each forest zones.

In order to evaluate whether different vegetation communities could be identified from pollen assemblages, discriminant analysis was performed using SPSS 17.0 (SPSS Inc., 1993-2007). This method has been efficiently used to aid pollen-based palaeovegetation reconstruction (e.g. Liu & Lam, 1985; MacDonald & Ritchie, 1986) and to assess the relationship between modern pollen and vegetation (e.g. Shen et al., 2008; Marcos & Mancini, 2012). The discriminant functions can be generated from known groups of sample sets, and then be applied to classify new cases which have measures for the predictor variables but unknown group membership (SPSS Inc., 1993-2007). In this study, percentage of major pollen types were used to create the discriminant function, these were used as *a priori* groups for discriminant analysis. The samples were then classified into predicted vegetation communities.

Counting error

Counting error is an important parameter which needs to be taken into account in determining whether the difference between pairs is a real difference in the underlying pollen assemblage, or an apparent difference caused by sampling effects. We used a Montecarlo approach to determine the difference between samples due solely to sampling effects, by taking a random sample pair in each of the 6 communities, using the recorded pollen proportions as a probability distribution, then simulating multiple pollen counts of the same assemblage. This procedure was repeated 5 times for each simulated sample, thus generating 25 simulated pairs in each community. These real and simulated pairs were reranked using PCA and then compared pairwise using Pythagorean distance based on the ordination scores from PCA.

Effect of vegetation composition on sample difference

We hypothesized that sample pairs from more diverse vegetation communities would tend to have larger intra-pair differences. We calculated the Shannon index (Shannon & Weaver,

1949) and the Simpson index (Simpson, 1949) for each community based on the composition data on the canopy species, choosing these metrics owing to their extensive application in the ecological literature (e.g. Duelli & Obrist, 1998; Keylock, 2005; Allen et al., 2009).

The Shannon index of diversity is defined as:

$$S_{Shannon} = -\sum_{i=1}^{N} p_i ln p_i$$

The Simpson index is calculated as follows:

$$S_{Simpson} = 1 - \sum_{i=1}^{N} p_i^2$$

Where N is the number of species in the community,

p_i is the proportion of species i

RESULTS

Differences between moss and soil samples

Generally, soil and moss samples show similar characteristics and ranges, but different mean values of key groups of taxa. The mean percentages of arboreal types are lower and of herb taxa are higher in soil samples than in moss samples (Figure 3).

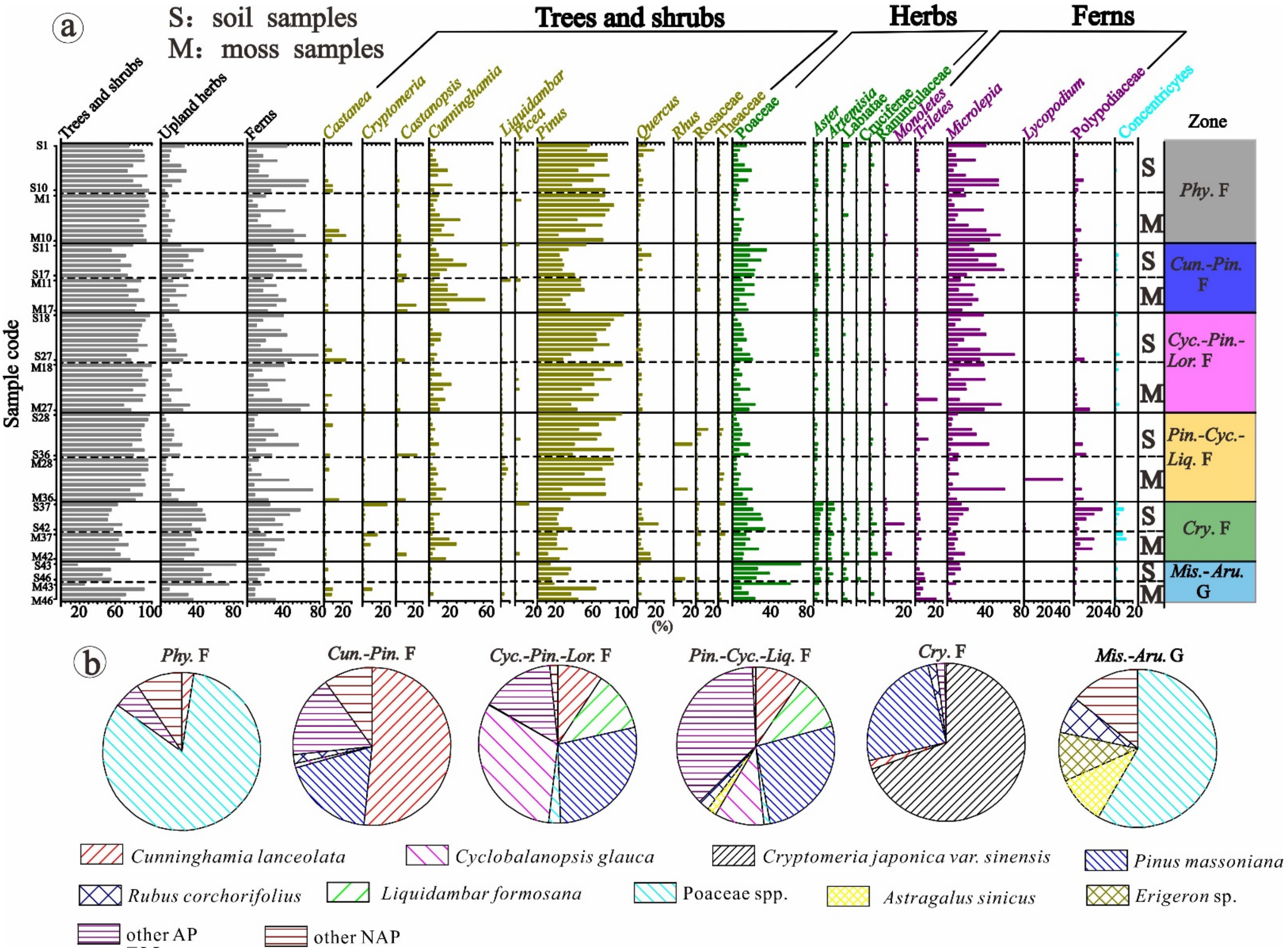

FIGURE 3 Pollen assemblages and vegetation composition in the six vegetation communities including a) pollen percentage diagram from paired surface soil and moss samples and b) pie chart showing the average vegetation percentage in the six communities.

Pollen assemblages in the six vegetation communities

Generally, *Pinus* and *Cunninghamia* dominate the pollen spectra of all forests, even in some communities where both of them are rarely found in vegetation (e.g. the bamboo forest, *Cryptomeria japonica* var. *sinensis* forest). Poaceae is the most abundant herbaceous pollen type in all the forest assemblages.

Compared to the pollen assemblage of the five forest zones, the pollen spectra in the grassland are characterised by higher upland herbs and lower arboreal types. The main species in the pollen spectra are *Pinus*, Poaceae and Compositae types. Although there is no *Pinus* present within the 100 m radius area around these sampling points, there are still *Pinus* pollen grains present in all grassland samples.

Ordination analysis

Figure 4 shows ordination plots of axes 1 and 2, which have eigenvalues of 0.533 and 0.266 respectively, and together explain 79.9% of the total variance in the dataset. Analysis was run with all samples together, but the results are plotted separately for soil and moss samples for clarity. The envelope encompassing the assemblages from the *Cun.-Pin.* F and the *Cry.* F are larger for soil samples than for moss samples, but the other four communities have similar envelope sizes for both sample types.

Many of the species are assigned low species scores and therefore have little impact on the distribution of samples. For clarity, only the top 20 scoring species are shown in Figure 4. Non-Arboreal Pollen (NAP) types and Arboreal Pollen (AP) types are not separated clearly along either axis, in fact the fern *Microlepia* seems to be the most important species in determining sample location (Fig. 4). The high value of *Microlepia* represents background noise by its high local over-representation, and this justifies our approach whereby the ferns were excluded from the pollen sum to avoid bias.

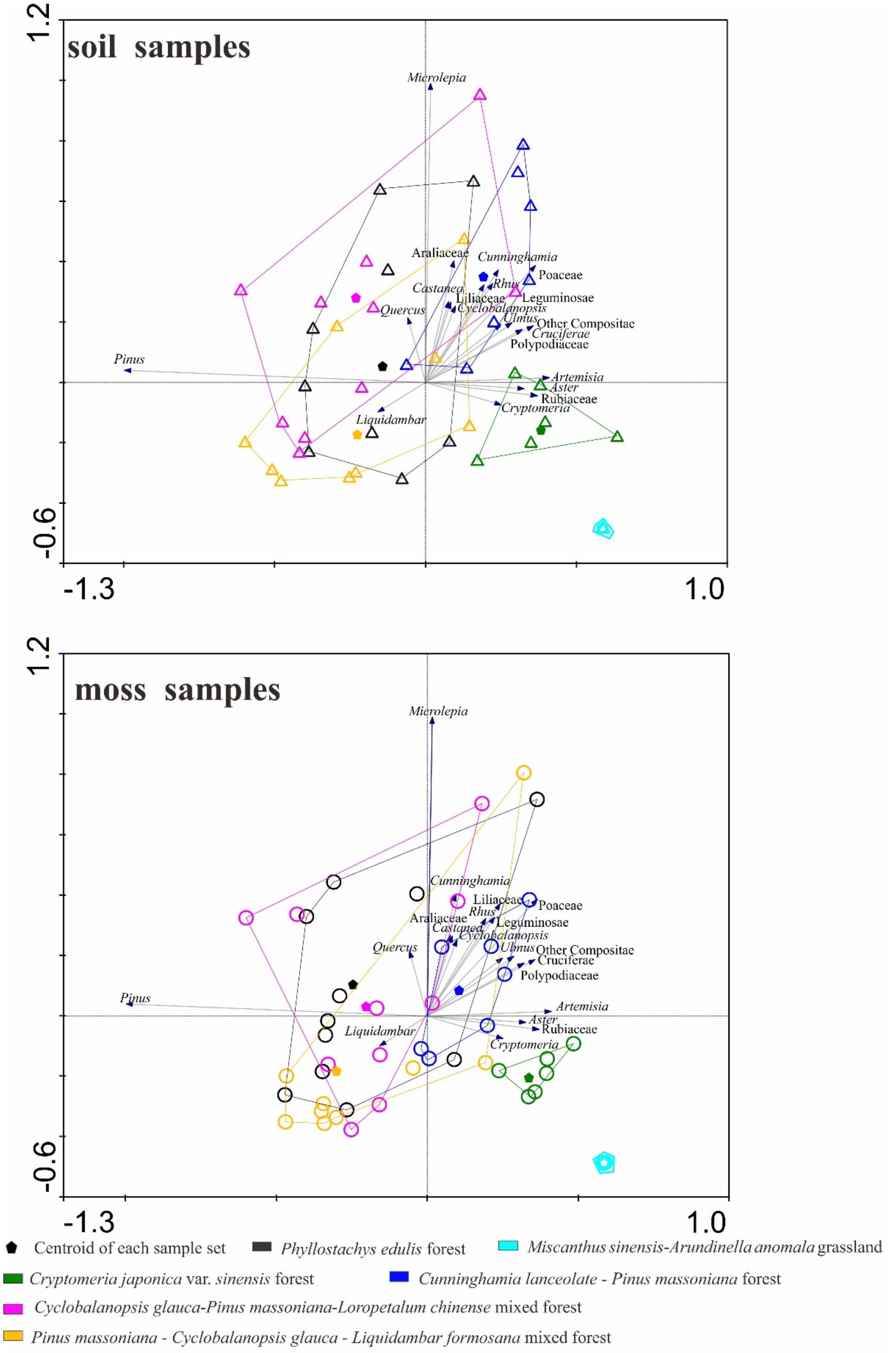

FIGURE 4 Ordination based on Principle Components Analysis (PCA) diagram showing pollen assemblages in the 6 vegetation zones. All data were included in the analysis, but are plotted on

separate diagrams for clarity. Ellipses are envelopes around samples from them. Centroids (multivariate centers of distribution) of each vegetation communities were plotted post hoc to visualize these relationships among sites.

Paired sample distances

Figure 5 shows the sample pairs plotted on the same axes as Figure 4, joined by lines to show the vector of difference. There is no common vector direction for individual pairs in any of the six communities, but when the centroids of each community group were considered (Figure 5 inset), all groups showed a dominant ‘north’ to ‘south’ trend, from the soil sample sets to the moss sample sets.

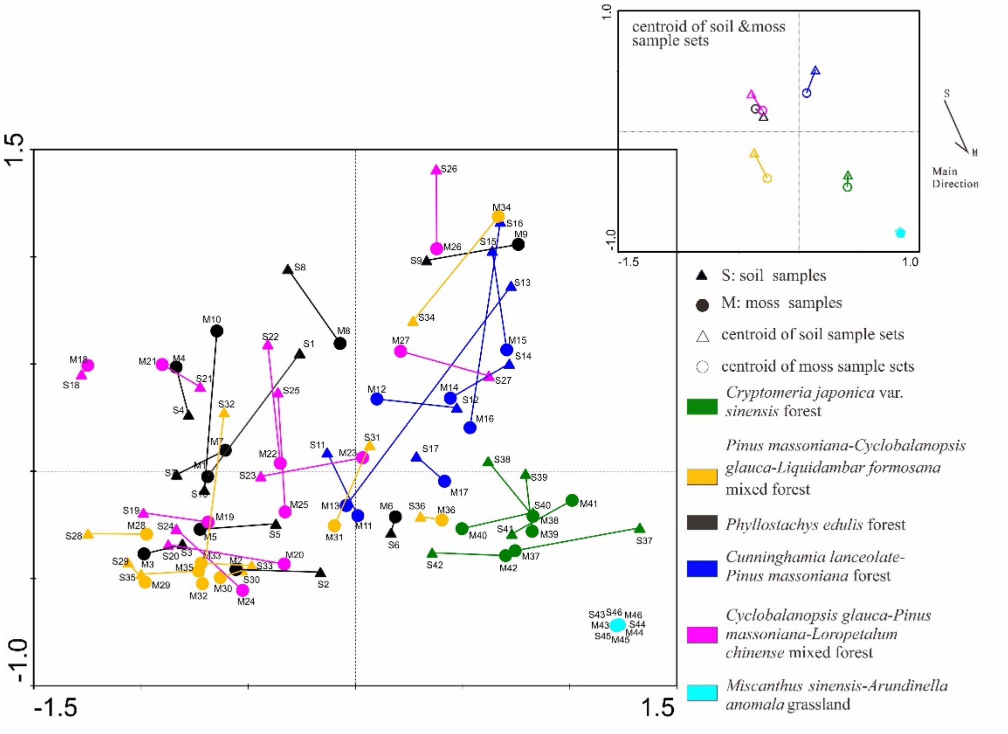

FIGURE 5 Ordination (PCA) diagram showing the patterns of change on paired samples. Filled up-triangle symbols: soil samples; filled circle symbols: moss sample. Insert: plot of centroids of soil (empty up-triangle) and moss (empty circle) samples for each forest zone.

Possible controls on paired sample difference

Vegetation diversity

For each of the communities, the Shannon index and the Simpson index were calculated and are presented in Figure 6.

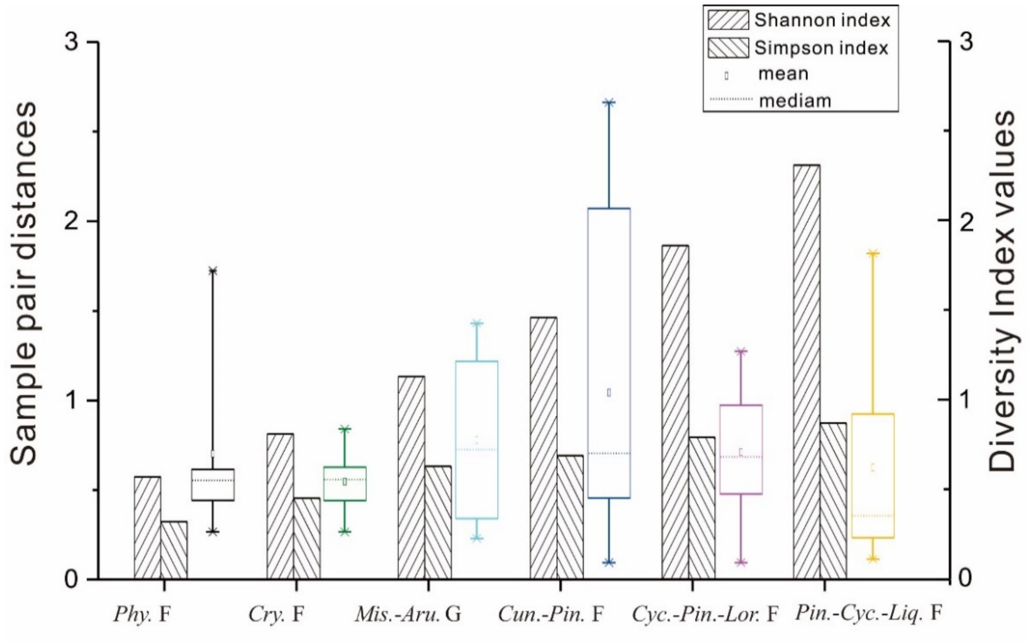

FIGURE 6 Boxplot showing paired sample distance in six communities. The middle line and the box represent the median and the first through third quartiles, respectively.

Both diversity indexes give the same rank order for the six vegetation communities. Maximum diversity is seen in the *Pin.-Cyc.-Liq.* F, and minimum values were found in the *Phy.* F. The median paired sample distance is the greatest in the *Cun.-Pin.* F, which also has relatively high vegetation diversity.

Counting error

After sorting all real and simulated samples again by PCA, the Pythagorean differences between all pairs were calculated according to the sample scores (Figure 7). The range of distances seen between the simulated samples, shown by the black dashed lines on Figure 7, indicate the range of difference values arising due to counting errors.

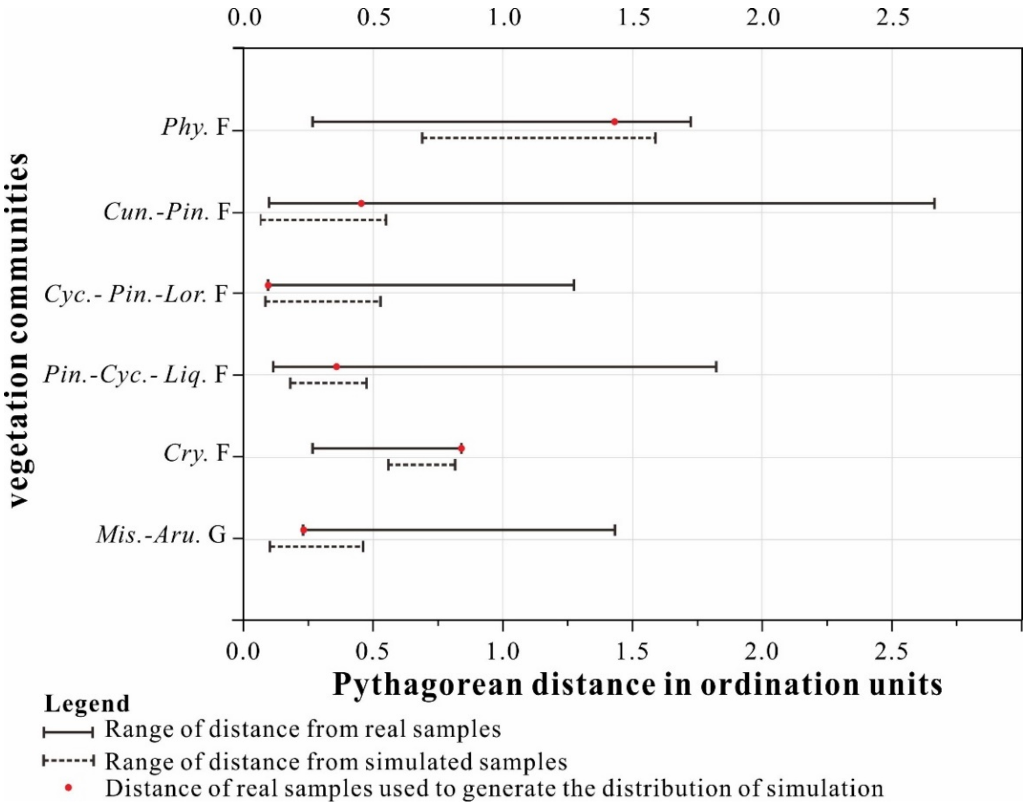

FIGURE 7 Comparison of Pythagorean distance in ordination units from real sample pair used for generating the simulation (black line) and simulated sample pairs (black dashed line) in six vegetation communities, the distances are calculated from sample scores from PCA output using 152 samples (92 real plus 60 simulated samples). The red dots show the distance of the real pairs used to create the distribution for simulation. The simulation count is generated using the recorded pollen proportions as a probability distribution.

The Pythagorean differences between paired soil and moss samples are greater than can be explained just by taking account of counting errors, especially in the *Cun.-Pin.* F, *Cyc.-Pin.-Lor.* F and *Pin.-Cyc.-Liq.* F communities, suggesting that there are some real differences in the pollen assemblages present in soils and mosses.

Identifying vegetation communities from pollen assemblages

Percentage data of the 20 main pollen types (those with high scores from the PCA) were used for discriminant analysis of surface soil and moss, respectively. The results show that 91.3% (42 out of 46) of the soil samples and 87% (40 out of 46) of the moss samples (Table 2) were correctly classified into their actual vegetation communities.

Samples from vegetation communities show clear grouping, with *Mis.-Aru.* G (grassland) and *Cry.* F (forest) clearly separate at the bottom right, and the other four forest communities overlapping in the upper portion of the ordination diagram (Figure 4). The discriminant analysis misclassifications all occurred within this group of four forest types, including S7, S10, M3 and M6 from *Phy.* F, M13 from *Cun.-Pin.* F, S21, M18 and M21 from *Cyc.-Pin.-Lor.* F, S35 and M33 from *Pin.-Cyc.-Liq.* F (Figure 8). This pattern is also demonstrated by their low probability of analogue (<0.5).

TABLE 2 Results of the discriminant analysis for soil and moss pollen assemblages

Sample type	Actual community	No. of samples	Predicted community					
			1	2	3	4	5	6
soil	*Phy.* F (1)	10	8(80%)	0	2(20%)	0	0	0
	Cun.- Pin. F (2)	7	0	7(100%)	0	0	0	0
	Cyc.- Pin.- Lor. F (3)	10	1(10%)	0	9(90%)	0	0	0
	Pin.-Cyc.-Liq. F (4)	9	0	0	1(11.1%)	8(88.9%)	0	0
	Cry. F (5)	6	0	0	0	0	6(100%)	0
	Mis.-Aru. G (6)	4	0	0	0	0	0	4(100%)
moss	*Phy.* F	10	8(80%)	1(10%)	1(10%)	0	0	0
	Cun.- Pin. F	7	0	6(85.7%)	0	1(14.3%)	0	0
	Cyc.- Pin.- Lor. F	10	2(20%)	0	8(80%)	0	0	0
	Pin.-Cyc.-Liq. F	9	1(11.1%)	0	0	8(88.9%)	0	0
	Cry. F	6	0	0	0	0	6(100%)	0
	Mis.-Aru. G	4	0	0	0	0	0	4(100%)

Percent of cases correctly classified: soil samples=91.3% ; moss samples=87%

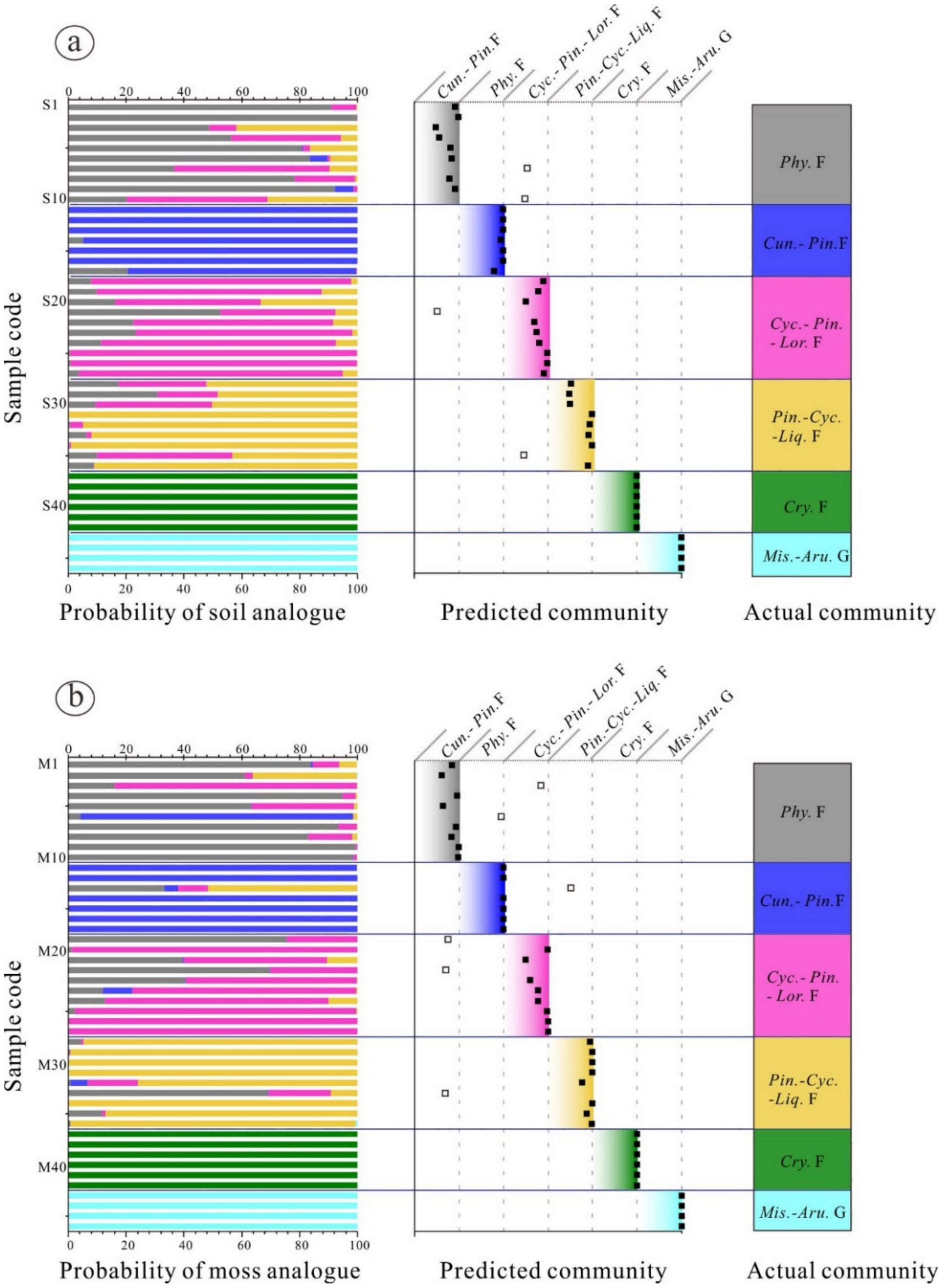

FIGURE 8 Comparison between predicted vegetation communities of discriminant analysis and actual vegetation types at sampling locations (a. soil samples, b. moss samples). ‘Probability of soil/moss analogue’ shows the probability of the sample in each of the six communities, which is determined by the chi-square distance between the sample and the group centroid defined by the discriminant functions. ‘Predicted community’ is assigned to the group for which it has the largest discriminant score. Misclassified samples were indicated by hollow box.

DISCUSSION

Pairwise comparisons between soil and moss samples

Figures 3 and 4 show that the pollen assemblages from soil and moss samples from different communities occupy the same space in the ordination diagram, but paired samples differ from each other (Figure 5). In some cases, the soil sample envelope is larger than moss sample envelope (Figure 4), which implies that the variation of soil pollen assemblages in those communities is larger than that of moss pollen assemblages.

Theoretically, Sugita (1994) estimates the relevant source area of pollen (RSAP) for basin with a radius of 2m (forest hollows) as 50-100m. Empirical study by Calcote (1995) supports the model prediction, and further confirms that 40%-50% of the pollen in the forest hollows comes from plants growing within 50-100m of the hollow. In this study, the samples in the forest are located beneath the forest canopy, and each pair was separated by at least 50 m and most by considerably more distance. Autocorrelation due to the sampling strategy is not likely to influence the pairwise differences since the sampling distance is close to the RSAP.

Counting a pollen assemblage produces an estimate of the true assemblage composition through sampling. Simulation (Figure 7) suggests that there are differences between paired soil and moss samples in excess of those arising due to counting errors. Other sources of uncertainty might be introduced during the analysis process, such as measurement error during sample collection (which would affect concentration but not percentage data), or different responses of soil and moss assemblages to treatments during sample preparation.

Vegetation diversity

Plant communities are innately more diverse than pollen communities since pollen taxonomy is derived from plant taxonomy and often cannot discriminate to the same level, and Figure 6 clearly shows that pollen assemblages are less biodiverse than plant assemblages in each community. However, vegetation diversity does not seem to be systematically related to sample pair distances. The variation between distance value for pairs within the same community is large, and there are only small differences in median values between communities. A difference might be expected if the less abundant plant types in the more diverse vegetation communities are under-represented, but the sample size seems to be sufficient to capture the overall diversity, likely because the community patches are small compared to the effective pollen source area, so the pollen assemblages are also picking up a general regional signal.

Preservation differences

Pollen trapped in soil is considered more likely than that from moss to experience post-depositional decay and therefore for assemblages to undergo systematic changes over relatively short periods of time (Havinga, 1964, 1967). Pollen types have differential susceptibility to oxidative damage and removal from the assemblage. Havinga (1984) found that spores and Cichorioideae (*Taraxacum*) were more resistant to decay than the other taxa, and Sangster & Dale (1961,1964) ranked pollen types from least to most resistant as '*Populus* < *Acer* < *Corylus* < *Alnus* < *Quercus* < *Fraxinus* < *Typha* < *Salix* < *Betula* < *Ulmus* < *Pinus*'.

If there was a systematic difference between moss and soil pairs, we would expect to see consistent ordination vector direction, at least within communities, since all soils would have more decay-resistant types and fewer decay sensitive types than their paired mosses. Figure 5 shows that there is no common direction of difference, therefore we consider it unlikely that observed differences are caused mainly by post-depositional changes. However, Figure 5 does show that the community centroids have a common vector of difference, which in the ordination seems to be largely driven by moss assemblages containing fewer fern-spores than soil pollen assemblages when averaged within communities (moss average between 15.0% and 31.8%; soil average between 17.1% and 44.6%). Fern spores are known to be fairly robust and resistant to decay (Havinga, 1984), and this might imply that the soil samples contain more spores because they represent a longer period of pollen deposition and/or because post-depositional biasing has acted to increase the apparent proportion of fern spores by removing other pollen types, but other explanations related to microhabitat are also possible (considered below).

Local taphonomy

Our study design implicitly assumes that the pollen deposition within the sampling quadrat was even and consistent and that differences between paired samples would reflect mainly counting and preservation differences. However, it is possible that pollen is not evenly distributed across the sampled 1m^2 quadrat, contributing to some of the observed differences. Tauber's (1965, 1977) model of the taphonomic routes by which pollen and spores arrive at moss and soil samples includes not just the canopy component (C_c) and long-distance component by precipitation (C_r), the components usually considered to be dominant in palaeorecords, but also three more local components, runoff (C_w – pollen deposited on a soil surface then moved by surface water flow), trunk space (C_t – pollen released from flowers located under the vegetation canopy and transported by local air currents), and gravity (C_g – grains and spores falling from flowering structures directly onto the sampling point under the influence of gravity) (Figure 1). In this study, sample locations were chosen on flat areas away from tree trunks to minimize contributions from C_w, but C_t and C_g are both plausible sources of pollen, and would contribute local elements.

For arboreal taxa, where all flowering structures are several meters above the ground, the assumption of even pollen rain is more reasonable than for understory taxa, which are smaller and grow closer to the ground. The quadrats for collecting the samples were placed in locations free from understory plants (wherever possible) to minimize the possible bias caused by C_g pollen input, but in subtropical forests, the contribution of nearby understory vegetation (mainly shrubs and ferns) through C_t cannot be neglected. Pollen transport through the trunk space is found to be an important source of pollen delivered to small lakes and forest hollows in a mixed deciduous forest (e.g. Tauber, 1965, 1967; Andersen, 1970). In this study, the trunk space component is likely to play a different role in different communities. The four mixed subtropical forest communities (i.e. *Cun.-Pin.* F, *Cyc.-Pin.* F, *Pin.-Cyc.-Liq.* F, *Cry.* F) have quite dense understorey vegetation, therefore might contribute to an uneven trunk-space pollen component. In the open grassland (*Mis.-Aru.* G), there is no clearly defined trunk space, and samples were taken at least 100m from the forest edge (beyond the likely "edge effect", which is often explained as a trunk space transport phenomenon; Bunting & Farrell, 2018), but a C_g component from local vegetation is more likely to contribute to these samples. The bamboo forest (*Phy.* F) is likely to be different from the other forest sites since the understory vegetation is generally sparse, which may increase the trunk space component from the arboreal taxa, but decrease the understorey contribution.

Tauber's model assumes that all pollen is transported in the air, but zoophily is also commonly found in sub-tropical taxa. Insects may have a preference for visiting soil or moss, affecting the pollen input. For example, mosses may provide shelter from wind, a warmer microclimate, or serve as a food source (Strong, 1967; Gerson, 1969), therefore attract more pollen-carrying insect visits than soil surfaces nearby. The influence of insects on pollen assemblages is considered to be more local than regional, therefore if this is an important process in these samples, there should be more local pollen components in moss samples than in soil samples.

Pollen grains deposited onto the surface of a moss or soil sample are assumed to stay in place for at least a few years, but this is not necessarily the reality. This study shows that the adjacent sites with similar vegetation may show differences in the pollen-vegetation relationships. Water movement through soil and mosses might be different. Pollen movement driven by exogenic process such as raindrops and local surface runoff are more likely to have an impact on soil than moss, especially in this hilly area. Another possibility is the difference in the ability to capture pollen grains between soil and moss. The growth-form and the surface texture of moss may affect the entrapment efficiency of pollen grains (Boyd, 1986). In order to minimize difference between pairs, all mosses used for this study have similar growth forms.

Differences in soil depth, microtopography, and the precise position relative to vegetation canopies (e.g. in the drip zone or under the crown of a tree) would likely mean that a consistent pattern of differences within communities would not be seen, making a difference due to this cause harder to detect.

Microfaunal activity is also an important contributor to soil mixing which can alter the surface pollen spectra (Moore et al., 1991; Walch et al., 1970), and since mosses tend to be damper than soil, and to be mainly made of living material rather than a decaying food source, burrowing microfauna are less likely to interact with mosses than with soils.

Differences between vegetation communities——can we tell them apart from modern pollen assemblages?

Based on the quantitative results of discriminant analysis conducted on 46 paired soil and moss samples, the six local vegetation communities can be distinguished by their modern pollen assemblages. Ordination showed overlapping envelopes for assemblages from four of the forest types but discriminant analysis was able to separate them effectively.

Selection of samples——moss or soil?

In some cases, the soil sample envelopes are larger than the moss sample envelopes in the ordination diagram. This indicates that there is less variability among moss samples collected in the same vegetation communities (Figure 4), which in turn suggests a greater likelihood that a small number of samples can be "representative" of the community pollen signal, therefore requiring less effort in collecting and processing samples. Although this study has not ruled out preservation and post-depositional reworking as factors altering soil samples, we do suggest that the former is not a dominant process since not all paired samples are altered in the same way. In some studies (e.g. Räsänen et al., 2004; Mazier et al., 2006; Fall, 2012), these very local effects are mitigated by collecting multiple samples within a small area and amalgamating them which might reduce very local effects such as uneven pollen distribution from nearby understory taxa, but this will not remove the overall differences seen here. Measuring the local-scale vegetation component in a quantitative way (Farrell et al., 2016), and the development of a standard sampling method which minimizes its effect, are needed for further study.

Soil samples contain more upland herb taxa and fewer arboreal types than the adjacent moss samples. The category "upland herbs" is made up of taxa which are not found in the forests and occur only rarely in the Meiling Mountains as weeds in areas of human activity, therefore most pollen in this category is believed to have come from sources beyond the mountains in the surrounding open agricultural landscape and can be considered a marker of the proportion of 'background' pollen in the assemblages. This suggests that soil sample pollen assemblages contain a larger background pollen component than the moss assemblages.

Is it possible to separate the ecologically distinct but Poaceae-dominated communities of grassland and bamboo forest from the pollen record?

In this study, the surface pollen assemblages include results from two typical subtropical communities dominated by Poaceae, i.e. abandoned farmland and bamboo forest, where the land use is strongly affected by human activity.

The bamboo forest stands out in this study, since it has the lowest diversity index, but relatively large distances between the pollen assemblages in sample pairs. Pollen spectra in the bamboo forest are dominated by *Pinus* (62.2% (soil) and 63.9% (moss) on average) and *Cunninghamia* (8.2% (soil) and 12.9% (moss) on average), both from plant taxa which are rarely present in the bamboo forest but frequently appear in adjacent forests of the Meiling Mountains. *Phyllostachys edulis* (Poaceae) is an important bamboo species which is widely cultivated in southeast China, and has larger pollen grains (an average diameter of 61µm) than those of grassland species (Zhang et al., 2016). However, little Poaceae is recorded in bamboo forests, therefore increasing the relative proportion of regional pollen input. Bamboo pollen was also found to be underrepresented in bamboo forest by Zheng et al. (2008) and Basumatary et al. (2014). A combination of factors may lead to this. The bamboo flowers irregularly (Bedell, 1997; Yuan et al., 2007), and it often surrounded by forests with high pollen producers, which can swamp the pollen signal of bamboo.

In the bamboo forest, the high variability between samples despite the relative lack of understory vegetation may be due to higher occurrence of overland water flow and therefore changes in soil pollen assemblages. The measured gross amount of runoff in bamboo forests was larger than that in broadleaved forests (Li & Wang, 2003), therefore this effect is likely to be stronger in the bamboo forest than in the other forest types studied here.

The *Mis.-Aru.* G is the only 'open area' involved in this study. The ordination figure separates the grassland in the bottom right corner. Unlike the datasets in the five forests, both moss and soil envelopes in the grassland are very small, and the distances between each pair can be negligible. One possible reason is the lack of trunk space transport in the grassland community, which therefore increased the relative proportion of long distance pollen input and effectively created a more even pollen rain. Another possible reason is that being out in the open land, the mosses are drier on average and behave more like soil.

CONCLUSION

This study finds that surface samples of moss or soil from adjacent sites with similar vegetation do differ in the pollen assemblages recorded. Soil samples contain more upland herb taxa and fewer arboreal types than the adjacent moss samples. Soil samples are more likely to be affected by post-depositional decay, faunal activity and soil mixing, which may contribute to the differences between soil and moss samples. Regardless of cause, our study implies that mosses provide a more accurate representation of the contemporary vegetation than soils. Pollen assemblages in soils are often biased by physical, chemical and biological factors, and understanding the preservation and decay of pollen in soil requires further investigation.

Although ordination analysis showed overlapping envelopes for assemblages from four of the forest types, discriminant analysis was able to separate vegetation communities effectively. The results of this study also found that there is less variability among the moss samples within the same vegetation community. Less variability in samples means there is a greater likelihood that a small number of samples are "representative" of the community, which saves time and effort. From this perspective, moss samples are a better choice for characterizing vegetation communities using pollen assemblages. Given the clear separation of vegetation types in the discriminant analysis, soil samples are also recording a clear pollen signal of vegetation.

Pollen assemblages from the bamboo forest are susceptible to contamination from the surrounding forest, which makes it difficult to identify the vegetation community by the surface pollen assemblage only. However, pollen spectra from the Poaceae dominated grassland are easy to separate from the other five subtropical forest communities, and samples collected from the grassland tend to be more similar to each other.

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AUTHOR CONTRIBUTIONS

M.J.B. and Y.F. contributed to the ideas and designed methodology; Y.F. collected and analysed the data; Y.F. and M.J.B. wrote the manuscript with input from all authors (C.M. and X.Y.). All authors contributed to the drafts and gave final approval for publication.

Data Availability

Surface pollen data will be made available through the University of Hull data repository.

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