INTEGRATED LANDSCAPE SCALE VEGETATION ASSESSMENT USING SURFACE SOIL AND BEE POLLEN DATA IN THE NILGIRIS AND THE COROMANDEL COAST, SOUTH INDIA - VISUALIZING POLLEN AS A REMOTE BIOLOGICAL SENSOR

Lazar J[1], Prasad S[1], Navya R[1], De Simone, D [2, 1], Anupama K[1*]

[1] Laboratory of Palynology and Paleoecology, Department of Ecology, French Institute of Pondicherry, No.11, Saint Louis Street, Puducherry 605001 India

[2] Department of Languages and Cultures, Ghent University Campus Boekentoren, Blandijn, Blandijnberg 2, 9000 Gent, Belgium

*corresponding author email ID: anupama.k@ifpindia.org

*https://orcid.org/0000-0003-3130-0113

prasad.s@ifpindia.org : https://orcid.org/0000-0002-8209-3647

lazar.j@ifpindia.org: https://orcid.org/0009-0008-7082-0414

daniela.desimone@ugent.be: https://orcid.org/0000-0003-1965-8219

Abstract

Modern pollen analogues remain a powerful tool in Quaternary palynology but classically the most favored repositories are moss cushions and surface soils. Here we use both surface soils and bee pollen to characterize modern pollen spectra from contrasting landscapes, evaluate their potential as biological proxies complementing each other in reconstructing vegetation comprised of anemophilous and entomophilous plants. The bee pollen assemblages are from honeycombs and corbicular loads from *Apis cerana* and *A. florea*. By framing classical palynology as an inherently geospatial sensor, we offer an integrative approach to landscape-level ecological analysis and generate baseline data on pollen transport mechanisms that remain less explored in the tropics using a case study in southern India in the upper montane Nilgiris and Coromandel coast. The proposed approach tweaks the standard protocol to fit better the tropics where, wind pollination is not the predominant mode and not much is understood about what we may miss in the record or what may be over represented. This also recognizes pollen analyses as a complementary method to understand the foraging preferences of native honeybees. Comparative analysis of the thirty-four samples (comprising >120,000 microscopically enumerated grains, with a target of 1,000 grains per soil

sample and significantly higher counts for bee-pollen samples) revealed a total richness of 151 pollen taxa with distinct exclusivity observed in each source. Data analyses broadly illustrate the potential to further integrate modern pollen data from diverse sources in the same sites and the same season to help quantify pollen-vegetation relationships more robustly in the monsoon-affected South Asian tropics.

Keywords: Palynology, South Asia, Vegetation reconstruction, pollen-vegetation relationships

1 Introduction

The use of pollen and spores in delineating current and historical vegetation patterns is now very well established (Manten, 1966; Moore *et al*., 1991; Gaillard et al, 2018). This application, especially in the Quaternary and, more specifically during the Holocene, uses a powerful method – the modern pollen analogue – in conjunction with both the surrounding vegetation and indirectly, the present day climate (Bonnefille *et al*., 1999; Broström *et al*., 2004; Bunting *et al*., 2013; Basumatary *et al*., 2014). This approach is grounded in the principle of uniformitarianism (MacDonald, 1996) that states that the relationships between pollen-producing plants and the environmental conditions remained unchanged during Quaternary and provides a well-established qualitative and quantitative method capturing the influence of climate, topography and human activity (Seppä & Bennett, 2003; Fyfe *et al*., 2015). While the classical/ traditional repositories for such modern analogues have been surface soil and mosses and the latter are readily available in the temperate landscapes but not in the hotter and drier tropical areas (Navya *et al*., 2026), several other natural traps such as spider-webs and bee loads (honey, corbicular pollen loads and honey combs) can also be harnessed (Anupama et al, 2002; Ponnuchamy *et al*., 2014; Quamar & Chauhan, 2011).

The regional vegetation, primarily of anemophilous taxa, is well reflected by pollen in soil while entomophilous taxa are mainly captured by bee pollen and help highlight actively foraged plant taxa (Dimou & Thrasyvoulou, 2007; Lazar *et al*., 2023, 2024). A diversity of human designed pollen traps (Anupama, 1992; Gimenez *et al*., 2024) exposed at varying periodic intervals also provide environmental data on the content of the aerosols that includes pollen, here providing not only snapshots of the local to regional vegetation but also acting as a proxy to the seasonally changing flowering phenology.

Widely used in biodiversity assessments that rapidly capture the dominant characteristics of the upper canopy of the forest or the agroecosystem (Kacic & Kuenzer, 2022; Turner et al., 2003), remote sensing of vegetation, relying on satellite data, is currently the most powerful method to map

vegetation at regional to continental scales. Here we visualize the classical discipline of palynology as one that provides a remote biological sensor – the pollen assemblage - which functions across two distinct modalities: (i) passive ground-based materials (soil, moss, or traps) on the ground at a single location capturing signals that reconstruct vegetation composition at local to regional landscape and temporal scales (Broström *et al*., 2004; Jones & Bryant, 2014; Liu *et al*., 2023) and (ii) active biological agents (bee loads) that integrate specific floral signatures from the landscape. By integrating these diverse sources, we obtain a better resolved signal of the vegetation that overcomes the limitations of single-source reconstructions. This is especially true in biodiverse and topographically complex regions like South India, which have, in addition to plant diversity a greater diversity and abundance of bees (Indhu *et al*., 2023; Sharma *et al*., 2025). Trees, rock crevices and other cavities are preferred nesting habitats for social bees, among which are honey bees with four native species in southern India (Schrader *et al*., 2018; Thomas *et al*., 2009). In tropical regions with limited wind pollination, insect-mediated dispersal dominates, making bee pollen a particularly informative source. Simultaneously, soil pollen at the same site complements this by capturing a broader area. In a different context of environmental pollution, soil, honey and bee pollen were considered as distinct environmental compartments regionally (Kastrati *et al*., 2021).

Comprehensive studies that integrate modern pollen data from diverse sources in the same sites to assess and quantify pollen vegetation relationships are vital to interpret present and past vegetation dynamics. This paper is an exploration of an approach to do this in southern India with a case study considering pollen assemblages from two sources, surface soil and bee pollen in two contrasting landscapes– upper montane Nilgiris and the Coromandel Coastal region around Pondicherry. The bee pollen assemblages are from honeycombs and corbicular loads of two native honeybees, *Apis cerana* and *A. florea*. The objectives are to characterize modern pollen spectra from bees and surface soil samples, evaluate their potential as biological proxies that complement each other in reconstructing vegetation comprised of both anemophilous and entomophilous plants. The aim here is to provide a case for a multi-pronged approach to understanding vegetation dynamics in

capturing local and regional vegetation patterns. This can also enable more precise reconstructions of how environments have been shaped through long-term, more-than-human interactions.

2 Materials and Methods

2.1 Study area, Sample collection and Preparation

The upper montane Nilgiri hills and the Coromandel Coastal region around Pondicherry are the two distinct landscapes where the investigations were carried out. In each landscape both surface soil samples and bee pollen samples were collected (Tables 1 & 2, Figure 1, Sup. Figures 1 and 2).

Samples were collected at eight sites in the upper montane Nilgiris, with surface soils being collected at seven sites mainly around grassland mounds in proximity to the settlements of the Todas, one of the Indigenous communities of the Nilgiris, At two of these sites, bee pollen was collected in the vicinity of the surface sample collection point and at one site, only bee pollen was collected. The surroundings of the sampling sites, all identified during the ongoing *Nilgiri Archeological Project*, comprise remnant shola (montane evergreen) forest patches mixed with plantations, with a mix of native and introduced species.

Information already available, as cited below, comprised the main data in the Coromandel coast, although one surface soil and one bee pollen sample (an *Apis florea* comb) from the same location (IFP: urban garden setting with diverse native and introduced flora and weeds in the vicinity) was also collected in April 2024 (Table 1) . The main data includes: a) 15 surface samples at 14 sites (Navya *et al*., 2026); and b) compiled data of corbicular loads of *Apis cerana* pooled as six monthly samples between January and April in 2021-2022 at French Institute of Pondicherry (IFP) (Lazar, 2024). The 15 surface samples are in the NEOTOMA data repository and can be accessed via the cited DOIs given at the end of the References section in this manuscript (Anupama 2025a-o).

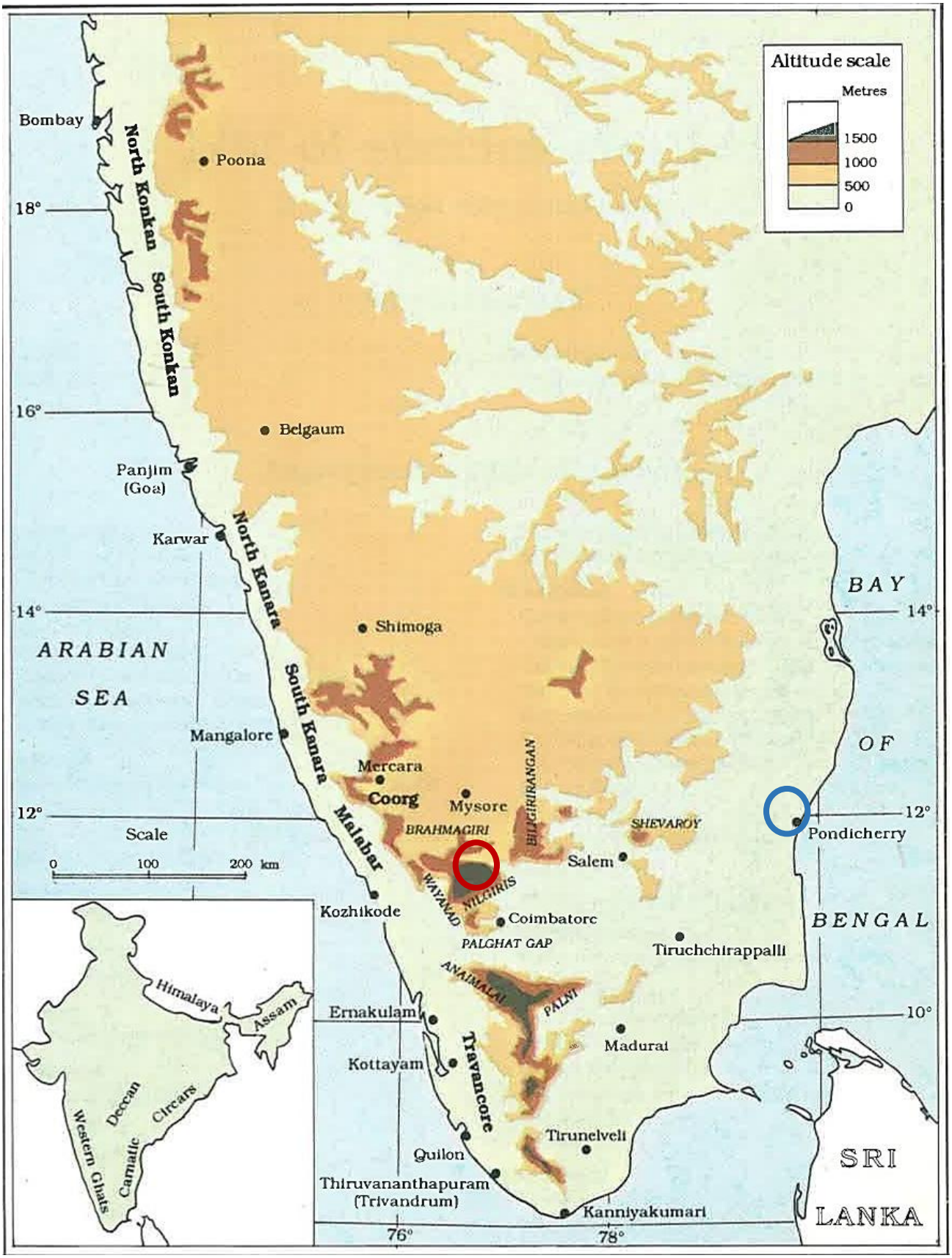


Figure 1. Physical map of southern India adapted from Tissot et al. (1994) showing the two contrasting landscapes chosen in this study – the upper montane Nilgiris (red circle) and the Coromandel coastal region around Pondicherry (blue circle). Please see Supplementary. Figures. 1 and 2 for detailed sampling site location

Table 1. Study sites in the Nilgiris and Pondicherry regions, sample collections (soil, moss, bee pollen and locations (+ indicates samples collected and – indicates no samples at sites).

Sl. No	Landscape / Region	Site Name/ Code	Coordinates (Lat, Lon)	Soil	Bee pollen (combs, loads)	Moss
1	**Nilgiris (Montane)**	Tenth Mile (TM)	11°27'31.30"N ;76°37'11.40"E	+	+	-
2		Pudhu-mund (PM)	11°25'53"N; 76°38'19"E	-	+	-
3		Aduthal -mund (ADM)	11°29'10.10"N ;76°37'12.80"E	+	-	-
4		Tarnad-mund (TNM)	11°29'30.10"N ;76°37'12.30"E	+	+	-
5		Muttanad-mund (MM)	11°26'51.80"N ;76°39'52.80"E	+	-	-
6		Seventh Mile (SM)	11°26'35.30"N ;76°38'19.10"E	+	-	-
7		Ninth Mile (NM)	11°26'17.20"N ;76°37'44.00"E	+	-	-
8		Sandynullah	11°26'18"N ;76°37'52"E	+		+
9	**Pondicherry (Coastal area)**	French Institute of Pondicherry (IFP)	11°56'13.12"N ;79°50'08.48"E	+	+	-

The subset of the core data of four matching soil surface and bee pollen samples, all collected between January – April 2024 are highlighted. For more details about the 34 pollen samples considered in this study, see Tables 2 &3, Figures. 2 and 3

Table 2: Details of the 34 samples considered in the study

No	Sample	Pollen count	% unidentified	No. of Pollen taxa	No	Sample	Pollen count	% unidentified	No. of Pollen taxa
Surface samples (soil except one)					*Bee Pollen samples (Ac - Apis cerana; Af: Apis florea)*				
1	Ousteri	1122	1.2	36	25	IFP (Jan 21) Ac	6240	1.6	19
2	Marakanam	1001	2.1	46	26	IFP (Feb 21) Ac	16223	1.3	14
3	Lawspet Season 1	1017	3.6	39	27	IFP (Mar 21) Ac	8657	0.5	11
4	Lawspet Season 2	1019	3.7	43	28	IFP (Apr 21) Ac	10938	0	14
5	Konerikuppam	306	1	27	29	IFP (Jan 22) Ac	11596	0	18
6	Elavalapakkam	1014	2.3	31	30	IFP (Feb 22) Ac	1663	0	6
7	Epakkam	1013	2.9	37	31	IFP Af	2547	1.7	10
8	Kadukkalur	1006	2.4	37	32	Tenth mile Ac	25215	0.1	24
9	PS Palayam	404	1.2	18	33	Taranad Mund Ac	5912	4.3	26
10	Aranya	1005	3.4	45	34	Pudhu Mund Ac	3538	1.2	17
11	Kattalai	1007	3.9	37	***Methodological note:*** We aimed for a count of 1,000 grains per soil sample and significantly higher counts for bee-pollen samples to catch even the rare entomophilous taxa. However, local site conditions—specifically in the agricultural landscapes of Konerikuppam and PS Palayam, and the anthropogenic setting of the IFP garden—inevitably resulted in lesser pollen preservation for some samples. Conversely, the first honeycomb sample from the Nilgiris (Tenth Mile) exhibited distinct chromatic stratification in the pollen stored within cells; these were processed and analyzed separately to capture this temporal/taxonomic variation, resulting in the highest count in the dataset. The significant divergence ($p < 0.001$) in the Chi-square test performed on the major taxa across subsamples validated this additional counting effort. The observed fluctuations in taxonomic richness per 1,000 grains across different landscapes and sample types underscore the distinct vegetation sensing properties of soil vs. bee – pollen.				
12	Kumalampattu	1007	3.8	43					
13	Paranganni	1008	3.2	37					
14	Muttakadu	401	6.2	31					
15	Karai	1010	3.5	42					
16	IFP	226	0.9	22					
17	Sandynallah	1921	1.2	43					
18	Sandynallah (Moss)	1693	1	43					
19	Taranad mund	1700	1.1	42					
20	Ninth mile	1552	1.3	39					
21	Tenth Mile	1544	1.2	34					
22	Aduthal Mund	2070	1	45					
23	Seventh mile	2080	0.6	39					
24	Muthanad mund	2016	0.9	34					

In total, the data comprised 34 samples compiled regionally under two heads (coastal, Nilgiris) and under each region two more heads (surface soil, bee pollen) making a total of four heads (Table 3). There are four matching soil surface and bee pollen samples, all collected between January – April 2024 constituting a subset of the core data to illustrate the potential of a more comprehensive palynological approach integrating modern pollen data from diverse sources. This subset allowing for a direct comparison of the remote biological sensor across two modalities: the 'passively accumulated surface soil pollen' and the pollen actively foraged by native honey bees under identical spatial and temporal conditions is a new methodological innovation put forth by this study.

Quantitative vegetation surveys were also carried out around the surface soil sampling points in both landscapes following standard protocols (Bunting *et al*., 2013; Navya *et al*., 2026). Surface samples of the top 2 cm of the soil, after clearing any litter, consisted of many subsamples within a 1 m^2 quadrat that was the centre of a circular distance weighted vegetation plant abundance survey, chosen for a quantitative pollen-vegetation analysis but we do not use or report these ongoing vegetation surveys in the present paper.

The laboratory protocol involved standard acid treatments for extracting pollen from sediments (Moore *et al*., 1991). Honeycombs were processed by acetolysis method as in Ponnuchamy *et al*., 2014.

2.2 Microscopy, data presentation and analyses

A light microscope (Olympus BX51) was used to study the processed slides in both the cases and all microscopic observations were made at x400 and at least 1,000 pollen grains were targeted for enumeration per surface soil sample, whereas more than 1000 grains were targeted for the bee pollen samples (Table 2) in order to help detect rare, possibly entomophilous taxa. Pollen identification was based on the Thanikaimani pollen slide collection and the photomicrographs available at the IFP and published literature (e.g. Vasanthy, 1988). Statistical analyses (PCA and CA) of the samples were

carried in PAST software version 3.26 (Hammer & Harper 2001). The complete data as well as the subset of the core data mentioned above were used for this multivariate statistics. Pollen diagrams were plotted using TILIA (Grimm, 1991) and CONISS (constrained incremental sum of squares) was applied within this environment to perform cluster analysis on the assemblages. The complete data was used to plot the pollen diagrams. (Figures 2 and 3).

3 Results

The thirty-four samples (24 surface soil and 10 bee pollen) in the two landscapes (Table 2) comprised of a total of 151 pollen taxa grouped under four heads (Table 3). Monolete and Trilete spores and Algal cysts were present exclusively in the surface samples while the bee pollen samples from the Nilgiris contained 14 distinct unidentified pollen types; overall <3% unidentified in all samples. Taken together in both landscapes, the honeycombs and bee loads comprised of 63 pollen taxa and the surface soils comprised 135 taxa. Methodological validation across six independent surface samples in the Nilgiris demonstrated high consistency in the primary vegetation signal. When comparing data from two different analysts, a ~40% gain in taxonomic richness was achieved with a mean Bray-Curtis Dissimilarity index of 0.11 (Supplementary Table S1).

Five pollen taxa (*Acacia*-t, Asteraceae (Echinate), Poaceae, Sapotaceae and *Syzygium*-t) were found in good proportions (2%-71%) under all four heads, i.e., in both landscapes and in both kinds of samples (Table 3; Figures 2 and 3). Eighteen taxa occurred under three heads: 11 in surface samples in both landscapes and in the coastal bee pollen sample (e.g., *Grewia*, Lamiaceae, *Mallotus*, Melastomataceae/ Combretaceae); 6 in surface samples in both landscapes and also found in the Nilgiris bee loads (Amaranthaceae, Asteraceae (Fenestrate), *Celastrus*, *Eucalyptus*, *Justicia*-t and *Toddalia*) while *Mimosa pudica* was found in the bee pollen in both landscapes and the Coromandel surface soil sample. Forty-four taxa occurred in two of the four heads as follows: taxa common to surface and bee pollen in the coastal landscape (14), in Nilgiris (10), taxa common to surface samples from both landscapes (19), and 1 taxon (*Coffea*) exclusively in bee pollen in both landscapes. Eighty-

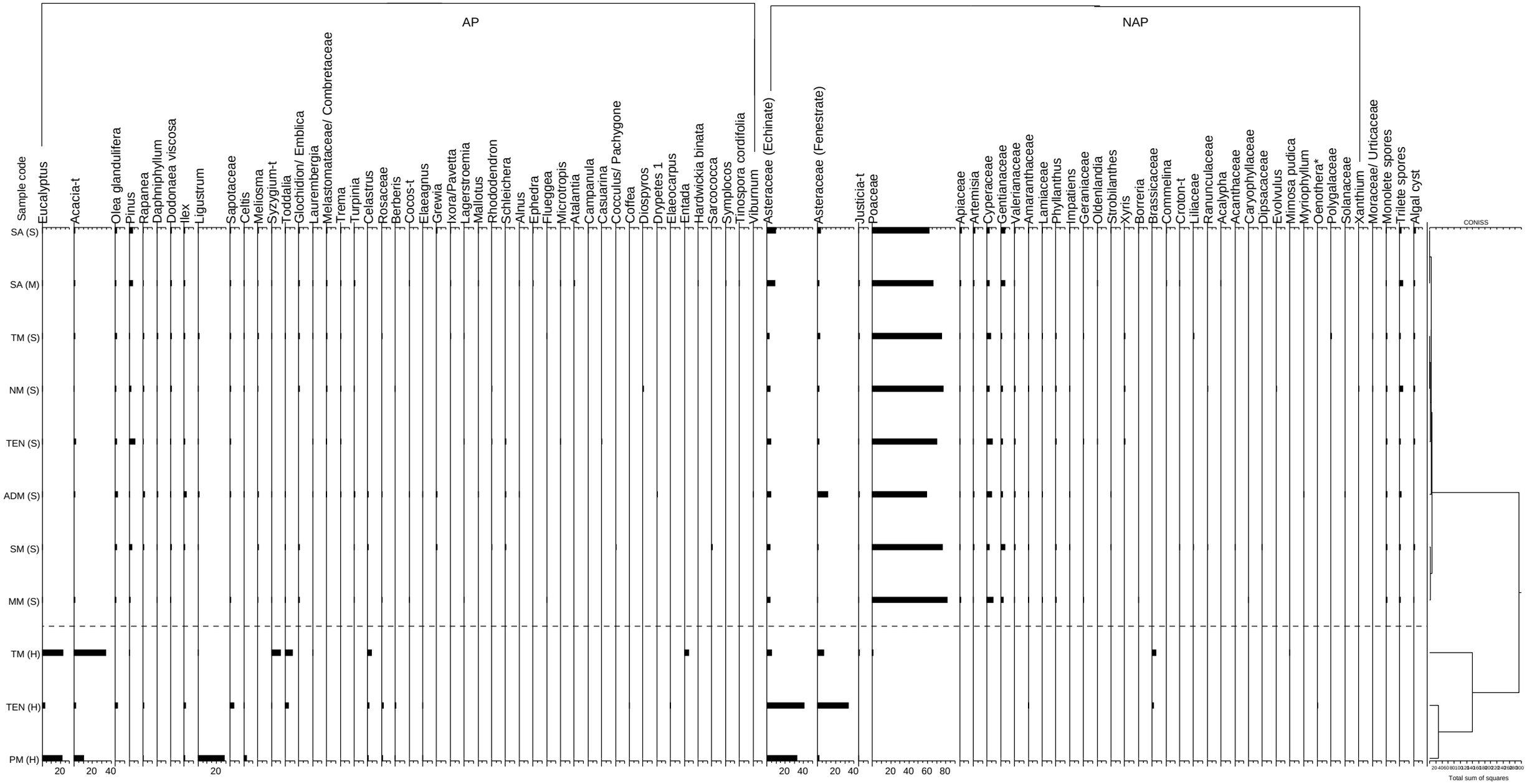


Figure 2. Diagram of pollen percentages for all the pollen taxa, monolete and trilete spores and algal cysts recovered from 8 surface soil (see Table 2, No. 17-24) and 3 bee pollen samples (see Table 2, No. 32-34) in the upper montane Nilgiris. Surface samples (abbreviated S or M for soil and Moss) were placed above and bee pollen samples (abbreviated with H) below the dotted line. CONISS cluster analysis shows the distinct separation of the bee pollen samples despite some overlap. The only non classified taxon here is Moraceae/ Urticaceae. At only one site Sandynullah both surface soil and moss were collected and analyzed separately and shown here as the first two samples in the plot. The overlap of taxa in both surface and bee pollen samples is very clear and more details of this in Table 3.

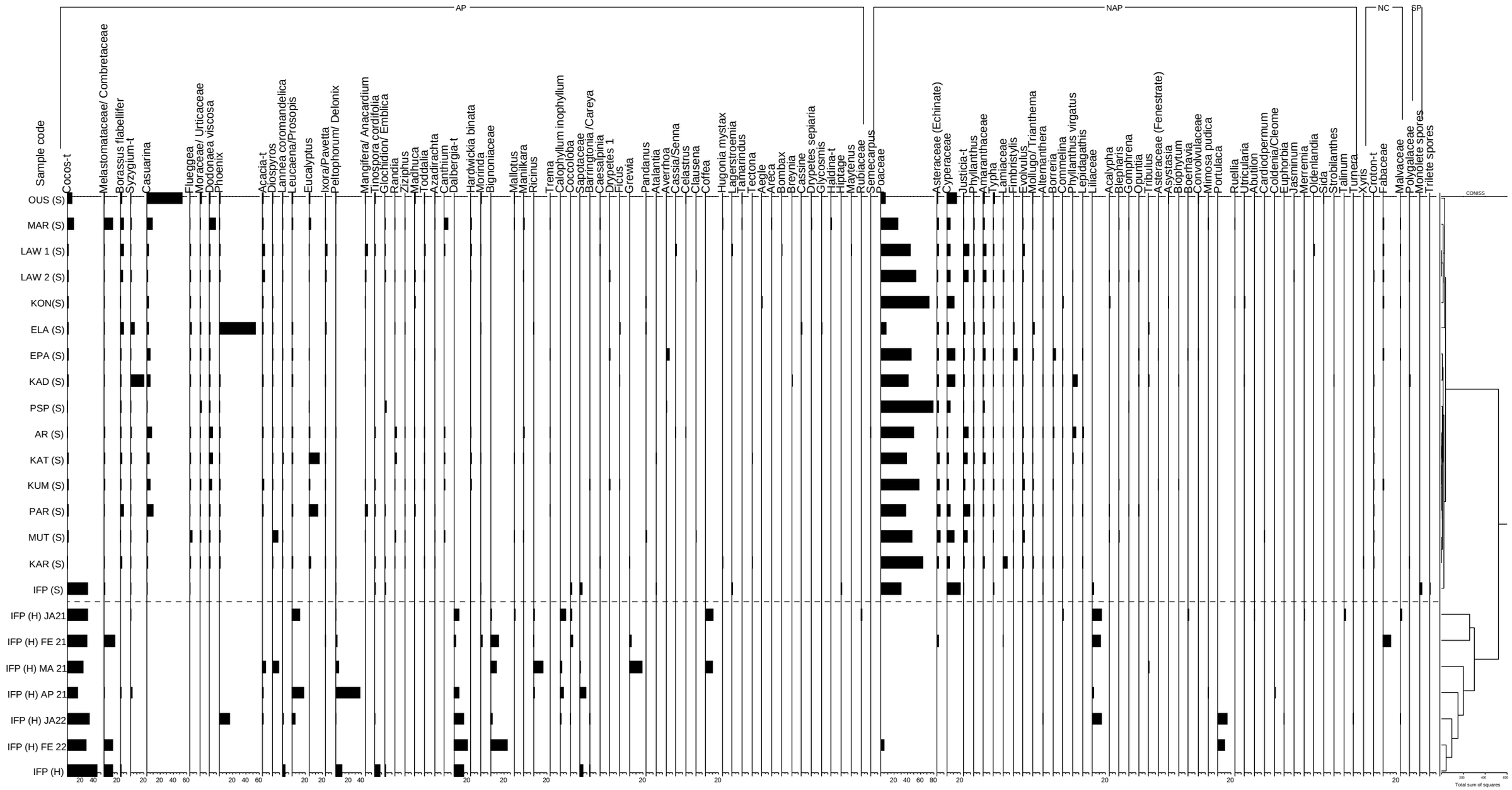


Figure 3. Diagram of pollen percentages for all the pollen taxa, monolete and trilete spores recovered from 16 surface soil (see Table 2, No. 1-16) and 7 bee pollen samples (see Table 2, No. 25-31) in the Coromandel coast. Surface samples (abbreviated S for soil) were placed above and bee pollen samples (abbreviated H) below the dotted line. CONISS cluster analysis shows the distinct separation of the bee pollen samples and, given this data is monthly, the cluster does exhibit seasonality. The overlap of taxa in both surface and bee pollen samples is very clear and more details of this in Table 3.

four taxa were found exclusively in both landscapes distributed as follows: in surface soils from the coast (43) and in the Nilgiris (26); in bee pollen samples from the coast (11) and the Nilgiris (4).

Multivariate analyses on the complete dataset of 34 samples show a separation of Nilgiris from the coastal samples and also the bee pollen from the surface soils, taking into account the first 3 PCA axes. Based on the results from the PCA and the pollen diagrams, Correspondence Analyses were also carried out on the full dataset (Figure 4). As expected, the separation of the samples according to our four different subheadings was more visible, with the bee pollen samples separating out from the surface samples and among the bee pollen samples those from the Nilgiris and the Coast clearly separated. The surface samples from both landscapes did separate but not as distinctly. Major taxa defining the first two axes in the PCA (Sup. Figures. 3a-g) are the ones that occur always and in higher percentages (eg; Poaceae, Asteraceae (Echinate), *Cocos*-t). Sample clustering was along similar lines when the analyses were repeated using a subset of the core data: four matching soil surface and bee pollen samples (Figure 5; Sup. Figures. 3a – 3g). The PCA and CA runs also show that a number of taxa cluster together and overlap.

Some light micrographs of pollen taxa retrieved from surface soils in the Nilgiris are shown in Figure 6; the taxa shown here are found in both kinds of assemblages. The pollen taxa from the Coromandel Coast are well illustrated in Appendix 3 (Navya *et al*., 2026 and in Lazar *et al*., 2023).

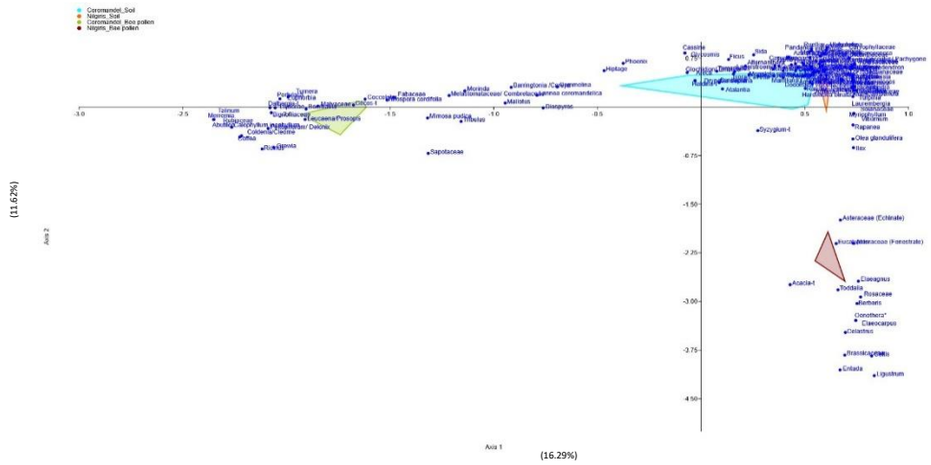
4 Discussion

Pollen assemblages from samples on the ground, or from honey combs or bee legs, each at a single location, act like biological sensors of the local to regional plant communities around them. These assemblages are a mixture of airborne and insect-mediated transports, providing another layer of biological information pertaining to the pollination mechanisms of the plant taxa in the assemblages. The taxa recovered (Figure 2 and 3) comprise all storeys of the forest and also Bryophyte and Pteridophyte spores and algal cysts attesting to the fine level of detail possible with

this remote biological sensor bridging the gap between wind-borne regional signatures and insect-mediated local pulses.

The clustering of Nilgiris versus Coromandel samples (Figure 4 and 5, Sup. Figures. 3a – 3g) demonstrates that pollen assemblages can discriminate ecological zones, paralleling remote-sensing classifications based on vegetation indices. Bee pollen spectrum represents the plants visited by the bees, revealing the targeted selection based on pollen and perhaps, nectar availability too. Conversely, surface soil pollen spectrum captures a broader selection, including local and regional vegetation, as also wind and other dispersal mechanisms (Broström *et al*., 2004). The low representation of some dominant tree taxa and the presence of highland species further suggest the combined effects of pollen dispersal, insect pollination, and long-distance transport (Nohro *et al*., 2020). It is theorized that many plants have evolved adaptations to maximize the chances for pollination, especially in the tropics (Barišić *et al*., 1994; Lazar *et al*., 2024).

Although different sampling media for trapping modern pollen rain have been compared (Jantz *et al*., 2013) and surface soils and moss cushions have been compared with bat guano (Basumatry & Bera, 2014), we are not aware of studies that explore both wind and insect borne pollen in the same sites and the same season and assess their complementarity – something that can have implications not only in past vegetation reconstruction but also as possible indicators of the chief pollination mechanisms, anemophily and entomophily. As many as 14 taxa in the coast and 10 in the upper montane area are present in both surface samples and in bee loads. Among these are taxa like *Lannea, Phoenix, Borassus flabellifer, Ricinus, Olea glandulifera, Ligustrum, Rapanea* that have been reported in regional Holocene and Quaternary records (Mahapatra *et al*., 2021; Sutra *et al*., 1997; Vasanthy, 1988) indicating the value of our approach in highlighting the complementarity of different kinds of modern pollen samples together to interpret past records better. Nearly 70% of the pollen taxa in Figure 6 are found in both surface soil and bee pollen samples. Further, our methodological validation (Supplementary Table S1; Mean BC = 0.11) confirms that even while we demonstrate how pollen as a remote biological sensor across two modalities (passively assimilated surface pollen and



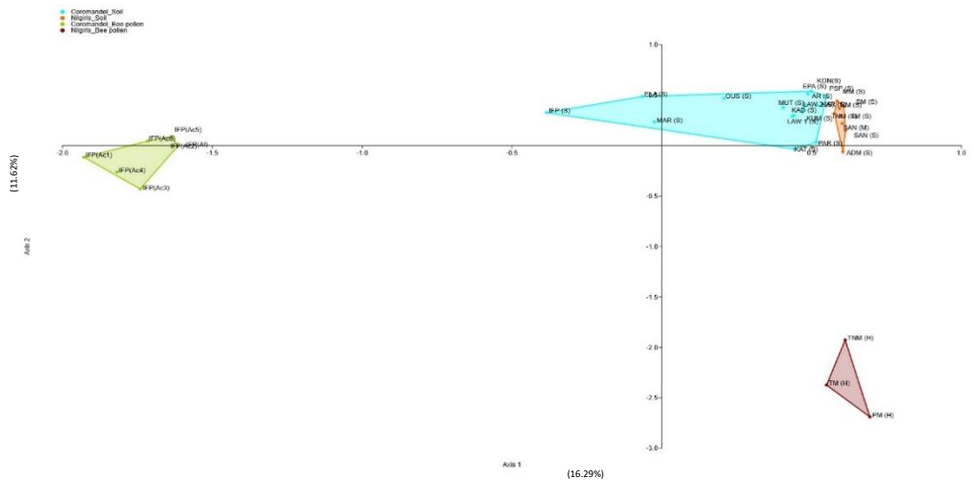


Figure 4 (a and b): CA of the core data of 34 surface soil and bee pollen samples from the two landscapes – upper montane Nilgiris and the Coromandel Coast. As indicated by the pollen diagrams the bee pollen samples from the upper montane Nilgiris are the best separated while the surface samples from both landscapes though separated are closer together. For more depictions of the multivariate analyses see Supplementary Figures 3 too.

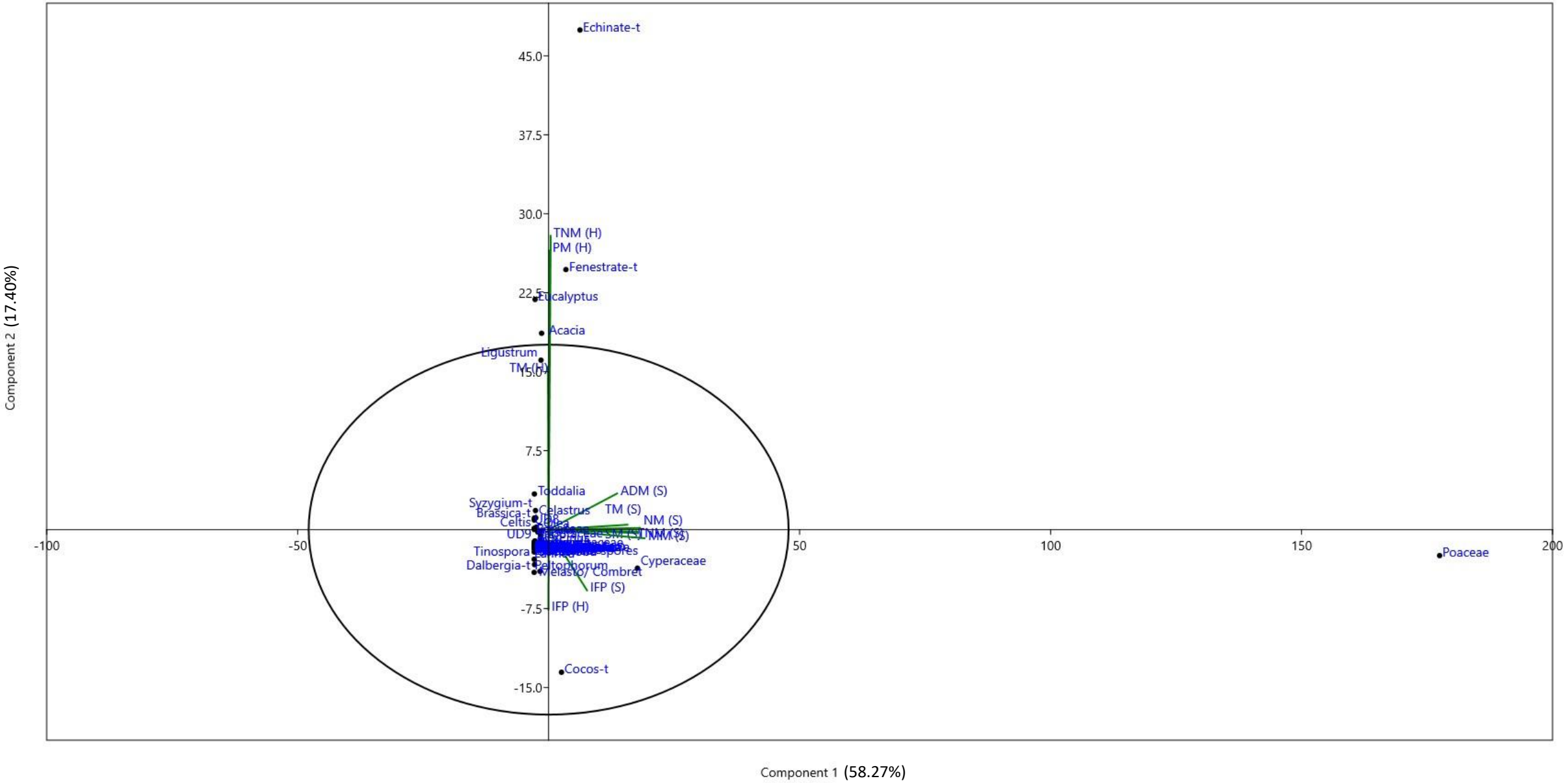


Figure 5. PCA of a subset of the core data, 4 paired samples of surface soil and bee pollen, 3 from the upper montane Nilgiris and 1 from the Coromandel coast. As indicated by the pollen diagrams, the cluster analyses and the correspondence analyses of all 34 samples (Figures 2-4), we expected a more visible separation of landscapes and sample types which is seen here: upper montane Nilgiris samples above the Axis 1 and the IFP coast samples below it; bee pollen samples away from the origin and surface samples closer to it in both landscapes. For more depictions of the multivariate analyses see Supplementary Figures 3 too.

actively foraged bee pollen) records different biological data, this data is internally consistent and reproducible. A further methodological point, underlined by the 40% gain in taxonomic richness by combining the data from two analysts, is the value of the high pollen counts ($n \geq 1000$) in capturing the tropical land cover including its rare, diagnostic taxa. Though beyond the purview of this paper, the inclusion of bee pollen studies not only provides an ecological index of the pollination mechanisms of plants but also offers an additional biological index of landscape history that complements archaeological surveys, ethnohistorical accounts, and palaeoecological cores.

Among the five taxa common to both landscapes and both kinds of samples, the two at family level, Poaceae and Sapotaceae, offer an important contrast in complementarity: Poaceae, largely regarded as an anemophilous taxon is also found in the bee loads and Sapotaceae with larger pollen size and largely not regarded as anemophilous is also found in the surface soils (Table 2). Poaceae along with other herbaceous taxa such as Amaranthaceae and *Justicia*-t seem to be collected by bees in the Nilgiris. This aligns with our earlier findings showing that *A. cerana* foraged extensively on many herbaceous taxa including grasses relying on a small set of essential plants while incorporating seasonal herbs to maintain nutritional balance in the Coromandel coast (Lazar *et al*., 2023a, b) and elsewhere (Bhalchandra *et al*., 2014; Layek & Karmakar, 2016). In coastal regions, plants visited by honey bees were clearly classified as pollen, nectar or dual resources, with Poaceae emerging as major pollen sources, a pattern that further supports the importance of herbaceous ground-flora. Notably, long-term surveys near Puducherry also recorded 49 herbaceous species among 145 forage plants, reinforcing that ground-flora consistently forms a substantial part of *A. cerana*'s foraging portfolio (Lazar *et al*., 2024c thesis). The inclusion of such herbaceous taxa in bee loads suggests that ground-flora plays an important supplementary role, particularly during periods when major woody or perennial resources are limited (Lazar *et al*., 2024a).

Asteraceae (echinate), largely considered an entomophilous taxon, though present under all four heads occurs most in the Nilgiris bee loads, as also Asteraceae (fenestrate), which is nearly absent in the coast. *Syzygium*-t and *Acacia*-t are found in both landscapes in all samples though both are

considered largely entomophilous; while *Syzygium*-t is a polyspecific genus occurring along different altitude gradients from the montane forest to the coastal plains, the presence of *Acacia*-t especially in the bee pollen loads of Nilgiris is due to its aggressive introduction.

Taxa such as *Toddalia* and *Celastrus,* though found in surface samples in both landscapes, were at maximum percentages only in the Nilgiris bee pollen and absent in the coastal bee pollen assemblages. This is consistent with their flowering in the vicinity at the time of the honeycomb collection in the Nilgiris and again highlights that some taxa considered predominantly entomophilous occur in the wind-borne surface samples too. The same pattern holds for *Eucalyptus* which like *Acacia* was introduced during the colonial period in the upper montane landscape and, together, they both constitute powerful archaeological markers of landscape changes.

That diversity matters to the foraging bees (Lazar *et al*., 2024) is well known. Our results validate this in both landscapes, highlighting the honeybees' reliance on trees as primary forage, as arboreal taxa were found in greater proportions. The assemblages also reflect well the greater foraging opportunities in montane regions, reflecting both the more varied vegetation and the behavior of *Apis cerana* that has been shown to exhibit a longer foraging range in the hill slopes (Nevard, 2017). This also attests to the fact that forests play an important role as pollinator reservoirs (Viswanathan *et al*., 2020). Though apparently more limited because of its urban garden setting, a similar diversity of foraging preference was exhibited by both *Apis* species at the IFP site in the Coromandel Coast too. Although *Apis florea* is known for its broad floral range and foraging adaptability (Layek & Karmakar, 2016), the pollen spectrum from the IFP site reveals selective foraging on a limited number of plant taxa, reflecting localized floral resource availability. However, more data on the foraging preference of *A. florea* is required for validating its behavior in different landscape settings. The Nilgiris host rich bee diversity (92 species) with strong floral associations, underscoring the need for conservation, supported by Sasidharan and Kunhikannan, 2010, who reported 113 plant species associated with bees in the Nilgiri Biosphere Reserve.

The consistent presence of taxa such as *Ilex, Ligustrum,* Sapotaceae, *Syzygium*-t and *Olea glandulifera* and some others such as *Impatiens, Laurembergia, Artemisia* and *Entada* in the upper montane bee samples highlights the role of these native taxa as key forage resources, while some introduced taxa like *Acacia* and *Eucalyptus* have also become important currently due to their recent aggressive spread as mentioned earlier. This observation is consistent with the melissopalynological findings of Padmavathy & Rehel (2014) that *Apis dorsata* honey from the Coonoor slopes in the Nilgiris exhibited a multifloral composition dominated by *Acacia* and *Syzygium cumini*. Other introductions such as *Pinus* in the hills and avenue and garden trees such as *Casuarina, Coccoloba, Lannea, Tinospora, Dalbergia*-t and *Glochidion/ Emblica* in the coastal plains were rare and site-specific, reflecting local vegetation influences on pollen spectra. *Tinospora cordifolia*, a key nectariferous pollen in *Apis florea* honey from Vikarabad (Chaya, 2019) also appeared as a minor yet significant component in the IFP sample. *Cocos*-t pollen is commonly associated with the widespread cultivation of coconut palms in the coastal areas of the Puducherry region (Lazar *et al*., 2024). The present findings highlight the significance of this pollen taxon as a major forage source for honey bees in this locality. Observation of the pollinator attests to their visiting ornamental palms *Chrysalidocarpus* and *Pritchardia* that share the same morphology as *Cocos nucifera* (see figures in Thanikaimoni, 1970).

The abundance of Poaceae in the Nilgiris and *Cocos*-t pollen taxon in both the IFP surface soil and the honeycomb of *A. florea*, further illustrates the influence of landscape heterogeneity and vegetation structure on the composition of pollen assemblages captured by different substrates (Figure 2 and 3). The greater diversity of pollen taxa in soil samples compared to honeycomb samples suggests that soil provides a more comprehensive record of local and regional vegetation, possibly because of a longer timeline covered by the soil. Conversely, in anthropogenic settings such as the IFP garden, the bee pollen records provide a high-fidelity 'filter' that isolates specific native flowering events from the general urban background noise captured in the surface soil. This distinction is further reflected in the prevalence of wind-pollinated taxa such as Poaceae and Cyperaceae in soil samples,

Table 3. Percentage pollen taxa retrieved regionally from surface soils and bee pollen in the coastal and upper montane landscapes in Southern India.

S.No	Pollen Taxa	Soil pollen %		Bee pollen %	
		Coastal	Nilgiris	Coastal	Nilgiris
1	*Acacia*-t	0.85	0.53	0.95	26.16
2	Asteraceae (Echinate)	2.29	4.95	0.47	14.00
3	Poaceae	41.18	70.67	0.15	0.13
4	Sapotaceae	0.04	0.12	2.12	0.65
5	*Syzygium*-t	2.65	0.06	0.60	6.77
6	*Cocos*-t	2.23	0.03	27.21	
7	*Commelina*	0.05	0.01	0.09	
8	*Diospyros*	0.39	0.01	1.46	
9	*Glochidion/ Emblica*	0.15	0.09	0.07	
10	*Grewia*	0.01	0.03	3.71	
11	*Ixora/Pavetta*	0.50	0.03	0.20	
12	Lamiaceae	0.68	0.05	0.03	
13	Liliaceae	0.02	0.03	7.82	
14	*Mallotus*	0.03	0.09	0.15	
15	Melastomataceae/ Combretaceae	1.55	0.24	5.84	
17	*Tinospora*	0.10	0.01	0.32	
16	*Mimosa pudica*	0.02		0.09	0.01
18	Amaranthaceae	1.80	0.11		0.11
19	Asteraceae (Fenestrate)	0.03	3.25		11.13
20	*Celastrus*	0.01	0.05		3.12
21	*Eucalyptus*	3.07	0.22		18.88
22	*Justicia*-t	3.61	0.47		0.90
23	*Toddalia*	0.22	0.05		6.33
24	*Alternanthera*	0.05		0.00	
25	*Boerhavia*	0.01		0.06	
26	*Borassus flabellifer*	2.63		0.24	
27	*Barringtonia /Careya*	0.01		0.02	
28	*Coccoloba*	0.05		1.43	
29	Fabaceae	0.16		3.02	
30	*Lannea coromandelica*	0.29		0.36	
31	*Leucaena/ Prosopis*	0.35		5.18	
32	Malvaceae	0.03		0.43	
33	*Morinda*	0.10		0.69	
34	*Peltophorum/ Delonix*	0.10		9.19	
35	*Phoenix*	4.62		3.06	
36	*Ricinus*	0.01		2.52	
37	*Tribulus*	0.03		0.10	
38	*Acalypha*	0.10	0.01		
39	*Atalantia*	0.04	0.01		
40	*Borreria*	0.48	0.01		
41	*Casuarina*	8.29	0.01		
42	*Coffea*			2.75	0.03
43	*Croton*-t	0.15	0.01		
44	Cyperaceae	6.37	3.59		
45	*Dodonaea viscosa*	1.75	0.41		
46	*Drypetes*	0.04	0.01		
47	*Evolvulus*	0.54	0.03		
48	*Flueggea leucopyrus*	0.99	0.01		
49	*Hardwickia binata*	0.12	0.02		
50	*Lagerstroemia*	0.04	0.03		
51	Moraceae/ Urticaceae	0.83	0.03		
52	*Oldenlandia*	0.01	0.03		
53	*Phyllanthus*	0.97	0.07		
54	Polygalaceae	0.03	0.01		
55	*Strobilanthes*	0.04	0.03		
56	*Trema*	0.05	0.10		
57	*Xyris*	0.02	0.08		
58	*Berberis*		0.01		0.10
59	*Celtis*		0.05		0.28
60	*Elaeagnus*		0.01		0.02
61	*Ilex*		0.56		0.21
62	*Laurembergia*		0.08		0.02
63	*Ligustrum*		0.36		2.89
64	*Olea glandulifera*		0.93		0.38
65	*Pinus*		2.24		0.00
66	*Rapanea*		0.40		0.09
67	Rosaceae		0.10		0.40
68	Brassicaceae				3.06

…contd

Table 2 contd...

S.No	Pollen Taxa	Soil pollen %		Bee pollen %	
		Coastal	Nilgiris	Coastal	Nilgiris
69	*Elaeocarpus*				0.01
70	*Entada*				3.36
71	*Oenothera*				0.01
72	*Abutilon*			0.02	
73	Bignoniaceae			6.25	
74	*Calophyllum inophyllum*			2.32	
75	*Coldenia/ Cleome*			0.26	
76	*Dalbergia*-t			6.51	
77	*Euphorbia*			0.00	
78	*Merremia*			0.04	
79	*Portulaca*			3.07	
80	Rubiaceae			0.20	
81	*Talinum*			0.30	
82	*Turnera*			0.02	
83	Acanthaceae		0.04		
84	*Alnus*		0.03		
85	Apiaceae		0.84		
86	*Artemisia*		0.64		
87	*Campanula*		0.01		
88	Caryophyllaceae		0.01		
89	*Cocculus/ Pachygone*		0.01		
90	*Daphniphyllum*		0.52		
91	Dipsacaceae		0.01		
92	*Ephedra*		0.01		
93	Gentianaceae		2.87		
94	Geraniaceae		0.04		
95	*Impatiens*		0.10		
96	*Meliosma*		0.30		
97	*Microtropis*		0.01		
98	*Myriophyllum*		0.02		
99	Ranunculaceae		0.02		
100	*Rhododendron*		0.02		
101	*Sarcococca*		0.01		
102	*Schleichera*		0.03		
103	Solanaceae		0.01		
104	*Symplocos*		0.01		
105	*Turpinia*		0.17		
106	Valerianaceae		0.32		
107	*Viburnum*		0.05		
108	*Xanthium*		0.01		
109	*Aegle*	0.01			

S.No	Pollen Taxa	Soil pollen %		Bee pollen %	
		Coastal	Nilgiris	Coastal	Nilgiris
110	*Areca*	0.01			
111	*Asystasia*	0.01			
112	*Averrhoa*	0.46			
113	*Azadirachta*	0.08			
114	*Biophytum*	0.07			
115	*Blepharis*	0.04			
116	*Bombax*	0.01			
117	*Breynia*	0.01			
118	*Caesalpinia*	0.04			
119	*Canthium*	0.48			
120	*Cardiospermum*	0.01			
121	*Cassia/Senna*	0.04			
122	*Cassine*	0.02			
123	*Clausena*	0.04			
124	Convolvulaceae	0.04			
125	*Drypetes sepiaria*	0.02			
126	*Ficus*	0.07			
127	*Fimbristylis*	0.85			
128	*Glycosmis*	0.02			
129	*Gomphrena*	0.04			
130	*Haldina*	0.01			
131	*Hiptage*	0.01			
132	*Hugonia mystax*	0.03			
133	*Jasminum*	0.04			
134	*Lepidagathis*	0.24			
135	*Madhuca*	0.13			
136	*Mangifera/ Anacardium*	0.69			
137	*Manilkara*	0.10			
138	*Maytenus*	0.01			
139	*Mollugo/ Trianthema*	0.36			
140	*Opuntia*	0.05			
141	*Pandanus*	0.04			
142	*Phyllanthus virgatus*	1.01			
143	*Randia*	0.52			
144	*Ruellia*	0.02			
145	*Semecarpus*	0.01			
146	*Sida*	0.01			
147	*Tamarindus*	0.04			
148	*Tectona*	0.02			
149	*Typha*	0.35			
150	*Utricularia*	0.01			
151	*Ziziphus*	0.18			

contrasted with their limited presence in honeycomb samples, reflects differences in pollen dispersal mechanisms and pollinator selectivity. Despite this, the opportunistic use of abundant ground-flora integrating available herbaceous resources to supplement seasonal nutritional gaps across landscapes by the native bee species is important in the context of conservation and management of bees and their rapidly changing native habitats.

The differential pollen capture observed in our study aligns with Anupama et al. (2002), that integrated samples (soil, moss, and spider web) provide a more reliable picture of vegetation dynamics and seasonal pollen patterns in modern studies. Surface soil pollen analysis from South India and Sri Lanka, and in Balpakram Valley, Meghalaya show that distinct pollen assemblages from evergreen and deciduous forests reflect vegetation and altitudinal zonations (Bonnefille *et al*., 1999; Basumatary *et al*., 2014). The present study departs slightly from these approaches by combining different kinds of modern pollen samples from the same sites and combining distance weighted vegetation surveys. In combination with traditional remote sensing and ecological field observations, pollen analysis enhances our capacity to interpret vegetation patterns and landscape transformations, not only in the past but also in the rapidly transforming earth today.

5 Conclusion and Perspectives

Integrative studies, that can help synchronize modern pollen datasets from varied sources at the same sites in the same season, seem to hold much potential to refine further the quantification of pollen-vegetation relationships across multiple spatial scales from the immediate surroundings to the broader regional landscape and validate the role of classical pollen analysis as a geospatial tool. Our study in two contrasting landscapes in the monsoon affected South Asian region ateempts this by comparing pollen assemblages from surface soil and bee loads of the native honey bees *Apis cerana* and *A. florea*. This multi-source approach has the potential to offer a more granular perspective on the tropical landscape dynamics though there is much more to be done to get a real handle on the complex, more-than-human interactions that have structured these environments over time. Our

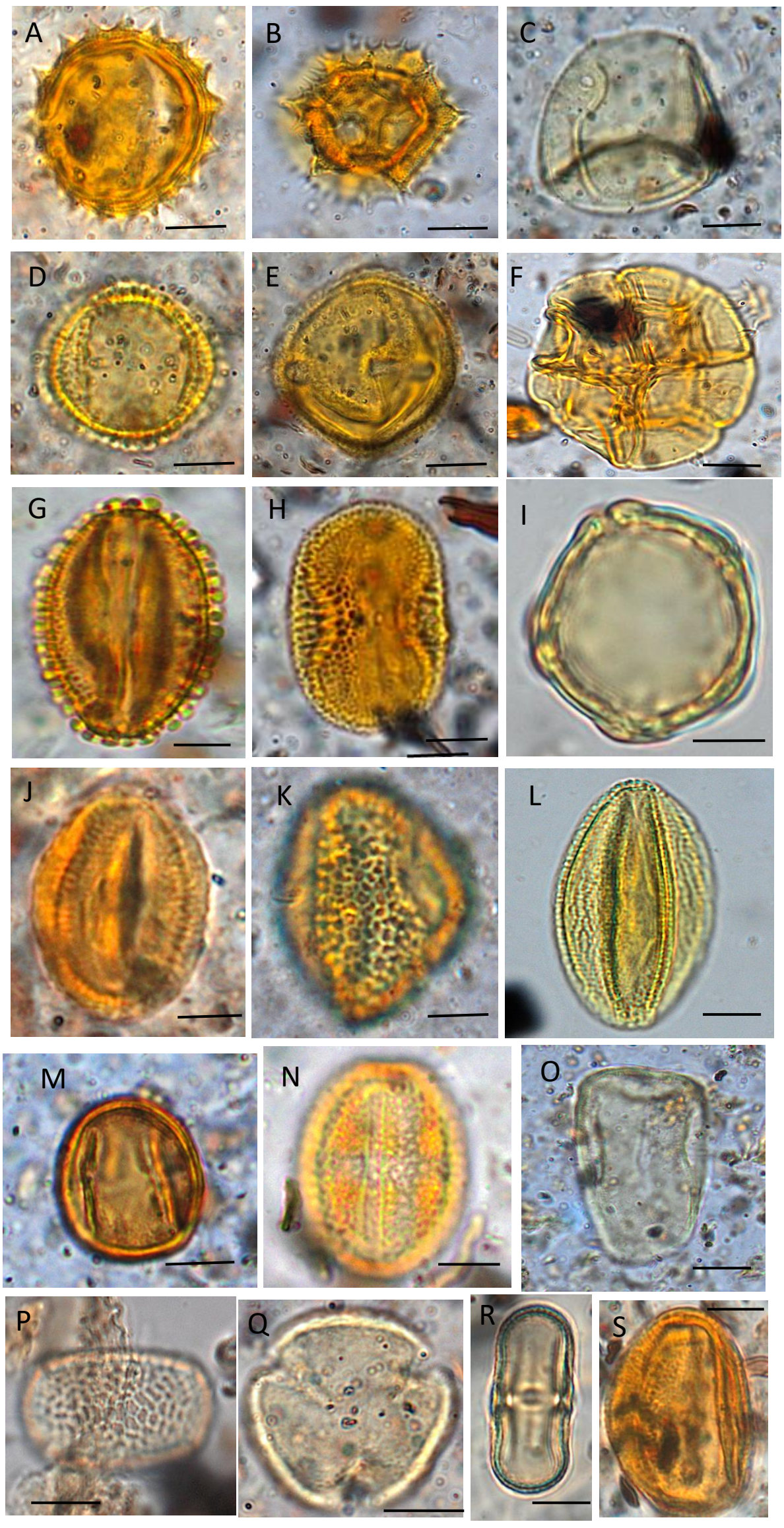


Figure 6. LM images of some pollen taxa from the Nilgiris. A. Asteraceae (echinate); B. Asteraceae (fenestrate); C. Poaceae; D. *Olea glandulifera*; E. *Dodonaea viscosa*; F. *Acacia*; G. *Ilex*; H. *Justicia*; I. *Laurembergia*; J. *Artemisia*; K. *Ligustrum*; L. Gentianaceae; M. *Rapanea;* N. *Meliosma;* O. Cyperaceae; P. *Impatiens' Q, Daphniphyllum;* R. Apiaceae; S. *Turpinia nepalensis.*
Scale bar: 10 µm

observation that certain taxa absent from vegetation surveys appear in both surface soil and honeycomb pollen spectra further attests to this "remote-sensing" capacity of the pollen record. It is also in this sense that classical palynology functions as an inherently geospatial sensor that captures overlapping ecological layers and temporal dynamics. When coupled with modern GIS and remote-sensing techniques, its ability to reconstruct and interpret vegetation patterns is greatly enhanced, offering a powerful integrative approach to landscape-level ecological analysis (Anupama et al., 2014). Data analysed here broadly show this; in particular, the data subset comprising four matching soil surface and bee pollen samples clearly illustrates the potential for further studies that integrate modern pollen data from diverse sources in the same sites and the same season to help quantify pollen vegetation relationships more holistically and robustly for past vegetation reconstructions as well as present day bee foraging preferences. Methodologically, our results show promise for future developments in the lesser studied tropical Asian landscapes where high volume pollen analyses are increasingly relevant. While the recent focus on automated pollen analyses and the digitization of reference collections (Zhang and Mao, 2026; Jaramillo et al, 2025; Feng et al, 2025; Gimenez et al, 2024) offer transformative potential for throughput, our results underscore the continued necessity of human taxonomic expertise (Anupama and Prasad, 2025).

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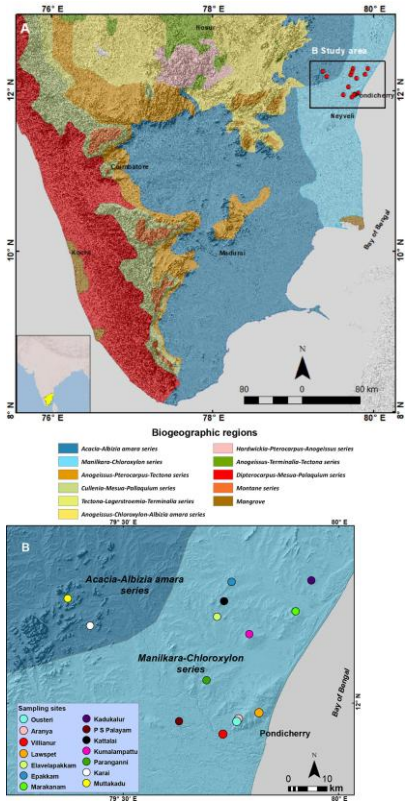
SUPPLEMENTARY MATERIALS (Supplementary Figure 1, 2, 3a-3g and Supplemantary Table 1 for the revised paper : INTEGRATED LANDSCAPE SCALE VEGETATION ASSESSMENT USING SURFACE SOIL AND BEE POLLEN DATA IN THE NILGIRIS AND THE COROMANDEL COAST, SOUTH INDIA - VISUALIZING POLLEN AS A REMOTE BIOLOGICAL SENSOR

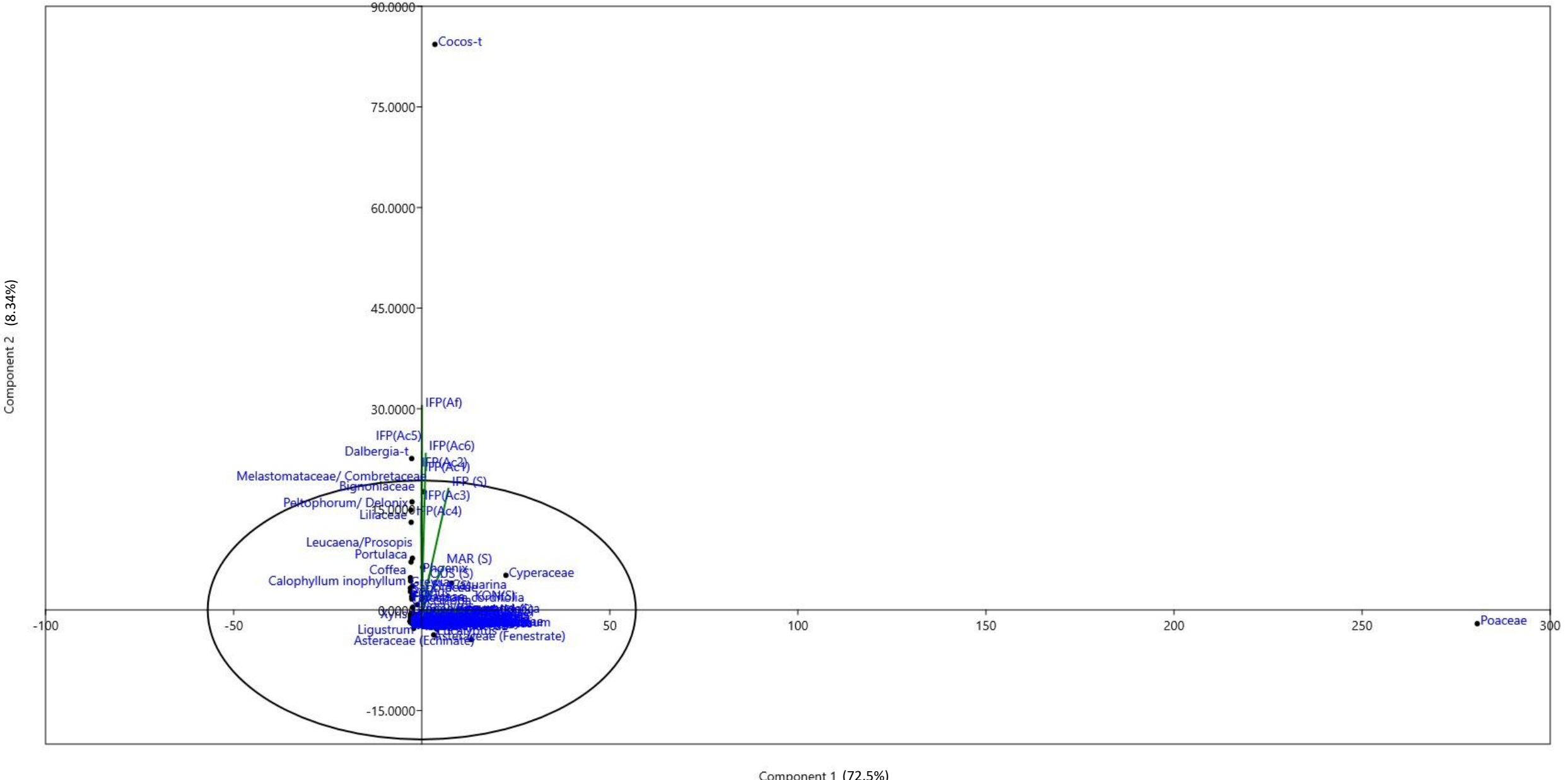
Lazar J, Prasad S, Navya R, De Simone, D , Anupama K

Supplementary Figure1. Location map showing the sites selected for surface soil and bee pollen sample collection in the Nilgiri Biosphere Reserve in southern India, (Source: Google Earth Pro) – the Site Sandynullah which was also sampled for both surface soil and moss samples, is very close to 9th mile and falls in the overlap between the circles around 7th mile and 9th Mile

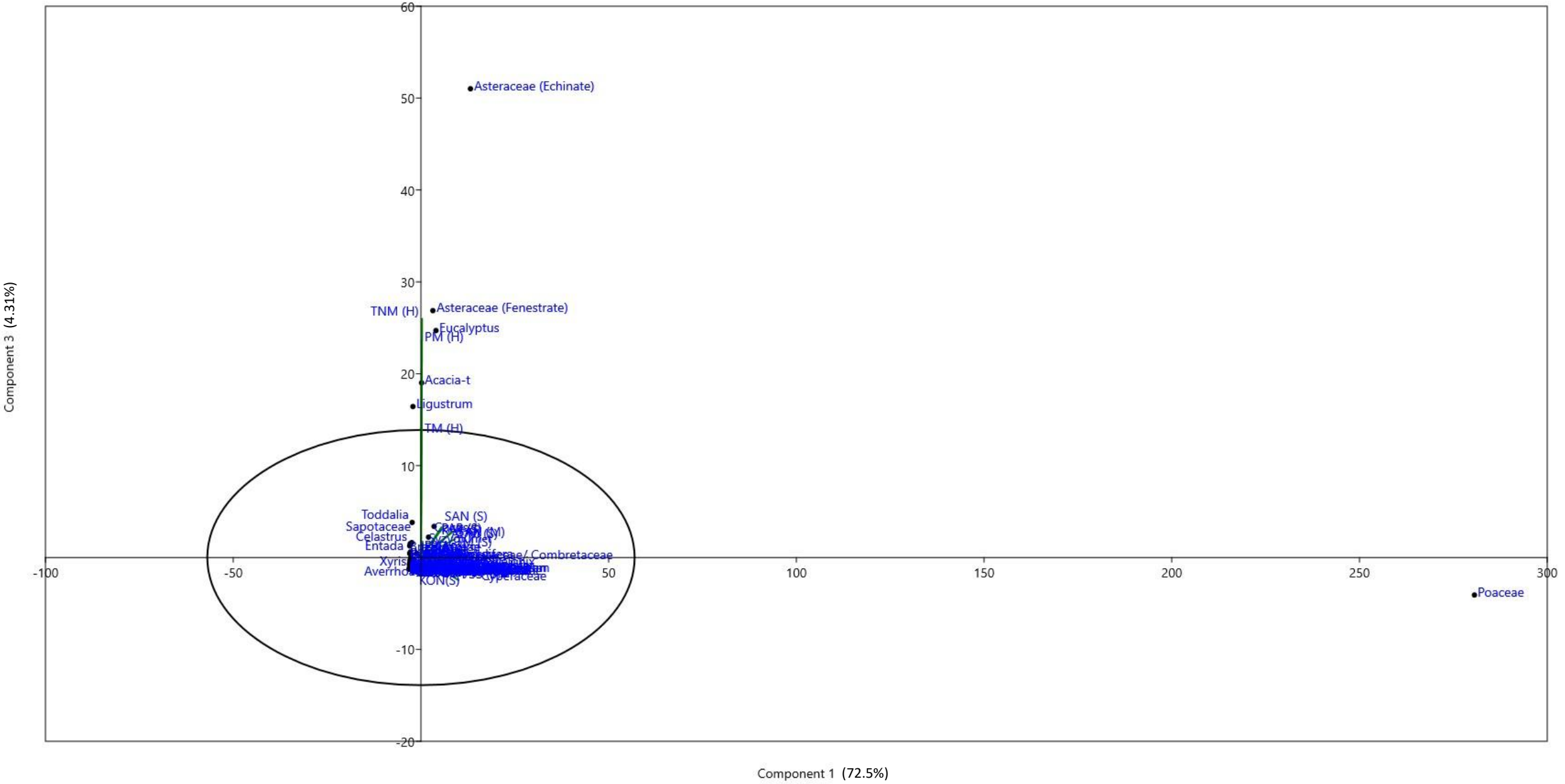


Supplementary Figure 2: Downloaded from - Ecosphere, Volume: 17, Issue: 2, First published: 19 February 2026, DOI: (10.1002/ecs2.70533)

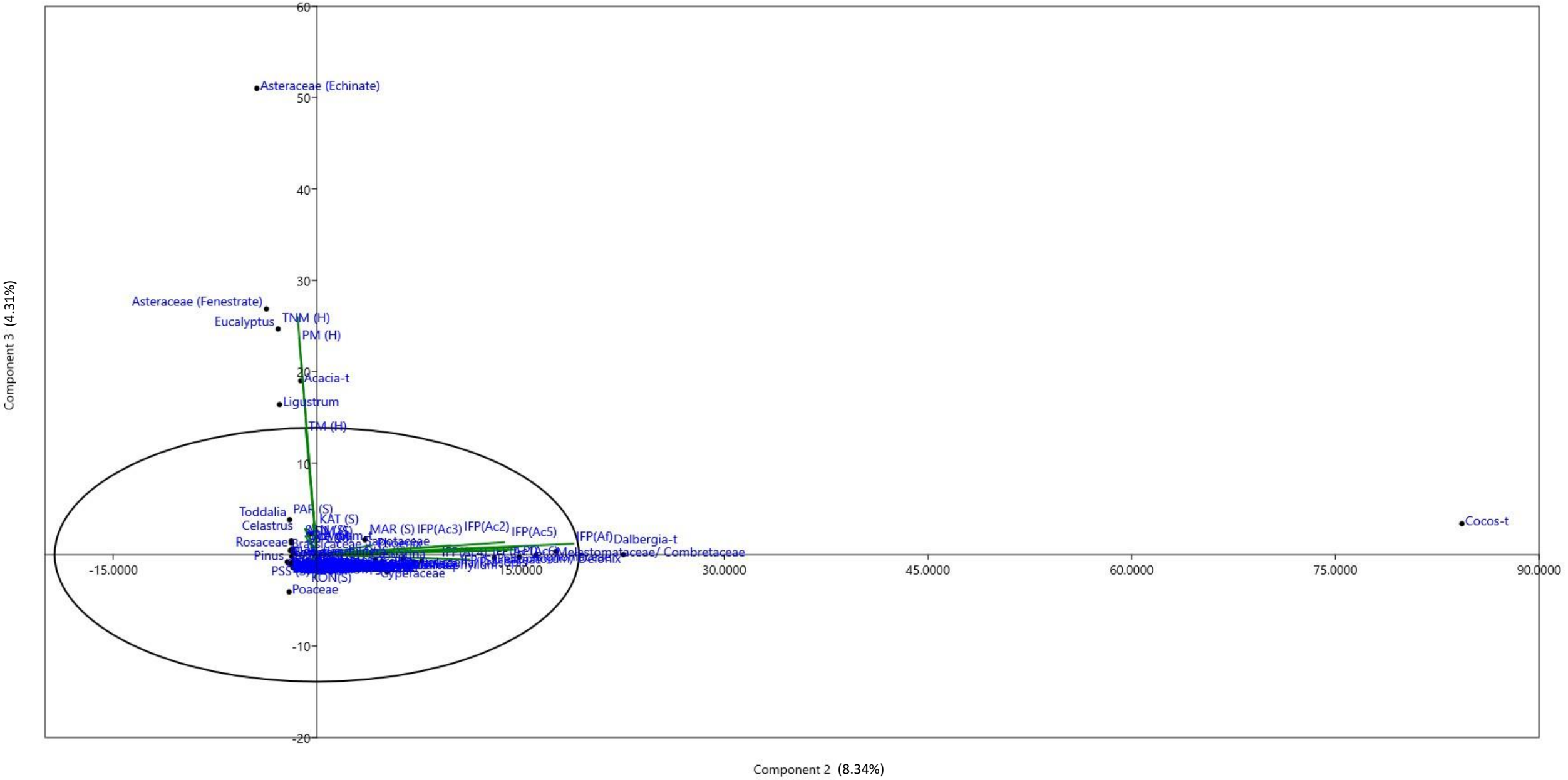
Supplementary Figure 3a: PCA of all 34 samples, AXIS 1_2



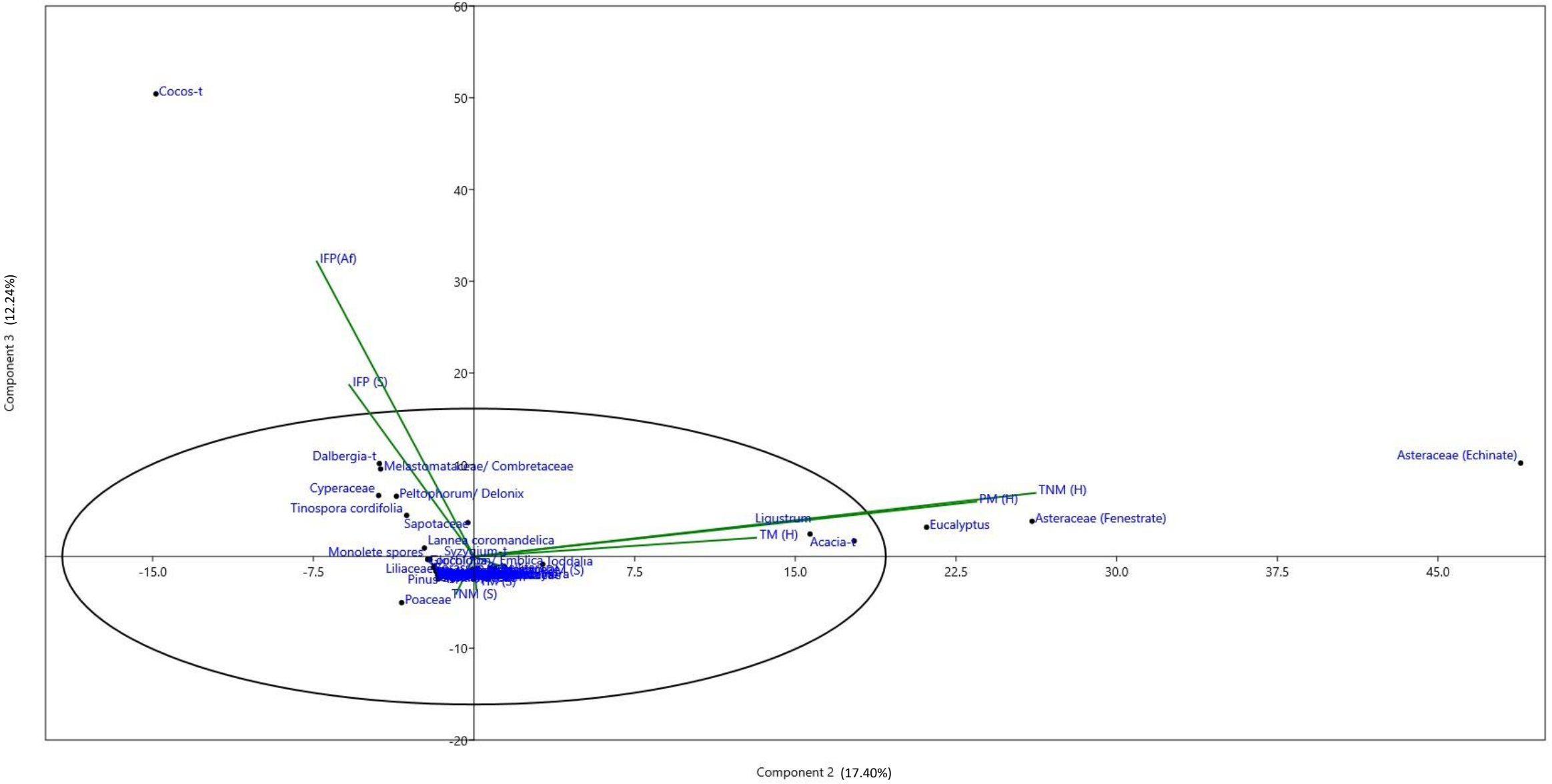
Supplementary Figure 3b: PCA of all 34 samples, AXIS 1_3



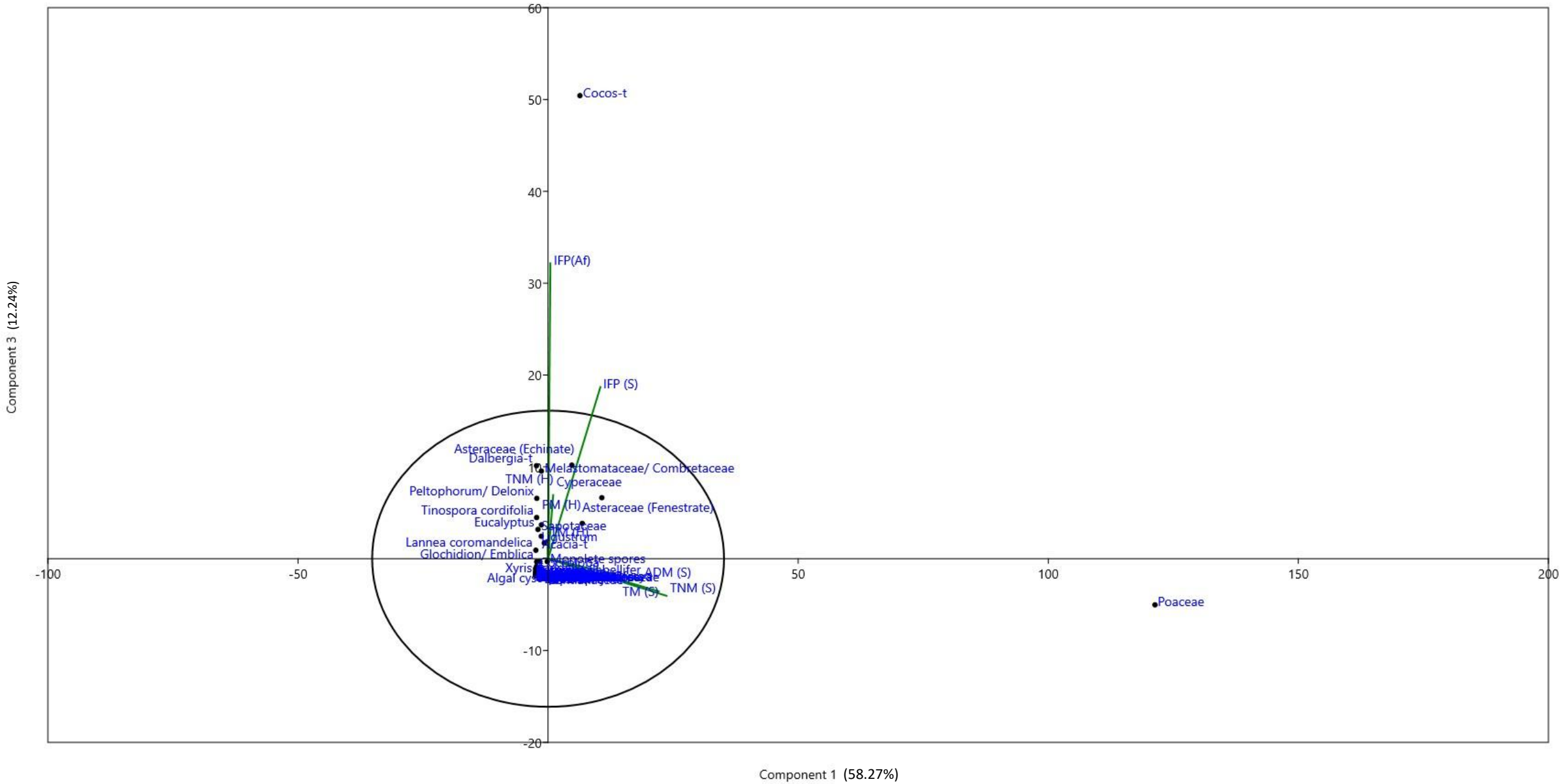
Supplementary Figure 3c: PCA of all 34 samples, AXIS 2_3



Supplementary Figure 3d: PCA of 8 samples (paired surface soil and bee pollen), AXIS 2_3

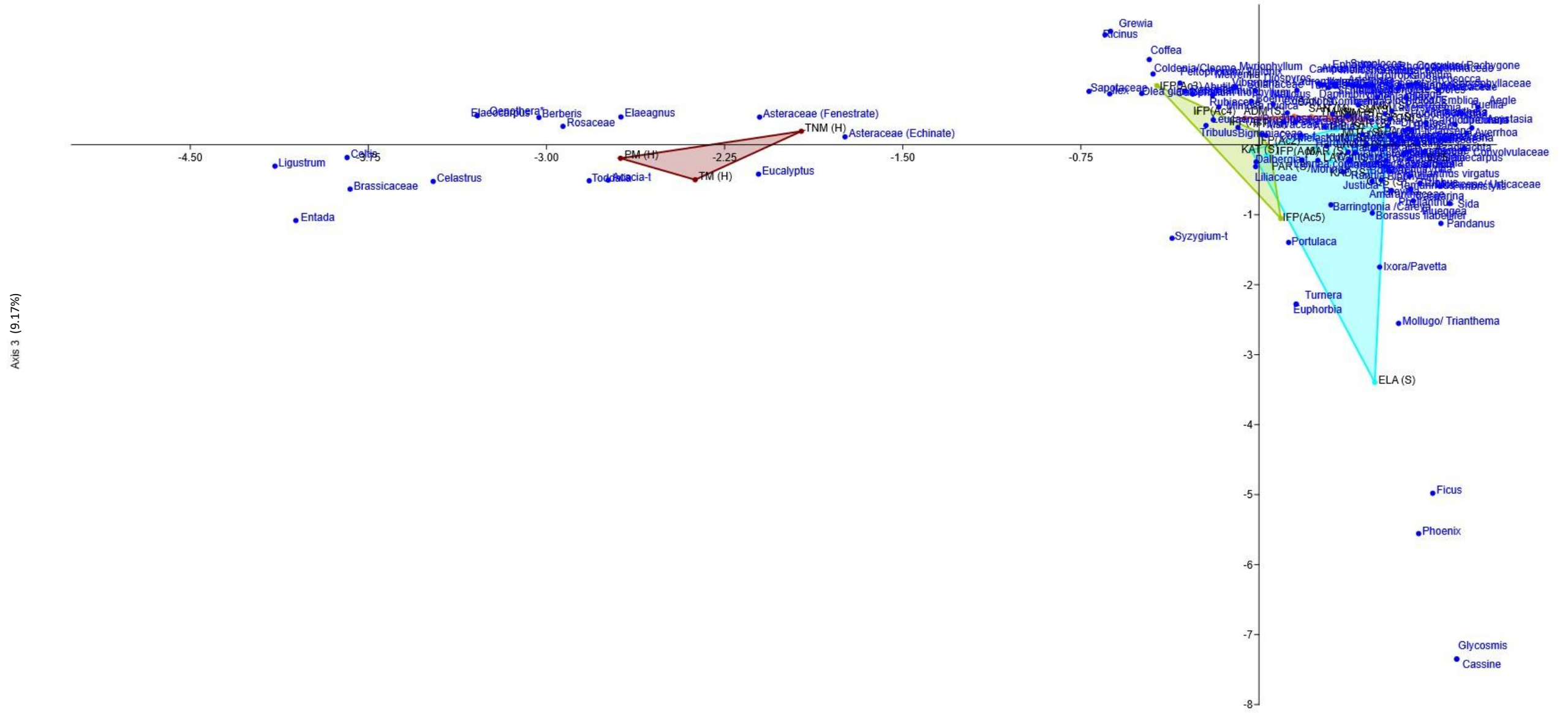


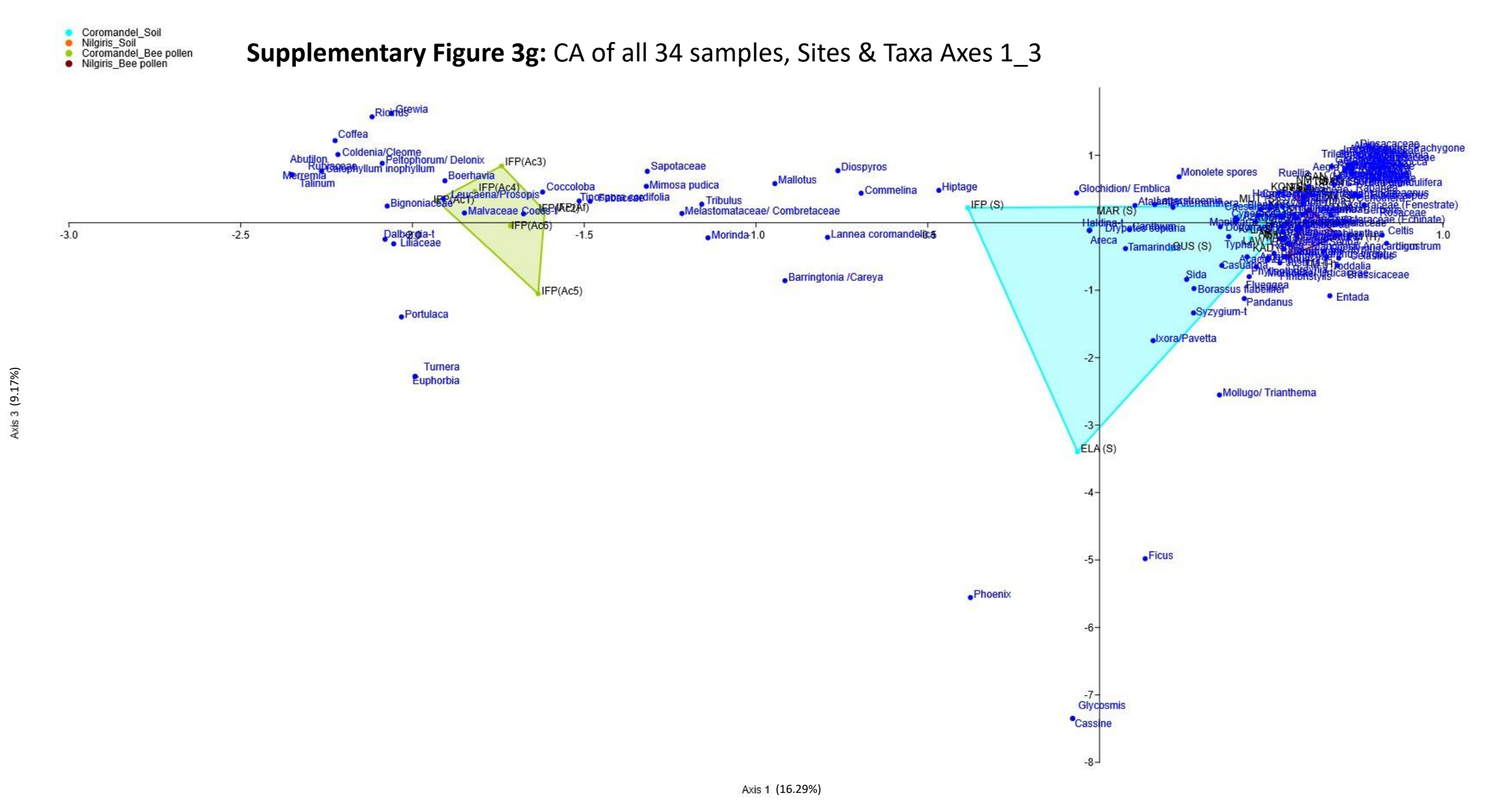
Supplementary Figure 3e: PCA of 8 samples (paired surface soil and bee pollen), AXIS 1_3



Coromandel_Soil
Nilgiris_Soil
Coromandel_Bee pollen
Nilgiris_Bee pollen

Supplementary Figure 3f: CA of all 34 samples, Sites & Taxa Axis 2_3





Supplementary Figure 3g: CA of all 34 samples, Sites & Taxa Axes 1_3