POLLEN ANALYSIS AS A REMOTE BIOLOGICAL SENSOR: USING MELISSOPALYNOLOGY AND SURFACE SOIL DATA FOR AN INTEGRATED LANDSCAPE SCALE VEGETATION ASSESSMENT IN SOUTH INDIA

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

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

[2] Department of Languages and Cultures, Ghent University, Belgium

*corresponding author: anupama.k@ifpindia.org

Abstract

We use pollen assemblages from two sources, surface soil 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*. We try to demonstrate how classical palynology functions as an inherently geospatial sensor, offering a powerful integrative approach to landscape-level ecological analysis and generating baseline data on pollen transport mechanisms that remain less explored in the tropics using a case study in southern India in two landscapes - the Coromandel coast and upper montane Nilgiris. The thirty-four samples compiled regionally under two heads (coast, Nilgiris) and under each region two more heads (surface soil, bee pollen) comprised of 151 pollen taxa. Taken together in both landscapes, the bee polen comprised of 63 pollen taxa and the surface soils comprised 136 taxa. Five taxa (*Acacia*-t, Asteraceae (Echinate), Poaceae, Sapotaceae and *Syzygium*-t) were found in good proportions under all heads, 17 under three heads (eg: *Mimosa pudica*, *Grewia, Toddalia*), 44 under two heads (eg: *Coffea, Olea glandulifera*). Eighty-four taxa were found exclusively in only one head distributed as follows: surface soils from the coast (43), Nilgiris (26); bee pollen from the coast (11), Nilgiris (4). 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 holistically and robustly.

Keywords: Palynology, Vegetation reconstruction, Nilgiris, Coromandel Coast, pollen-vegetation relationships

POLLEN ANALYSIS AS A REMOTE BIOLOGICAL SENSOR: USING MELISSOPALYNOLOGY AND SURFACE SOIL DATA FOR AN INTEGRATED LANDSCAPE SCALE VEGETATION ASSESSMENT IN SOUTH INDIA

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

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

[2] Department of Languages and Cultures, Ghent University, Belgium

*corresponding author: anupama.k@ifpindia.org

Introduction

Palynology, the study of pollen and spores, provides a robust method for interpreting both current and historical vegetation patterns (Faegri & Iversen, 1989; Moore et al., 1991) by identifying pollen taxa that correspond to plant taxa. Modern pollen assemblages, that are frequently considered as analogues to reconstruct the surrounding vegetation, are preserved naturally in surface soils and in bee loads (honey, corbicular pollen loads and honey combs). Since the relationships between pollen-producing plants and the environmental conditions were the same in the past (during Quaternary) as today (MacDonald, 1996), the interpretation of the pollen assemblages of these samples can directly be applied in the past scenarios. These assemblages can also be obtained using traps of various kinds, including natural ones such as spider-webs. They provide a well-established qualitative and quantitative method capturing the influence of climate, topography and human activity (Seppä & Bennett 2003; Stephen, 2014; Fyfe et al., 2015; Lazar et al., 2024).

Pollen in soil reflects regional vegetation, primarily anemophilous taxa, while bee pollen captures primarily entomophilous taxa, highlighting actively foraged plant taxa (Dimou & Thrasyvoulou, 2007; Ponnuchamy et al., 2014; Lazar et al., 2023, 2024). Different kinds of pollen traps (Anupama, 1992, 2001; Gimenez et al., 2024) exposed at varying periodic intervals also provide environmental data on the content of the aerosols that includes pollen which here becomes a proxy to the seasonally changing flowering phenology in addition to providing snapshots of the local to regional vegetation.

Remote sensing of vegetation, relying on satellite data, is currently the most powerful method to map vegetation at regional to continental scales and hence widely used in biodiversity assessments that rapidly capture the dominant characteristics of the upper canopy of the forest or the agroecosystem (Turner et al., 2003; Kacic & Kuenzer, 2022). Here we visualize the classical century old discipline of palynology as one that provides a remote biological sensor (pollen assemblage) on the ground at a single location that reconstructs vegetation composition at local to regional landscape and temporal scales (Broström et al., 2004; Jones & Bryant, 2014; Liu et al., 2023). The diverse sources of modern pollen assemblages can be complementary in their vegetation reconstruction. Thus, they offer fine-scale, biologically integrated signals of the vegetation. 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., 2021; 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 (Thomas et al., 2009; Schrader et al., 2018). 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).

There remains a need for comprehensive studies that integrate modern pollen data from diverse sources in the same sites to assess and quantify pollen vegetation relationships that are vital to interpret present and past vegetation dynamics. The present communication explores 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 soil samples, evaluate their potential as biological proxies that complement each other in reconstructing vegetation comprised of both anemophilous and entomophilous plants. This study aims 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.

Materials & Methods

Study area, Sample collection and Preparation

The investigation was conducted in two distinct landscapes: the upper montane Nilgiri hills and the Coromandel Coastal region around Pondicherry. In each landscape both surface soil samples and bee pollen samples were collected (Table 1, Figure 1 and Appendix 1 Sup.Figs. 1 & 2).

In the Nilgiris, samples were collected at eight sites: surface soils were collected at seven sites mainly around grassland mounds in proximity to the settlements of the native tribals of Nilgiris, Todas. At two of these, bee pollen was collected in the vicinity of the surface sample collection point and at one, 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, dominated by native and introduced species.

In the Coromandel coast, information already available comprised the main data. This includes: a) 15 surface samples at 14 sites (Navya et al, 2025); and b) compiled data of corbicular loads of *Apis cerana* pooled as 6 monthly samples between January to April in 2021-2022 at French Institute of Pondicherry (IFP) (Lazar, 2024). In addition, an *Apis florea* comb and surface soil from the same location (IFP) (Table 1) were collected in the urban garden setting with diverse native and introduced flora and weeds in the vicinity. The data from the 15 surface samples is in the NEOTOMA data repository and can be accessed via the cited DOIs given before the References section in this manuscript (Anupama, 2025a-o).

In total, the data altogether 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 2). 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.

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, 2025 (accepted)). 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.

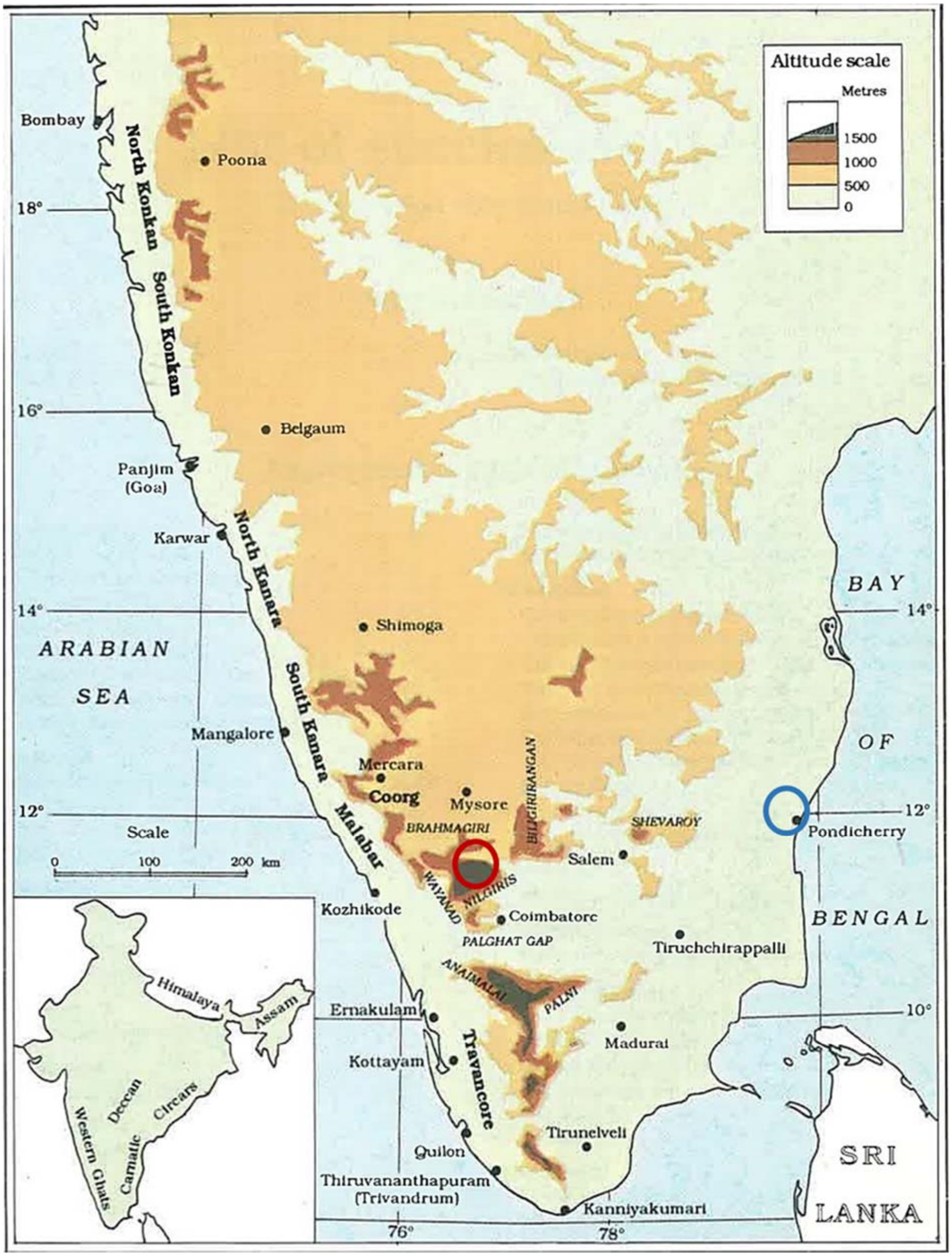


Fig.1 Physical map of southern India adapted from Tissot et al. (1994) showing the two contrasting landscapes chosen in this study – the upper montane Nilgiris (red circle) and the Coromandel coastal region around Pondicherry (blue circle). Please see Appendix 1, Sup.Figs. 1 & 2 for detailed sampling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

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. The core data from 34 samples is presented in Table 2, Figs. 2 & 3

The laboratory protocol involved acid treatments as indicated in Anupama et al. (2014). Honeycombs were processed by acetolysis method as in Ponnuchamy et al. (2014).

Microscopy, data presentation and analyses

The processed slides in both the cases were observed at x400 under a light microscope (Olympus BX51) and at least 1,000 pollen grains were enumerated per sample. Pollen identification was based on the Thanikaimani pollen slide collection and the photomicrographs available at the IFP and published literature (Guinet, 1962; 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). The complete data was used to plot the pollen diagrams (Figures 2 &3).

Results

The thirty-four samples (24 surface soil and 10 bee pollen) in the two landscapes comprised of a total of 151 pollen taxa grouped under four heads (Table 2). 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.

Five 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 2; Figures 2 &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 coast 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-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 (Figures 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 (Online Resouce 1 Sup.Figs 3a – 3g) 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; Online Resouce 1 Sup.Figs 3a – 3g). The PCA and CA runs also show that a number of taxa cluster together and overlap.

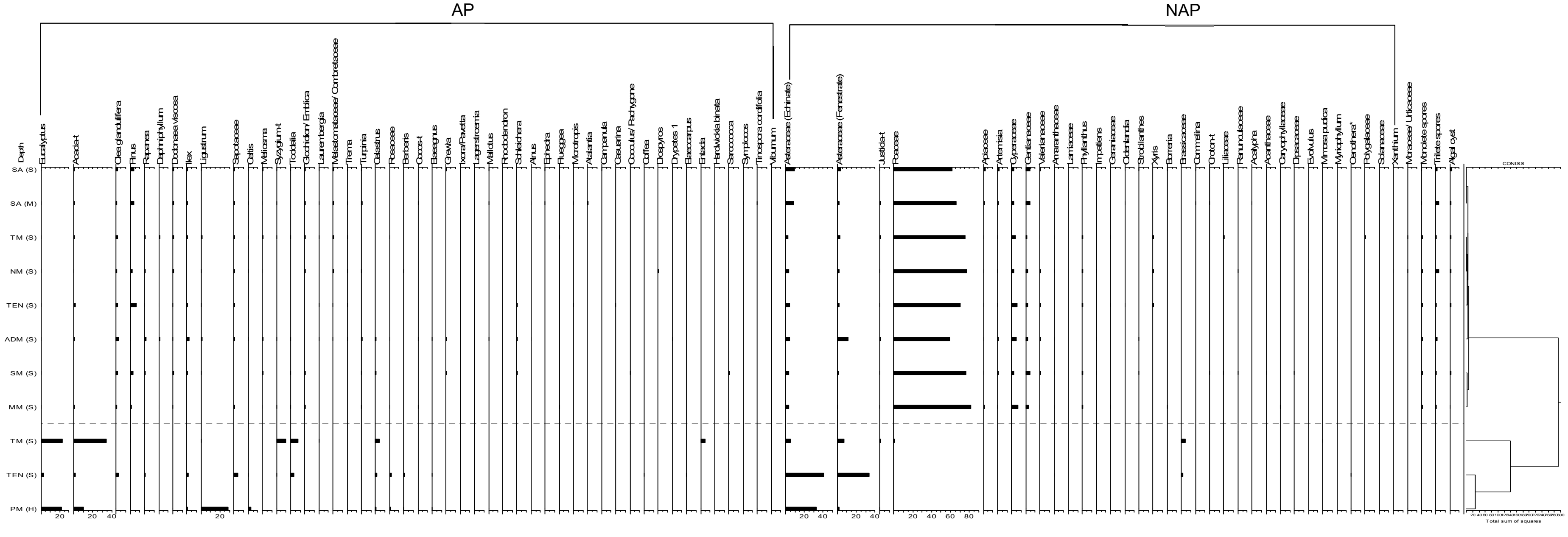


Fig. 2: Diagram of pollen percentages for all the pollen taxa, monolete and trilete spores and algal cysts recovered from 8 surface soil and 3 bee pollen samples in the upper montane Nilgiris. Surface samples were placed above and bee pollen samples below the dotted line. CONISS cluster analysis shows 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 2.

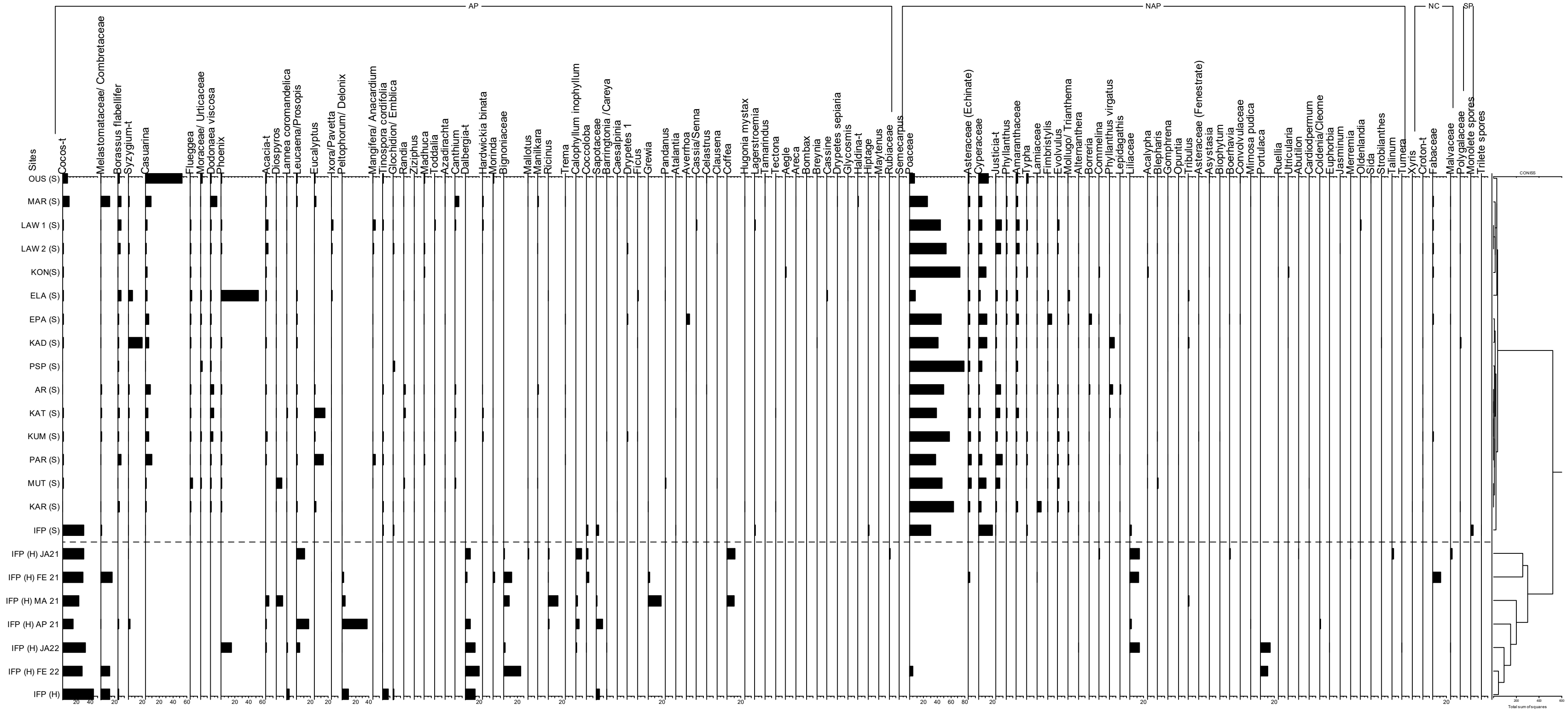


Fig. 3: Diagram of pollen percentages for all the pollen taxa, monolete and trilete spores recovered from 16 surface soil and 7 bee pollen samples in the Coromandel Coast. Surface samples were placed above and bee pollen samples below the dotted line. CONISS cluster analysis shows the distinct separation 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 2.

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., 2025 and in Lazar et al., 2023).

Discussion

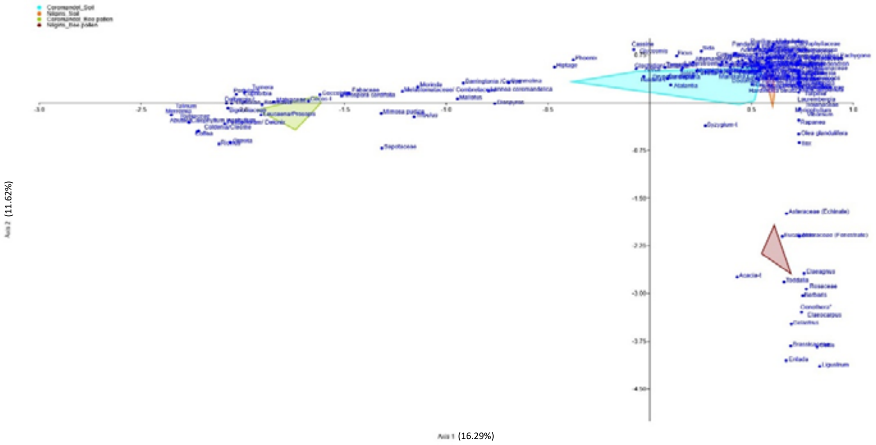
Pollen assemblages from samples on the ground, or from honey combs or bee legs, each at a single location, act like biological sensors of the local to regional plant communities around them. These assemblages are a mixture of airborne and insect-mediated transports, providing another layer of biological information pertaining to the pollination mechanisms of the plant taxa in the assemblages. The taxa recovered (Figs. 2 & 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.

The clustering of Nilgiris versus coastal samples (Figures 4, 5, Appendix 1 Sup.Figs 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 (Vasanthy, 1988; Sutra et al., 1997; Anupama et al., 2014; Mahapatra et al., 2021) 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 Fig. 6 are found in both surface soil and bee pollen samples. 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. 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

a) Taxa



b) Samples

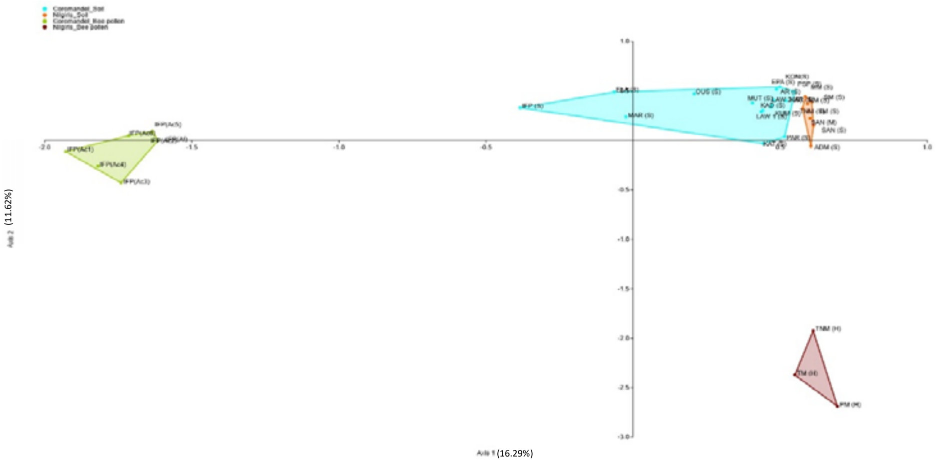


Fig. 4 (a & b): CA of the core data of 34 surface soil and bee pollen samples from the two landscapes – upper montane Nilgiris and the Coromandel Coast. As indicated by the pollen diagrams the bee pollen samples from the upper montane Nilgiris are the best separated while the surface samples from both landscapes though separated are closer together. For more depictions of the multivariate analyses see Appendix 1 Sup.Figs 3a, 3b …3g.

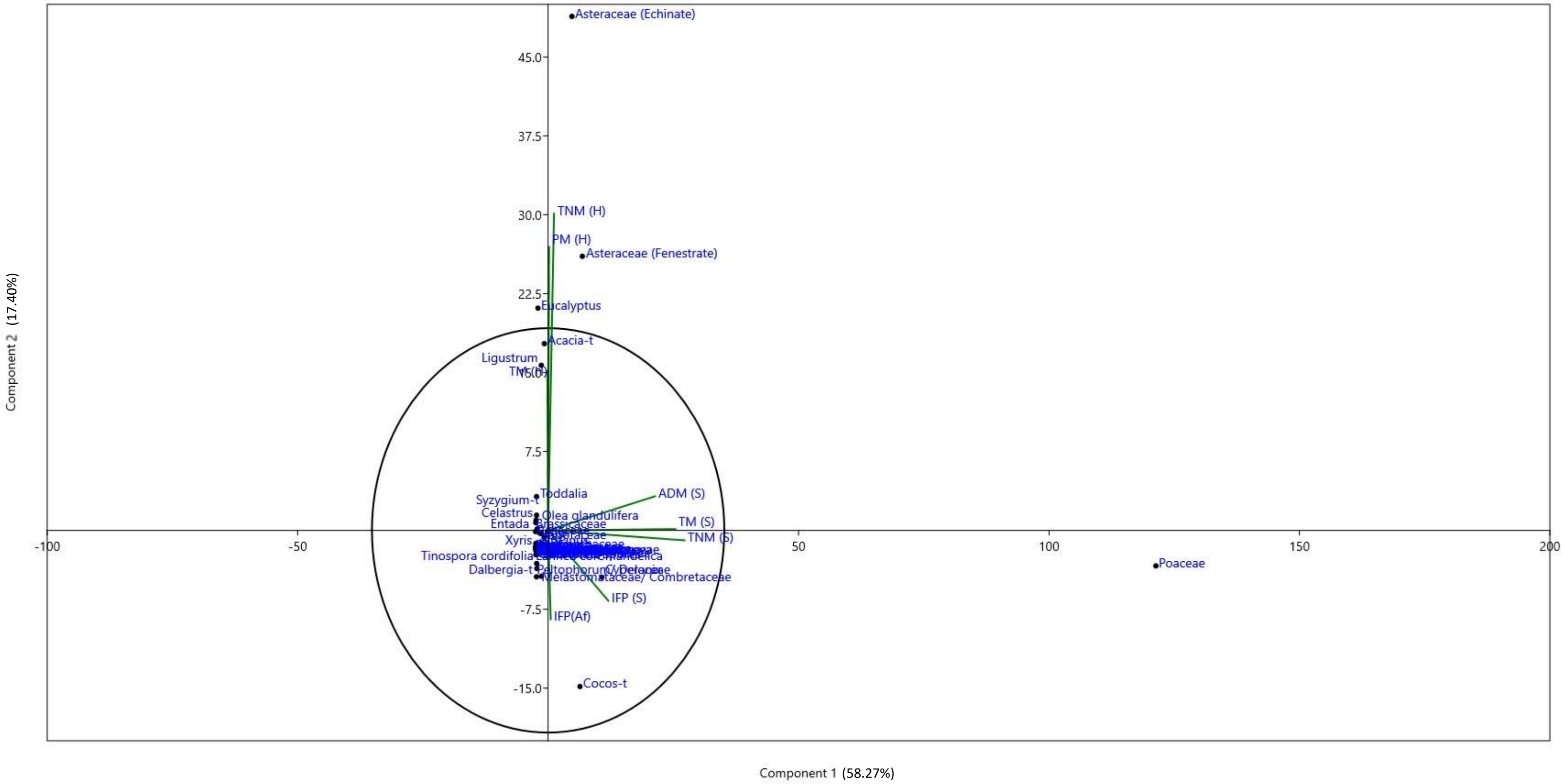


Fig. 5: PCA of a subset of the core data, 4 paired samples of surface soil and bee pollen, 3 from the upper montane Nilgiris and 1 from the Coromandel coast. As indicated by the pollen diagrams, the cluster analyses and the correspondence analyses of all 34 samples (figures 2-4), we expected a more visible 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 Appendix 1 Sup.Figs 3a, 3b …3g.

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 and 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* (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 (Figures 2 & 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. The prevalence of wind-pollinated taxa

Table 2: 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			
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			

such as Poaceae and Cyperaceae in soil samples, contrasted with their limited presence in honeycomb samples, reflects differences in pollen dispersal mechanisms and pollinator selectivity.

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; Anupama et al., 2000; 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.

Conclusion

Pollen analysis itself can be viewed as a geospatial tool, as it integrates information from vegetation across multiple spatial scales from the immediate surroundings to the broader regional landscape. Pollination occurs through various transport mechanisms, including wind, water, and insects, which carry pollen beyond its source vegetation, often through several secondary pathways. The 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. In this sense, 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. 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.

Acknowledgements

This paper was conceived in the course of the Nilgiri Archaeological Project and benefitted partly from funding by the Research Foundation–Flanders (FWO) through an Odysseus Type II grant (no. G0F0621N) and partly through the IFP PhD Fellowship granted to JL (2020-2023). We thank the Tamil Nadu Forest Department for permissions to sample and in particular Mr Nagaraj and all the staff at the Nilgiris Division office for their kind cooperation. All the people in all the Toda villages especially Mr Puthu Raj, Attas Kuttan and Jai for all their support and guidance during our fieldwork.

Competing Interests: There are no competing interests

Author Contributions: All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by [Lazar J], [Prasad S] and [Anupama K]. The first draft of the manuscript was written by [Lazar J] and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

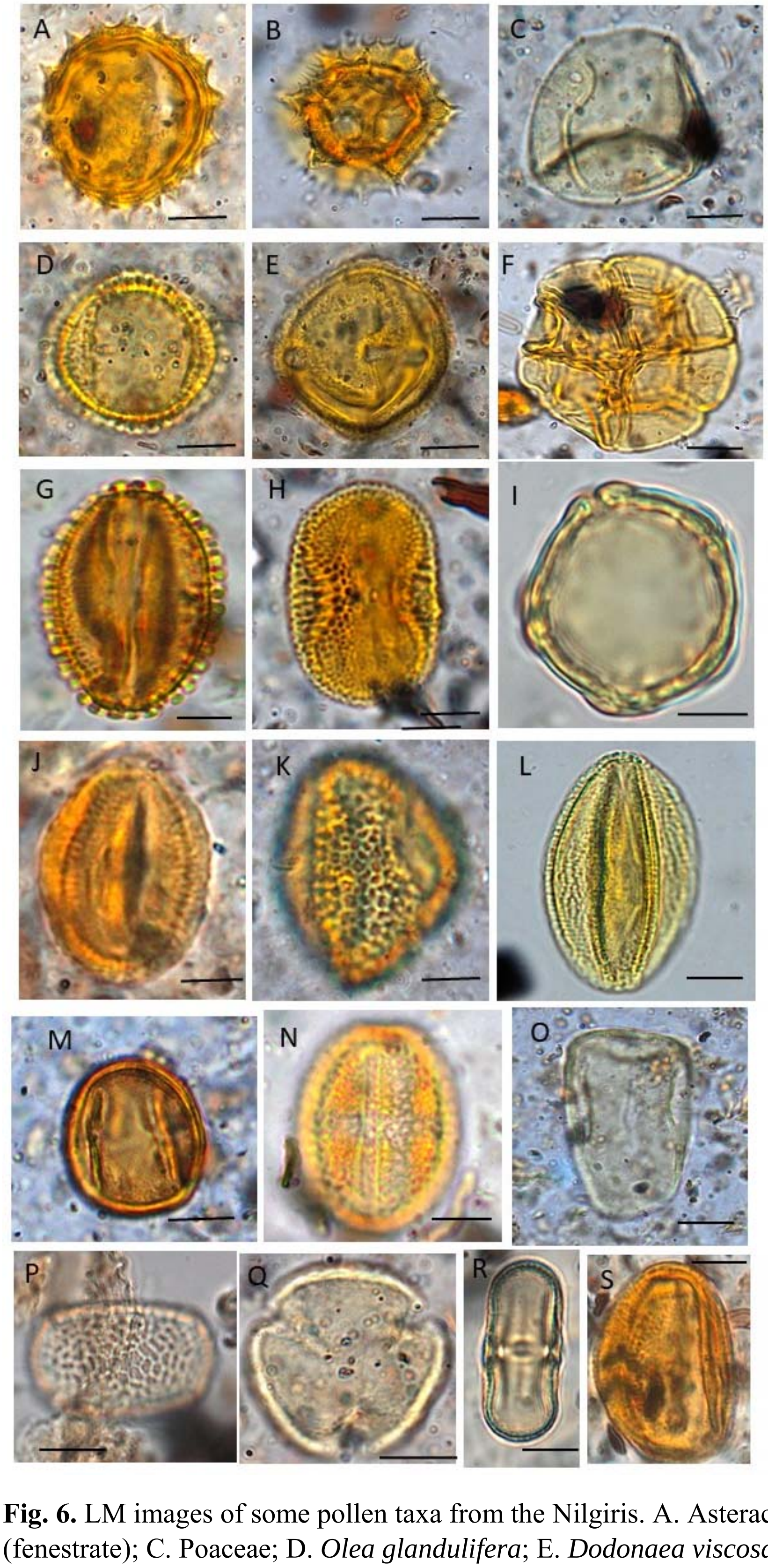


Fig. 6. LM images of some pollen taxa from the Nilgiris. A. Asteraceae (echinate); B. Asteraceae (fenestrate); C. Poaceae; D. *Olea glandulifera*; E. *Dodonaea viscosa*; F. *Acacia*; G. *Ilex*; H. *Justicia*; I. *Laurembergia*; J. *Artemisia*; K. *Ligustrum*; L. Gentianaceae; M. *Rapanea;* N. *Meliosma;*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

Pollen data Repository access for 15 surface soil samples

Anupama, K. 2025a-o. “Lawspet Season 1”, “Muttakadu”, “Karai”, “Kadukkalur”, “Epakkam”, “Kattalai”, “Marakanam”, “Elavalapakkam”, “Kumalampattu”, “Paranganni”, “PS Palayam”, “Konerikuppam”, “Aranya”, “Ousteri” and “Lawspet Season 2” pollen surface sample dataset” (Version 1.1) [Dataset]. Neotoma Paleoecology Database:

a: https://doi.org/10.21233/SMTR-7V46

b:https://doi.org/10.21233/Z57B-EP96

c:https://doi.org/10.21233/SJKJ-7F33

d: https://doi.org/10.21233/9M1M-QN58

e: https://doi.org/10.21233/ZDFA-7X33

f: https://doi.org/10.21233/SFWK-EN12

g: https://doi.org/10.21233/NTS4-8A48

h: https://doi.org/10.21233/J69X-BJ14

i: https://doi.org/10.21233/KECE-M591

j: https://doi.org/10.21233/9VRS-VP74

k: https://doi.org/10.21233/48J5-NW77

l: https://doi.org/10.21233/5ESP-XG68

m: https://doi.org/10.21233/SCV7-2B34

n: https://doi.org/10.21233/K86Q-7G20

o: https://doi.org/10.21233/Q9TH-R979

References

Anupama, K. (1992). Airborne pollen in Pondicherry in May, a period of shift in wind direction. *Indian Journal of Aerobiology, special volume*, 43–48.

Anupama. K. (2001). Representation of Dipterocarpaceae pollen grains in a low elevation wet evergreen forest in Karnataka, India. 6th Round Table Conference on Dipterocarps, Bangalore, India, 8-12 February 1999, Curtin University of Technology, Perth, Australia.

Anupama, K., Aravajy, S., & Prasad, S. (2002). Pollen and ecological studies in the Southern Eastern Ghats: a new methodological approach. In *Proc. National Seminar on Conservation of Eastern Ghats*, 88–102.

Anupama, K., Prasad, S., & Reddy, C. S. (2014). Vegetation, land cover and land use changes of the last 200 years in the Eastern Ghats (southern India) inferred from pollen analysis of sediments from a rain-fed tank and remote sensing. *Quaternary International*, *325*, 93–104.

Anupama, K., Ramesh, B. R., & Bonnefille, R. (2000). Modern pollen rain from the Biligirirangan–Melagiri hills of southern Eastern Ghats, India. *Review of Palaeobotany and Palynology*, *108*(3-4), 175–196.

Barišić, D., Lazarić, K., Lulić, S., Vertačnik, A., Dražić, M., & Kezić, N. (1994). 40K, 134Cs and 137Cs in pollen, honey and soil surface layer in Croatia. *Apidologie*, *25*(6), 585–595.

Basu, P., Bhattacharya, R., & Ianetta, P. (2011). A decline in pollinator dependent vegetable crop productivity in India indicates pollination limitation and consequent agro-economic crises. *Nature Precedings*, 1–1.

Basumatary, S. K., Bera, S. K., Sangma, S. N., & Marak, G. (2014). Modern pollen deposition in relation to vegetation and climate of Balpakram valley, Meghalaya, northeast India: Implications for Indo-Burma palaeoecological contexts. *Quaternary International* 325 (2014), 30–40.

S.K. Basumatary and S.K. Bera – Modern pollen record on bat guano deposit from Siju Cave and its implication to palaeoecological study in South Garo Hills of Meghalaya, India. Journal of Cave and Karst Studies, v. 76, no. 3, p. 173–183. DOI: 10.4311/2013PA0119

Bell, K. L., Turo, K. J., Lowe, A., Nota, K., Keller, A., Encinas-Viso, F., & De Vere, N. (2023). Plants, pollinators and their interactions under global ecological change: The role of pollen DNA metabarcoding. *Molecular Ecology*, *32*(23), 6345–6362.

Bhalchandra, W., Baviskar, R. K., & Nikam, T. B. (2014). Diversity of nectariferous and polleniferous bee flora at Anjaneri and Dugarwadi hills of Western Ghats of Nasik district (MS) India. *Journal of Entomology and Zoology Studies*, *2*(4), 244–249.

Bonnefille, R., Anupama, K., Barboni, D., Pascal, J., Prasad, S., & Sutra, J. P. (1999). Modern pollen spectra from tropical South India and Sri Lanka: altitudinal distribution. *Journal of Biogeography*, *26*(6), 1255–1280.

Broström, A., Sugita, S., & Gaillard, M. J. (2004). Pollen productivity estimates for the reconstruction of past vegetation cover in the cultural landscape of southern Sweden. *The Holocene*, *14*(3), 368–381.

Bunting, M. J., Farrell, M., Broström, A., Hjelle, K. L., Mazier, F., Middleton, R., ... & Twiddle, C. L. (2013). Palynological perspectives on vegetation survey: a critical step for model-based reconstruction of Quaternary land cover. *Quaternary Science Reviews*, *82*, 41–55.

Chandrasekaran, S., Nagendran, N. A., Krishnankutty, N., Pandiaraja, D., Saravanan, S., Kamaladhasan, N., & Kamalakannan, B. (2011). Disposed paper cups and declining bees. *Current Science 101*(10): 1262.

Chaya, P. (2019). Floral composition and pollen morphological studies of *Apis florea* honey sample from Vikarabad district of Telangana state. *International Journal of Research and Analytical Reviews, 6(2),* 321–327.

Cunningham, S. A. (2000). Depressed pollination in habitat fragments causes low fruit set. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1448), 1149–1152.

Daugaliyeva, S., Daugaliyeva, A., Amirova, K., Yelubayeva, A., Toktarov, N., & Peletto, S. (2025). Identifying Honey Species Composition and Verifying Label Accuracy Using Melissopalynological Analysis and DNA Metabarcoding. *Food Analytical Methods*, *18*(11), 2634–2650.

Devy, M. S., & Davidar, P. (2006). Breeding systems and pollination modes of understorey shrubs in a medium elevation wet evergreen forest, southern Western Ghats, India. *Current Science*, 90(6), 838–842.

Dimou, M., & Thrasyvoulou, A. (2007). Seasonal variation in vegetation and pollen collected by honeybees in Thessaloniki, Greece. *Grana*, *46*(4), 292–299.

Erdtman, 1960. The acetolysis method. A revised description. *Svensk Bot. Tidskr.* 54: 561–564.

Fyfe, R. M., Woodbridge, J., & Roberts, N. (2015). From forest to farmland: pollen-inferred land cover change across Europe using the pseudobiomization approach. *Global Change Biology*, *21*(3), 1197–1212.

Gallai, N., Salles, J. M., Settele, J., & Vaissière, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological economics*, *68*(3), 810–821.

Grimm, E. C. (1991). TILIA and TILIA GRAPH: PC spreadsheet and graphics software for pollen data. INQUA working group on data-handling methods. *Newsletter*, *4*, 5–7.

Gimenez, B., Joannin, S., Pasquet, J., Beaufort, L., Gally, Y., de Garidel-Thoron, T., ... & Peyron, O. (2024). A user-friendly method to get automated pollen analysis from environmental samples. *New Phytologist*, *243*(2), 797–810.

Gupta, D., Chauhan, H., Gupta, S., & Gupta, R. (2019). Effect of colony collapse disorder on honeybees. *Journal of Computational and Theoretical Nanoscience*, *16*(10), 4149–4152.

Gupta, R. K. (2014). Taxonomy and distribution of different honeybee species. In *Beekeeping for poverty alleviation and livelihood security* (pp. 63–103). Springer, Dordrecht.

Hammer, Ø., & Harper, D. A. (2001). Past: paleontological statistics software package for educaton and data anlysis. *Palaeontologia electronica*, *4*(1), 1.

Hepburn, H. R., Radloff, S. E., Otis, G. W., Fuchs, S., Verma, L. R., Ken, T., ... & Wongsiri, S. (2005). Apis florea: morphometrics, classification and biogeography. *Apidologie*, *36*(3), 359–376.

Indhu, A., Lazar, J., Prasad, S., & Anupama, K. (2023). Pollinators in tropical ecosystems of Southern India with emphasis on the native pollinators *Apis cerana indica* and *Tetragonula iridipennis*. *Indian Journal of Entomology,* e22025.

Jantz, N., Homeier, J., León-Yánez, S., Moscoso, A. and Behling, H., 2013. Trapping pollen in the tropics—comparing modern pollen rain spectra of different pollen traps and surface samples across Andean vegetation zones. *Review of Palaeobotany and Palynology*, *193*, pp.57-69.

Jones, G. D., & Bryant, V. M. (2014). Pollen studies of East Texas honey. *Palynology*, *38*(2), 242–258.

Kastrati, G., Paçarizi, M., Sopaj, F., Tašev, K., Stafilov, T. and Mustafa, M.K., 2021. Investigation of concentration and distribution of elements in three environmental compartments in the region of Mitrovica, Kosovo: Soil, honey and bee pollen. *International Journal of Environmental Research and Public Health*, *18*(5), p.2269.

Kwaiser, K. S., & Hendrix, S. D. (2008). Diversity and abundance of bees (Hymenoptera: Apiformes) in native and ruderal grasslands of agriculturally dominated landscapes. *Agriculture, Ecosystems & Environment*, *124*(3-4), 200–204.

Laxmikant, B., & Devandra, M. (2018). Pollen analysis of summer honey from forest area of Pombhurna Tahsil in Chandrapur District of Maharashtra State. *World. J. Pharm. Res*, *7*, 1059–1072.

Layek, U., & Karmakar, P. (2016). Bee plants used as nectar sources by *Apis florea* Fabricius in Bankura and Paschim Medinipur districts, West Bengal. *Geophytology*, *46*(1), 1–14.

Lazar, J., Prasad, S., Barboni, D., Das, L., Kumaresan, V., & Anupama, K. (2024). Diversity matters: Diet of Apis cerana in southeast India includes one consistently occurring and several seasonally available floral sources. *Palynology*, *48*(1), 2255990.

Lazar, J. 2024 Foraging Preferences of the Honey bee *Apis cerana* Fabr. In the Puducherry region, India using corbicular pollen: Insights from microscopic and field observations.Unpublished PhD Thesis Pondicherry University.

Leontidou, K., Vokou, D., Sandionigi, A., Bruno, A., Lazarina, M., De Groeve, J., ... & Cristofori, A. (2021). Plant biodiversity assessment through pollen DNA metabarcoding in Natura 2000 habitats (Italian Alps). *Scientific Reports*, *11*(1), 18226.

Liu, L., Wang, N., Zhang, Y., Yu, X., & Cao, X. (2023). Performance of vegetation cover reconstructions using lake and soil pollen samples from the Tibetan Plateau. *Vegetation History and Archaeobotany*, *32*(2), 157–169.

MacDonald, G.M. (1996). Non-aquatic Quaternary. In *Palynology: Principles and applications*, Vol.2., 879-910. ed.: Jansonius, J. and McGregor, D.C. AASP, USA. 3 volumes.

Malekar, H. D., Matte, R., Rajurkar, A., & Ukey, S. (2024). Melissopalynological Investigation in India: A Review. *International Journal of All Research Education and Scientific Methods, 12* (7), 889–894.

Moore, P. D., Webb, J. A., & Collinson, M. E. (1991). *Pollen Analysis* (2nd ed.). Blackwell Scientific Publications, Oxford.

Navya, R. (2019). Pollen based estimates of Holocene vegetation in southern India: An LRA (Landcover Reconstruction Algorithm) approach, PhD thesis, Pondicherry University.

Navya, R. Prasad, S. Gaillard M-J., Mazier, F., Li F., & Anupama K. (2025) Relative Pollen Productivity estimates from India: a step towards quantitative reconstruction of past plant abundance – Accepted for publication in *Ecosphere*

Nevard, L. (2017). *Foraging behaviour and niche differentiation in two South Asian bee species*. University of Exeter (United Kingdom).

Nohro, S., Bera, S. K., & Jayakumar, S. (2020). Modern pollen spectra from the Pala Wetland Reserve Forest, Siaha District, Southern Mizoram, north-eastern India. *Palynology*, *44*(2), 205–216.

Padmavathy, S., & Rehel, S. M. (2014). Bee plants of *Apis dorsata* during winter season from Coonoor Region, Nilgiri, Tamil Nadu, India. *Journal of Academia and Industrial Research*, *2*(10), 570–572.

Ponnuchamy, R., Bonhomme, V., Prasad, S., Das, L., Patel, P., Gaucherel, C., ... & Anupama, K. (2014). Honey pollen: using melissopalynology to understand foraging preferences of bees in tropical South India. *Plos one*, *9*(7), e101618.

Potts, S. G., Vulliamy, B., Dafni, A., Ne'eman, G., & Willmer, P. (2003). Linking bees and flowers: how do floral communities structure pollinator communities?. *Ecology*, *84*(10), 2628–2642.

Ruttner, F. (2013). *Biogeography and taxonomy of honeybees*. Springer Science & Business Media.

Sadafale, G. V. R., Vishnupandi, M., Sami, A.., Sudalaiyandi, Y., Subal, B. K., Kamal, P. A., & Shukla, A. (2025). Global Decline of Pollinators: Drivers, Consequences and Mitigation Strategies. *Journal of Biology and Nature*, *17*(2), 356–379.

Sasidharan, K. R., & Kunhikannan, C. (2010). Bee faunal diversity in the Nilgiris part of the Western Ghats, Tamil Nadu.

Schrader, J., Franzén, M., Sattler, C., Ferderer, P., & Westphal, C. (2018). Woody habitats promote pollinators and complexity of plant–pollinator interactions in homegardens located in rice terraces of the Philippine Cordilleras. *Paddy and Water Environment*, *16*(2), 253–263.

Seppä, H., & Bennett, K. D. (2003). Quaternary pollen analysis: recent progress in palaeoecology and palaeoclimatology. *Progress in Physical Geography*, *27*(4), 548–579.

Sharma, M. V., Viswanathan, P., Leo, R., Gemmill-Herren, B., Mammides, C., & Ngo, H. T. (2025). Factors influencing pollinator abundance in Indigenous coffee farms of the Nilgiris, Western Ghats, India. *Journal of Apicultural Research*, 1–14.

Stephen, A. (2014). Pollen: A microscopic wonder of plant kingdom. *International Journal of Advanced Research in Biological Sciences*, *1*(9), 45–62.

Sukumar, R. (2000). Climate and ecosystem change: what does it mean for biodiversity conversation in India. *Journal of the Indian Institute of Science*, *80*(6), 609.

Thanikaimoni, G. (1970). *Les Palmiers. Palynologie et systématique* (pp. 286-p). Institut Français de Pondichéry.

Thapa, R. B. (2006). Honeybees and other insect pollinators of cultivated plants: a review. *Journal of the Institute of Agriculture and Animal Science*, *27*, 1-23.

Thomas, S. G., Rehel, S. M., Varghese, A., Davidar, P., & Potts, S. G. (2009). Social bees and food plant associations in the Nilgiri Biosphere Reserve, India. *Tropical Ecology*, *50*(1), 79.

Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E., & Steininger, M. (2003). Remote sensing for biodiversity science and conservation. *Trends in ecology & evolution*, *18*(6), 306–314.

Vasanthy, G. (1988). Pollen analysis of Late Quaternary sediments: evolution of upland savanna in Sandynallah (Nilgiris, South India). *Review of Palaeobotany and Palynology*, *55*(1-3), 175–192.

Verma, R. C., Waseem, M. A., Sharma, N., Bharathi, K., Singh, S., Anto Rashwin, A., ... & Singh, B. V. (2023). The role of insects in ecosystems, an in-depth review of entomological research. *International Journal of Environment and Climate Change*, *13*(10), 4340–4348.

Viswanathan, P., Mammides, C., Roy, P., & Sharma, M. V. (2020). Flower visitors in agricultural farms of Nilgiri Biosphere Reserve: Do forests act as pollinator reservoirs?. *Journal of Apicultural Research*, *59*(5), 978–987.

Wagner, D. L. (2020). Insect declines in the Anthropocene. *Annual review of entomology*, *65*(1), 457–480.

Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D., & Coomes, D. (2019). Advances in microclimate ecology arising from remote sensing. *Trends in Ecology & Evolution*, *34*(4), 327–341.

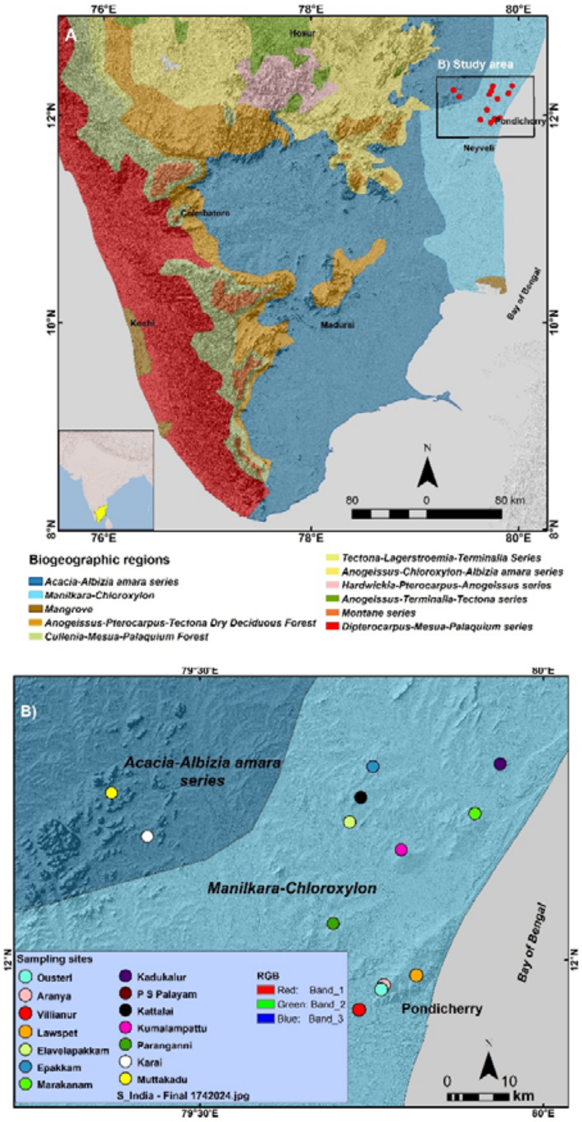
POLLEN ANALYSIS AS A REMOTE BIOLOGICAL SENSOR: USING MELISSOPALYNOLOGY AND SURFACE SOIL DATA FOR AN INTEGRATED LANDSCAPE SCALE VEGETATION ASSESSMENT IN SOUTH INDIA

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

Appendix 1

Comprises SupFigs. 1, 2, 3a, 3b, 3c, 3d, 3e, 3f and 3g

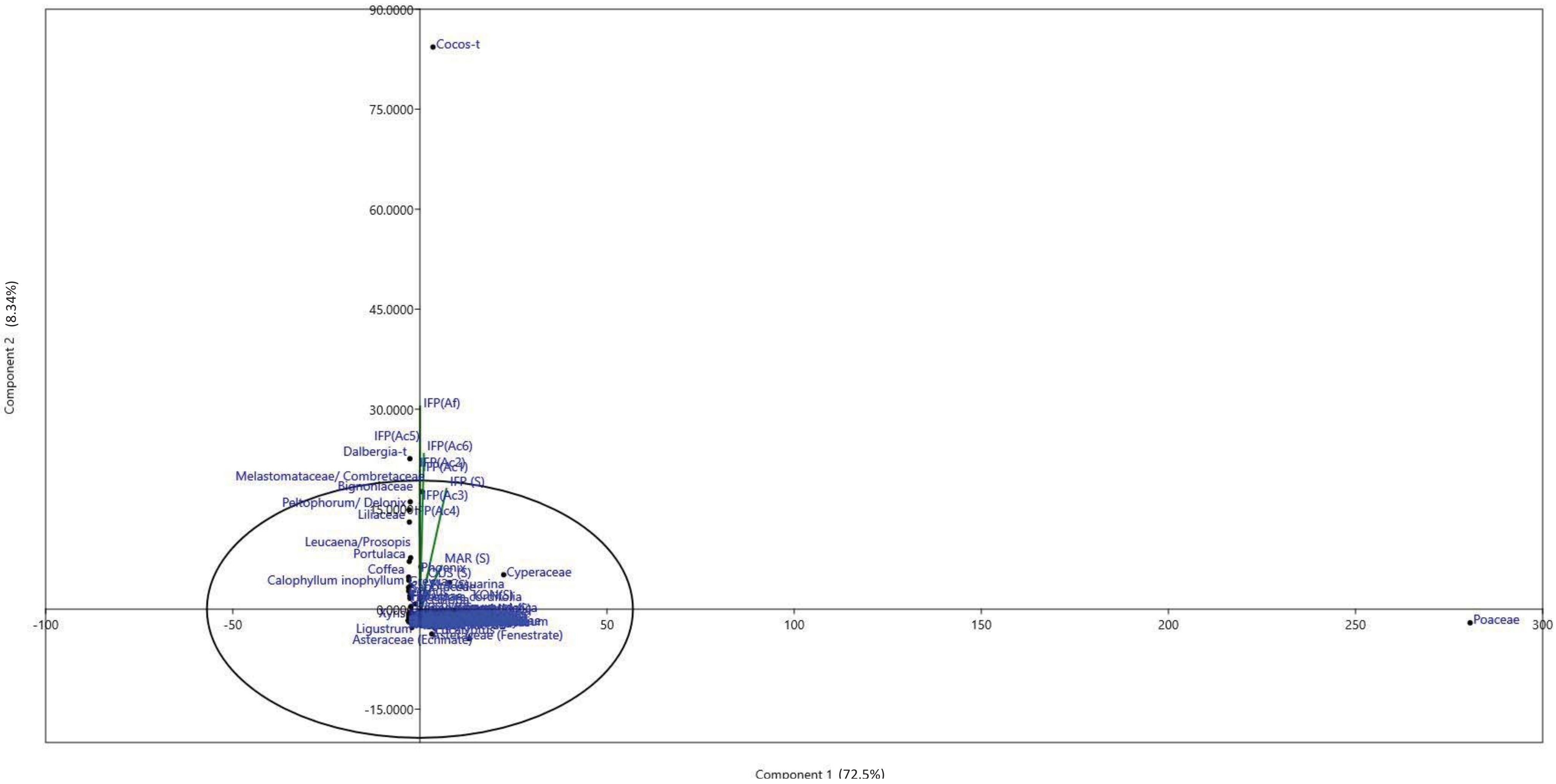
SupFig.1. Location map showing the sites selected for surface soil and bee pollen sample collection in the Nilgiri Biosphere Reserve in southern India, (Source: Google Earth Pro)



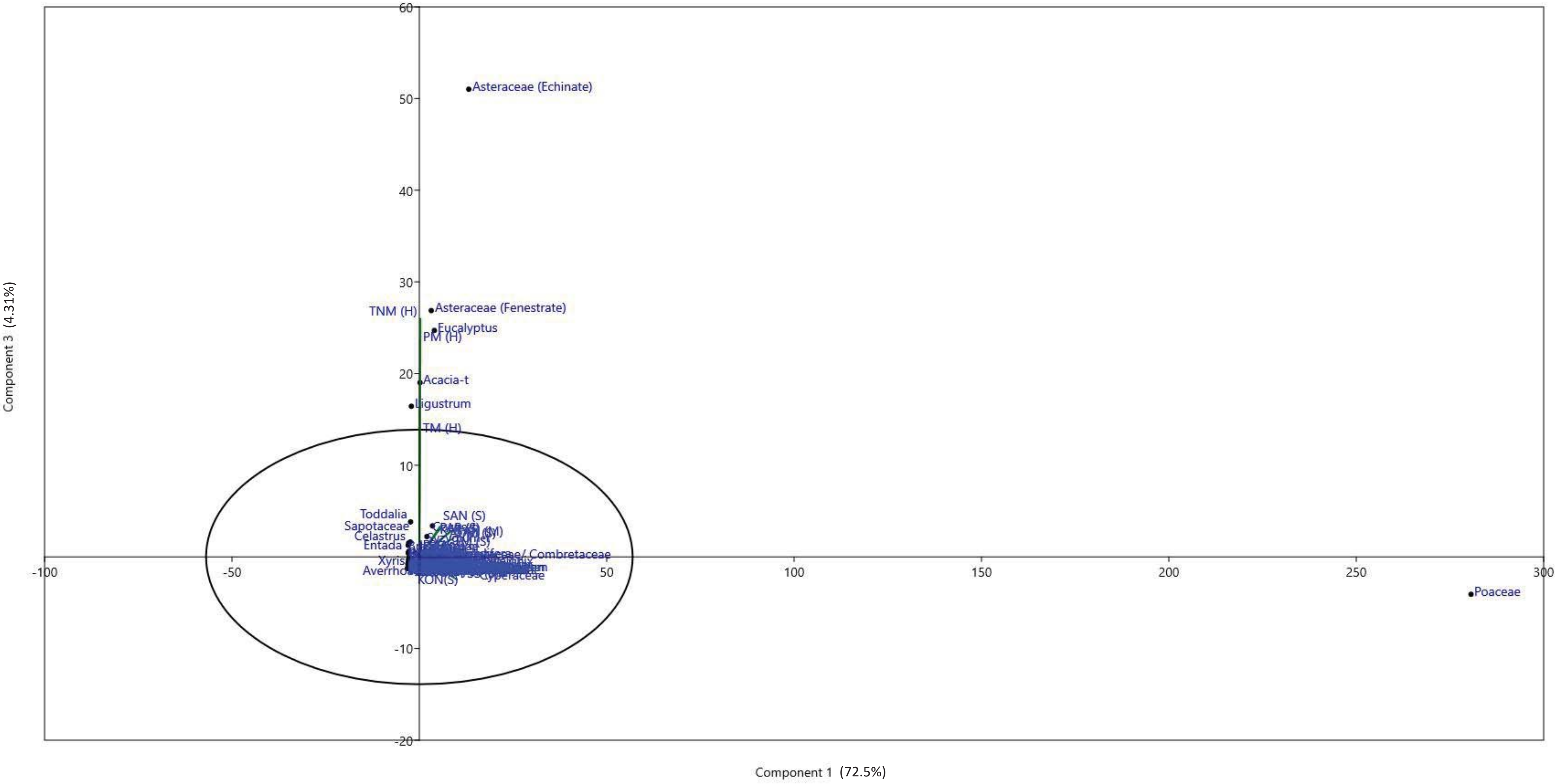
SupFig. 2: Location map showing the sites selected for surface soil and bee pollen sample collection in the Coromandel coast

Surface sample locations and maps from Navya et al, 2025 (accepted for publication in *Ecosphere*)

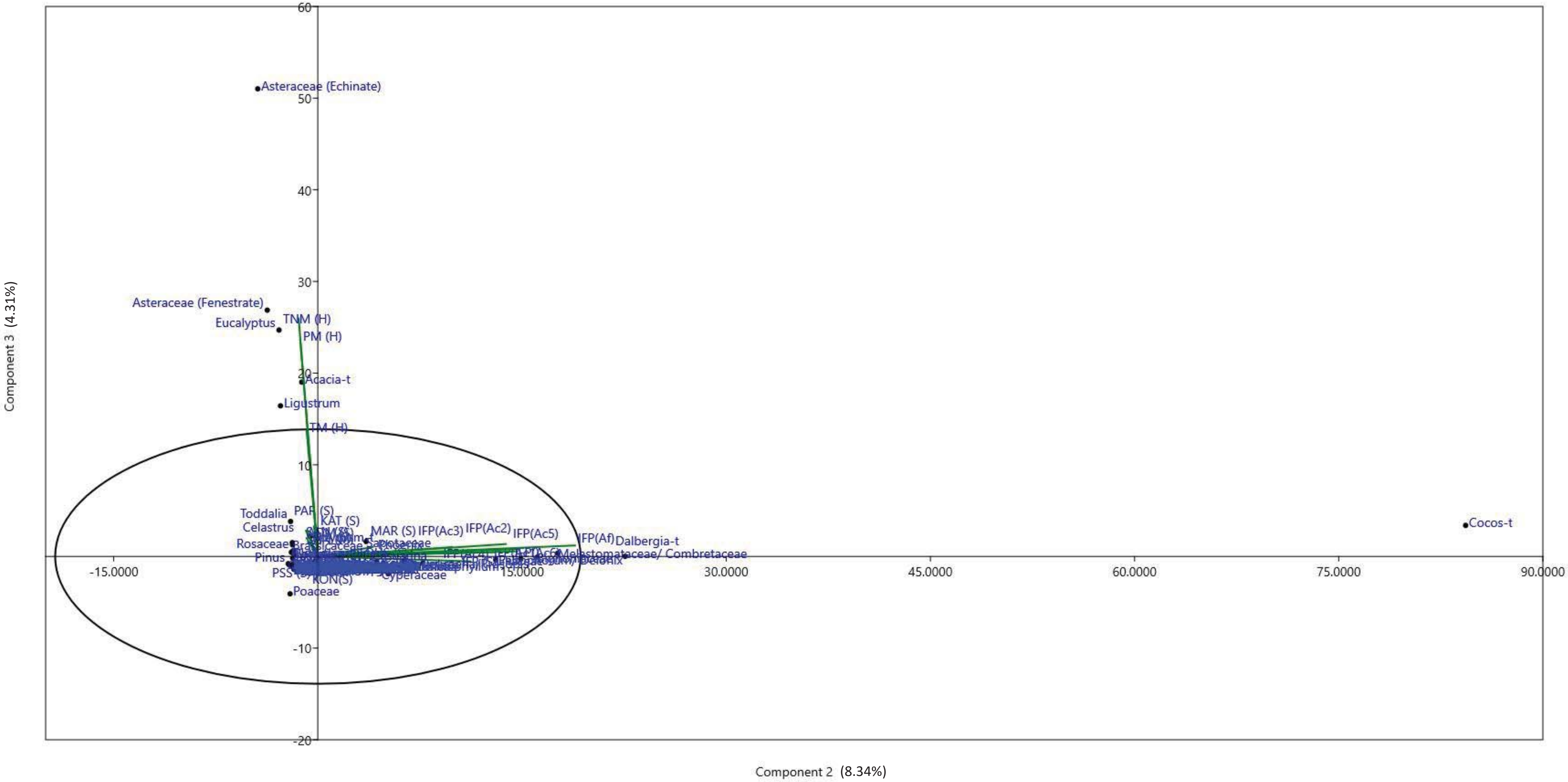
SupFig. 3a: PCA of all 34 samples, AXIS 1_2



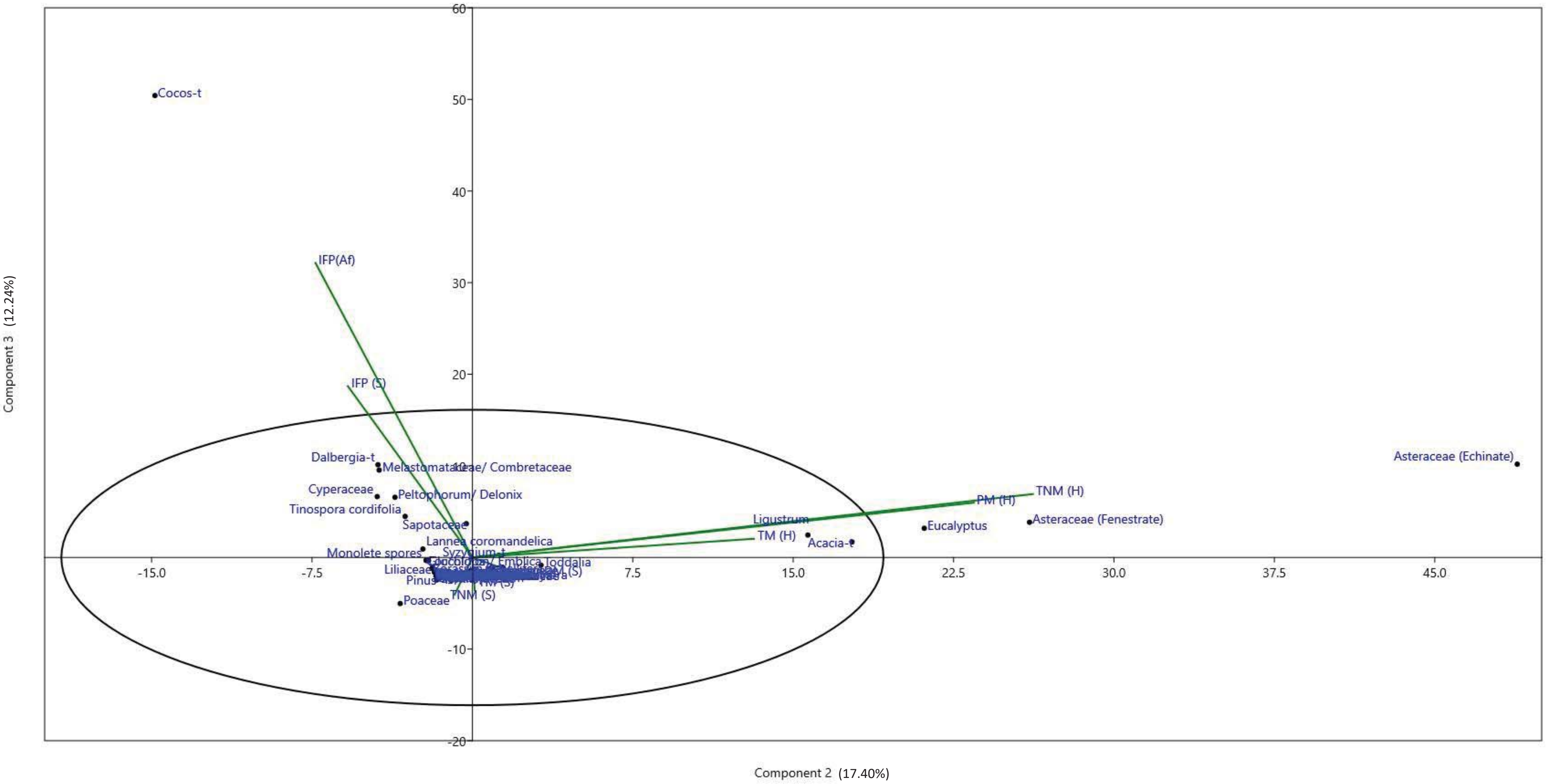
SupFig. 3b: PCA of all 34 samples, AXIS 1_3



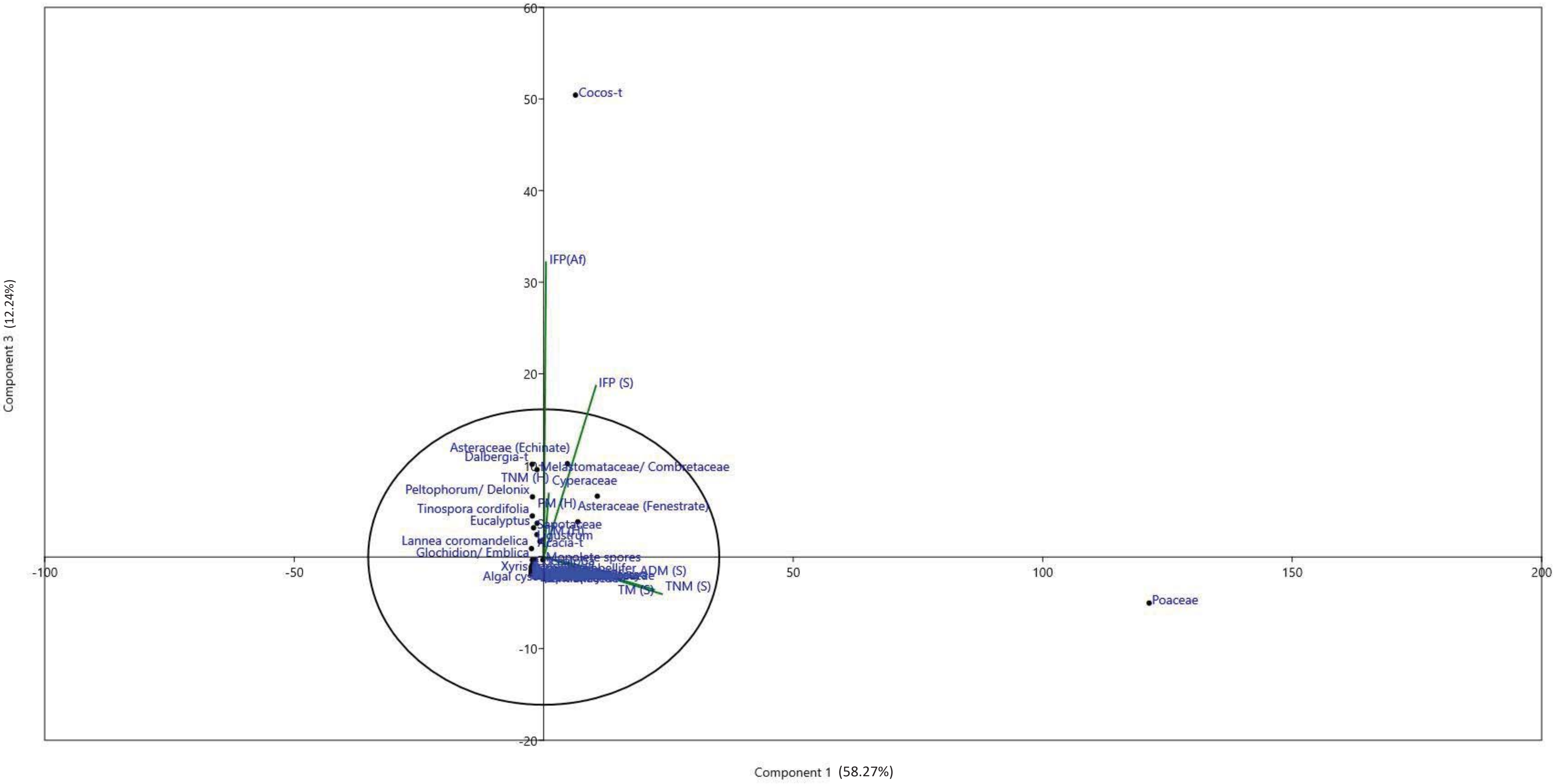
SupFig. 3c: PCA of all 34 samples, AXIS 2_3



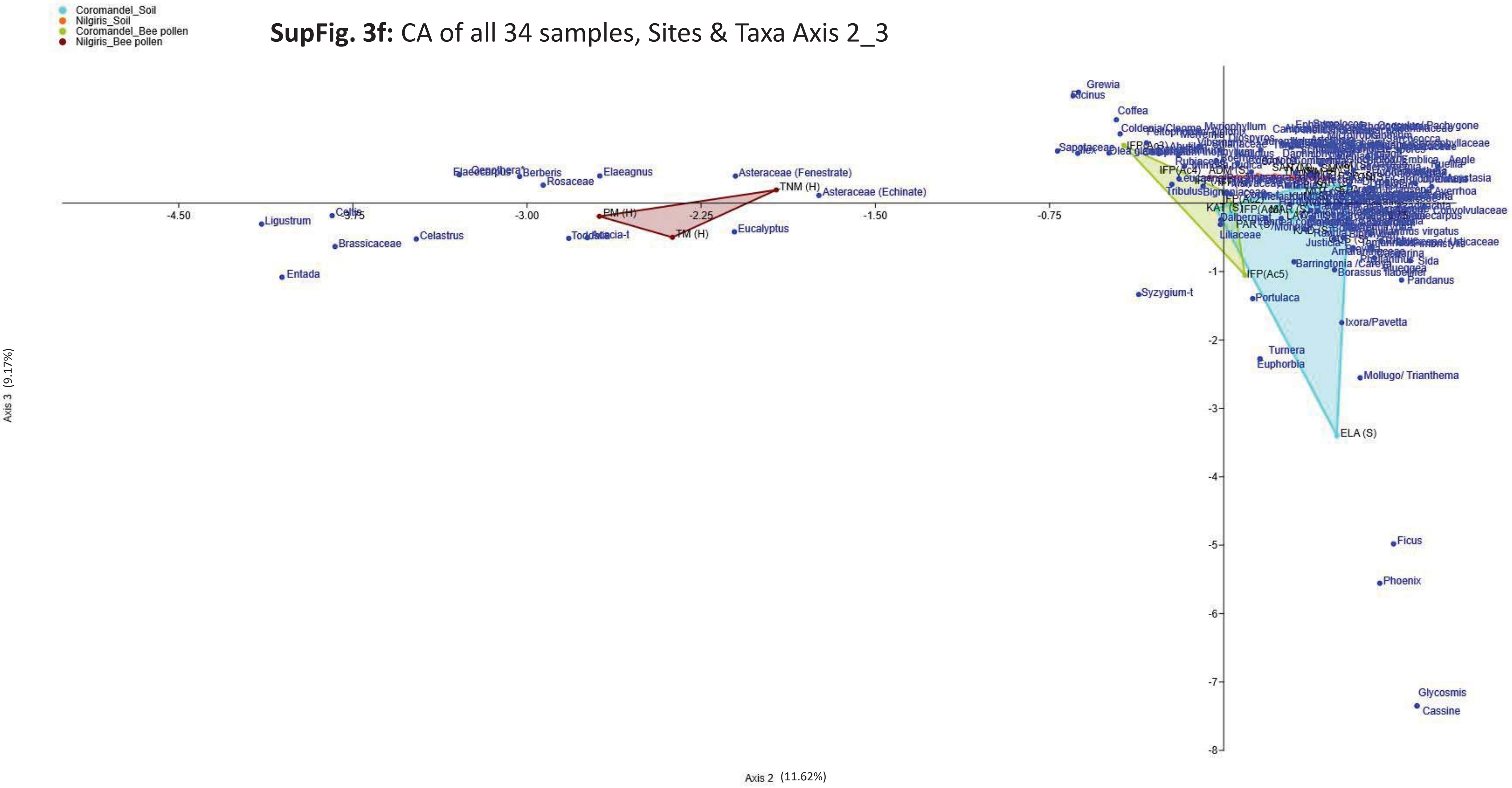
SupFig. 3d: PCA of 8 samples (paired surface soil and bee pollen), AXIS 2_3



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



SupFig. 3f: CA of all 34 samples, Sites & Taxa Axis 2_3



SupFig. 3g: CA of all 34 samples, Sites & Taxa Axes 1_3