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## ORIGINAL RESEARCH ARTICLE

# Pollen diversity and protein content in differentially degraded semi-arid landscapes in Kenya

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In Africa there is a scarcity of information on how plant species that can provide forage for honey bees vary across differentially structured landscapes, and what are the implications of such variabilities on colony integrity. This research presents new insights into the diversity and richness of pollen collected by *Apis mellifera scutellata*, a subspecies of the Western honey bee native to sub-Saharan Africa, at six study sites of different degradation levels within a semi-arid landscape in Kenya. Ten colonies were established at each site and land cover characteristics were extracted using novel remote sensing methods. The sites differed by the proportions of natural vegetation, cropland, grassland and hedges within each site. Bee bread was collected five times, with three colonies in each of the six sites repeatedly sampled during the period from May 2017 to November 2018. Pollen identification and protein analysis within the study sites were thereafter conducted to establish the linkage between landscape degradation levels and abundance and diversity of pollen. Out of 124 plant species identified, *Terminalia* spp., *Cleome* spp. and *Acacia* spp. were identified as the most abundant species. Moreover, species richness and diversity were highest in the two sites located in moderately degraded landscapes. Pollen protein content showed statistically significant differences across season rather than geographical location. This study demonstrated that landscape degradation negatively affected the diversity and richness of pollen collected by honey bees. Consequently, this helps our understanding of native honey bees' forage resource usage and plant species preferences in landscapes with varying degrees of degradation.

**Keywords:** *Apis mellifera*; landscape degradation; honey bee nutrition; natural habitats

## Introduction

Honey bees (*Apis mellifera* L.) provide valuable ecosystem services via pollination, consequently contributing immensely to crop production globally (Hung et al., 2018; Potts et al., 2010). This crucial ecosystem service occurs because the pollinators forage and harvest the nectar and pollen which they need for their development (Di Pasquale et al., 2013). Pollen is the most important and almost exclusive source of proteins, vitamins, lipids and minerals for bees (Brodschneider & Crailsheim, 2010; Danner et al., 2016; Filipiak et al., 2017). Protein content in pollen has served as a measure of the quality of pollen (Roulston et al., 2000; Vaudo et al., 2015). Honey bees preserve their collected pollen in the form of 'bee bread' which is a blended mix of honey/nectar, pollen and worker bee glandular secretions (Anderson et al., 2014; Brodschneider & Crailsheim, 2010). This 'bee bread' is used by the nurse bees for feeding the growing bee brood and is essential for their development, because it provides a balanced diet consisting of all the molecules required by the bee for optimal growth (Alaux et al., 2017; DeGrandi-Hoffman et al., 2010; Keller et al., 2005a). Subsequently, honey bee health has been reported to be dependent on the abundance and diversity of pollen mainly for the brood (Rasmont et al., 2005; Somerville & Nicol, 2006) as well as nectar for the adult honey bees, which ensures a wide variety of nutrients for the honey bees (Di Pasquale et al., 2013). Important too for honey bee health is the consideration of the general nutritional health and nutritional ecology of the honey bee (Wright et al., 2018).

However, shifts in landscape characteristics mainly due to increasing landscape fragmentation and subsequent habitat degradation, have altered honey bees' pattern of utilization of the foraging landscape for nectar and pollen (Dolezal et al., 2016). Pollen diversity has been directly linked to landscape structure and composition (Matthias et al., 2015), as various plants tend to provide different quality of protein in various proportions (Andrada & Tellería, 2005; Estevinho et al., 2012; Seeley, 1995; Vaudo et al., 2020). For instance, pollen harvested from landscapes composed of mainly intensive

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farmlands were shown to have lower nutritional value than those collected from landscapes with high floral diversity (Dolezal et al., 2016; Donkersley et al., 2014; Requier et al., 2015). Consequently, honey bees fed on pollen with lower nutritional status, especially with regard to protein, demonstrated higher vulnerability to pathogens (Di Pasquale et al., 2013), thereby affecting overall health of the bees and possibly contributing to the observed decline in honey bee populations (Vaudo et al., 2015). Likewise, the importance and contribution of pollen from croplands as part of honey bees nutrition has also been demonstrated (Odoux et al., 2012). Moreover, early honey bee colony growth has been shown to be positively correlated with amounts of pollen from woody vegetation (Kämper et al., 2016). However, it has been shown that other stresses also affect the honey bee including the increase of pesticide application, competition from alien species, pathogens as well as changes in climate conditions (Potts et al., 2010).

Additionally, landscape degradation and fragmentation have been shown to affect floral availability and diversity. For instance, reduced patch fragment sizes were shown to have fewer plant communities when evaluated against bigger fragments (Raghubanshi & Tripathi, 2009). Furthermore, the larger fragments were generally characterized by diverse and richer plant species (Raghubanshi & Tripathi, 2009). Conversely, it has also been demonstrated that species may thrive in fragmented landscapes which are composed of both semi-natural and man-made landscapes which provide varied resources during the different seasons of the year (Krauss et al., 2003; Mandelik et al., 2012). Previous studies on the linkage between landscape structure and pollen have indicated that landscape composition has an influence on the distances which honey bees travel to forage for pollen (Danner et al., 2014; Steffan-Dewenter & Kuhn, 2003) which is therefore likely to affect their health. Moreover, habitat degradation has been shown to affect bee species mainly due to the reduction of floral resources as well as the introduction of agricultural insecticides which negatively affect the bees (Potts et al., 2010). Further, it has also been demonstrated that honey bees will most likely forage on particular plants based on their preferences and not necessarily proximity of the floral resources (Olsen et al., 1979; Visscher & Seeley, 1982). Temporal variation in protein content has also been shown to occur considerably with increases in protein content seen during late spring season (Keller et al., 2005). Likewise, in the study region, colony growth closely follows the bimodal rainy season patterns (March–May is the long rains and October–December is the short rains), hence March–May and November are the main honey bee colony reproductive seasons. November is the midpoint of the short rain season following a prolonged dry season (June – Mid October) (McMenamin et al., 2017).

To the best of our knowledge, there is no documented information in Kenya and most of Africa as to the linkage between landscape degradation levels and abundance and diversity of pollen. The current study therefore intends to fill this knowledge gap, given the high rate of conversion of natural and semi-natural landscapes into croplands in the region (Nkonya et al., 2015). The effects of landscape degradation level on pollen diversity and protein content were examined in six sites (apiaries) situated within three distinctly varying landscapes in the study area in Kenya, (as defined in Ochungo et al., 2019). The study area is a semi-arid agroecological landscape, typical of most rural landscapes in Kenya and several other African countries. The specific objectives of this study were to (i) establish the pollen sources for the honey bees at study sites of varying degrees of landscape degradation, and (ii) to determine the protein content of the pollen at the same sites and in different time periods. Generally, it was hypothesized that the pollen diversity and protein content would be higher in the least degraded landscapes.

## Materials and methods

### *Study area and landscape characteristics*

We established six experimental sites (apiaries, each with 10 hives) in Mwingi, a subcounty in the Eastern region of Kenya (Figure 1). Mwingi falls within the Lower Midland (LM4) agroecological zone (FAO, 1996) and is made up of largely heterogeneous landscapes, mainly consisting of farmlands interspersed with shrublands, woody vegetation and grasslands. Some sites of the subcounty have more natural vegetation than others that have been highly degraded mainly due to agricultural expansion (Fening et al., 2008). The six study sites were chosen based on landscape degradation severity gradients, defined within a 3 km radius as following: (1) if the proportion of woody vegetation, grassland and hedges occupied the largest share of the landcover composition, compared with the proportion of croplands, it was considered to have low degradation, (2) if the proportion of woody vegetation, grassland and hedges occupied an almost equal share of the landscape as the proportion of croplands, then it was considered moderately degraded, and (3) if the proportion of croplands was greater than the proportion of woody vegetation, grasslands and hedges, then it was considered highly degraded (Table 1 and Figure 2). The landscape composition data for the six study sites were extracted from fused remotely sensed data sets, combining 10-meter Sentinel-1 (S1) (radar) and 10-20 meter Sentinel-2 (S2) (optical) bi-temporal satellite imagery (European Space Association (ESA), 2017). Each site consisted of an apiary and each was located at least 3 km apart. This 3 km radius was chosen based on approximated honey bees foraging distance which is on average within 3 km from an apiary (Hepburn & Radloff, 1998; Roubik, 1989). Initially, each apiary comprised 10 Langstroth

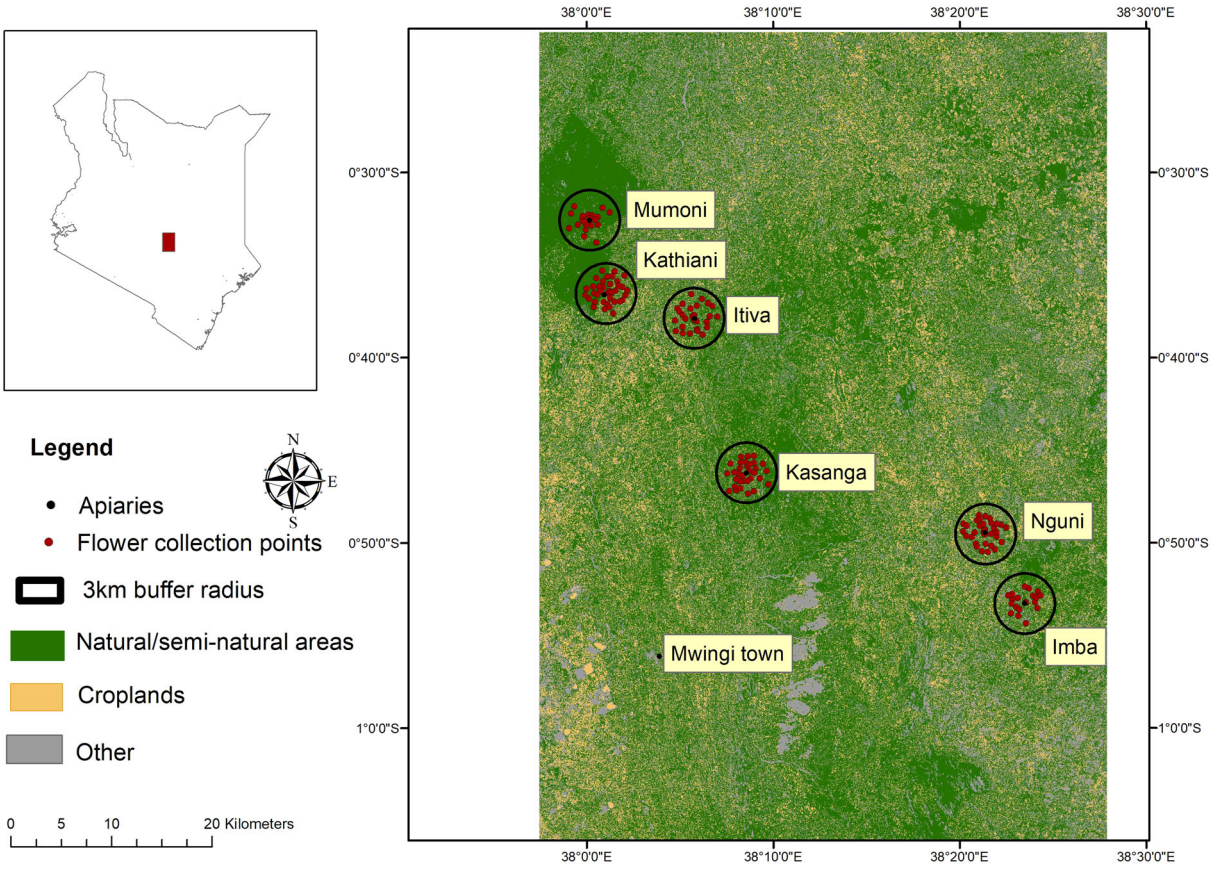


Figure 1. Location of the study area in Kenya (left) and classified map showing natural/semi-natural (woody vegetation, grasslands, and hedges) and cropland areas (predicted using the S1-S2 fused data) of the study area. The red points are the locations where flowers were collected for reference plant species throughout the study period.

Table 1. Landscape characteristics of the experimental sites (apiaries) in Mwingi study area. Landscape composition comprising of proportions of woody vegetation, grasslands, hedges and croplands for each apiary site is calculated within a 3-km buffer zone.

| Name of apiary | Latitude (East) | Longitude (South) | % woody vegetation | % grassland | % hedges | % croplands |
|---|---|---|---|---|---|---|
| Nguni | 38.3561 | 0.8217 | 8.52 | 16.09 | 6.94 | 46.69 |
| Imba | 38.3913 | 0.88783 | 10.76 | 16.14 | 3.8 | 49.37 |
| Itiva | 38.0964 | 0.63146 | 18.61 | 16.72 | 11.04 | 45.43 |
| Kasanga | 38.1427 | 0.77026 | 31.13 | 15.72 | 4.09 | 43.71 |
| Kathiani | 38.0160 | 0.61022 | 41.64 | 9.46 | 5.05 | 39.43 |
| Mumoni | 38.0026 | 0.5430 | 76.97 | 1.58 | 0 | 19.24 |

hives, thus a total of 60 hives. However, throughout the study period, we only inspected and sampled 30 hives (i.e., colonies) which were the only ones that were occupied by natural swarms as observed during the first field data collection. The data collection was repeated five times during the two rainy (May and November) and three dry seasons (January, February, and June). The number of colonies during the different data collection periods were as follows: May 2017 (30), January 2018 (15), February 2018 (14), June 2018 (8) and November 2018 (6). By the end of the last data collection in November 2018, 24 colonies had been abandoned by the bees (8 from the highly degraded areas, 7 from the moderately degraded, and 9 from the least degraded).

Collection of flowering materials for pollen referencing were carried out within a 3 km buffer zone from each apiary, mimicking the average foraging distance for honey bees (Hepburn & Radloff 1998; Roubik, 1989). The major documented flowering plant species in Mwingi are *Acacia* spp., *Boscia, Grewia* spp., *Aspilia mozambensis, Cassia diambotia, Cassia semea, Euphobia* spp., *Terminalia brownii and Solonium incunum*, of which most of them flower after the rainy seasons in December-January and May (Abdel-Rahman et al., 2015).

### *Pollen collection*

We conducted the study between May 2017 and November 2018 during which a total of five data collection periods were carried out. The five data collection periods spanned the wet and dry seasons of the year i.e., May and November are typically wet seasons, while

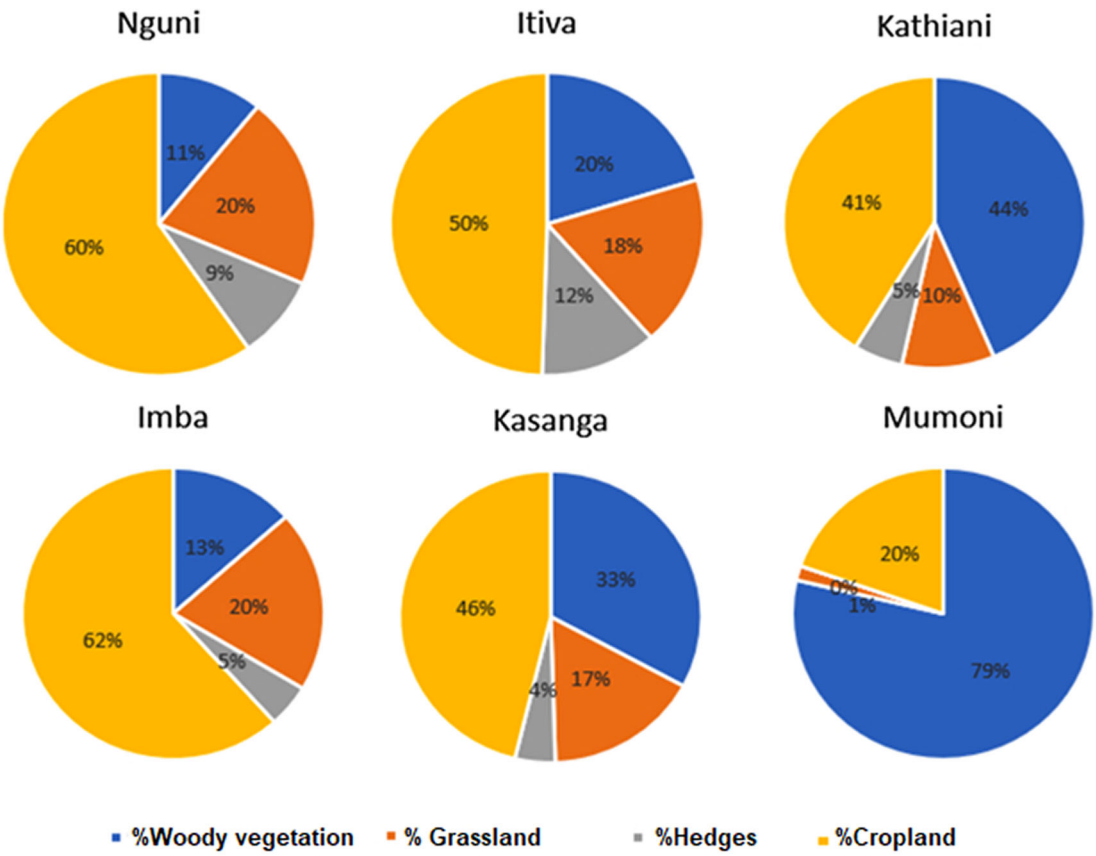


Figure 2. Pie charts showing the relative proportion of four potential honey bee foraging habitats i.e. proportions of woody vegetation, hedges, grasslands and croplands in the six study sites.

January, February and June are dry seasons. Experimental colonies were obtained from natural swarms and housed in standard 10-frame Langstroth hives. Pollen samples in the form of bee bread were collected as follows: 11 in May 2017, 6 in January 2018, 6 in February 2018, 6 in June 2018 and 6 in November 2018. An attempt to collect corbicular pollen using pollen traps failed after the bees declined to use the entrance with the trap, hence the alternative was to collect bee bread. Pollen freshness was based on lack of fermenting odor (Hoover & Ovinge, 2018; Menezes et al., 2013; Vollet-Neto et al., 2017). In total, 35 separate bee bread samples (11 in low, 14 in moderate, and 10 in high landscape degradation classes) consisting of mixed pollen were collected. The bee bread was stored in falcon tubes at −20 °C while in the field, and subsequently at −80 °C in the laboratory for long term storage and analysis.

### *Protocol for processing pollen samples for taxonomic identification*

Distilled water (2 mL) was added to each bee bread sample, vortexed and then 1 mL of each sample was used for pollen identification. We used an acetolysis method (Erdtman, 1969) where 9 parts of acetic anhydride and one part of concentrated sulfuric acid were thoroughly mixed to form the acetolysis mixture. Approximately 10 mL of the mixture was added to each vial containing the pollen sample to remove exine to allow accurate morphological identification of the pollen. Each sample was then washed using $dH_20$, centrifuged and the supernatant was decanted to obtain the pollen residue. Lastly, the pollen samples were washed with 50% glycerin, centrifuged and decanted. Then 100% glycerin was added to the samples for storage and mounting purposes.

Pollen residue (20 µL) was mounted on the microscopic slides, then a cover slip was placed over it carefully to ensure no bubbles trapped. Prepared slides were studied to determine pollen diversity to a genus level and tallied the identified pollen grains. For slides rich in pollen, counting stopped after counting more than 800 grains. For the slides with less pollen grains, a second slide was prepared, and complete slides were studied. Identification and counting of pollen was done using the standard pollen atlases (Bonnefille, 1971a, 1971b; Gosling et al., 2013; Riollet & Bonnefille, 1976) and consultation of the modern pollen reference collection available at the National Museums of Kenya (NMK), Palynology and Paleobotany laboratory. Any unidentifiable pollen was subsequently labelled as 'unknown'. Thereafter, pareto charts were generated for all sites combined.

### *Pollen protein extraction and determination test*

Using a pestle and mortar, each bee bread sample was crushed, and a sample of 0.025 g was taken as per de

Sá-Otero et al. (2009) suggestions and then transferred into a microcentrifuge tube. We extracted protein from the samples by applying the method used by de Sá-Otero et al. (2009) with slight modifications. Onto each of the samples, 4 mL of 30 mM TE buffer was added and vortexed to ensure uniform mixing. The sample mixture was centrifuged for 20 min at 3000x g and afterwards, the supernatant was collected in 0.1 mL aliquots. We added 5 mL of Bradford reagent, leaving the setup for 2 min at room temperature (Bradford, 1976). The samples were measured using a spectrophotometer at an absorbance of 595 nm. TE buffer of 0.1 mL was used as blank. 50 μL, 150 μL, 200 μL, 250 μL and 400 μL dilutions of Bovine Serum Albumin (BSA) served as the standards for generating a calibration curve.

The absorbance values of the BSA standard were plotted against protein concentrations and the protein content in samples was determined by a linear regression model. This allowed the crude protein values of the pollen to be quantified using the standard curve generated (expressed in g/100 g). The protein content was conducted for all the samples in triplicates.

### *Pollen diversity and crude protein data analysis*

#### *Alpha diversity*

All data and statistical analyses as well as figure generation were implemented using the 'vegan' package (Oksanen, 2017) in R version 3.5.3 (R core team, 2019) and PAST version 4.0.1 (Hammer et al., 2001). Pollen composition at species and family levels were first calculated for each of the six sites and number of taxa computed. Thereafter, species accumulation curves (sample and individual rarefaction, Mao Tau's) were generated to determine the species richness of the pollen as a function of the quantity of samples (sampling effort). Further, rank abundance dominance (RAD) models were produced to compare species evenness in all the sites. These plots were used to indicate the logarithmic species abundances versus plant species rank order for the study sites (Gardener, 2014). For each site, five RAD models were utilized in the 'vegan' package *viz*., Broken stick, Lognormal, Mandelbrot, Preemption and Zipf models (Appendix A). Each of these models takes the logarithmic abundance and rank of abundance as input data, and uses various parameters to fit models (Gardener, 2014). For each site, the model with the lowest Akaike Information Criterion (AIC) was selected and the curve was plotted (Appendix A). Furthermore, in order to compare alpha-diversity at the six sites, diversity ordering using the Renyi index was used and the output plotted (Oksanen, 2017). Since the data were not normally distributed (Shapiro-Wilks, $w = 0.95368$, p-value $= 0.00986$), the Kruskal–Wallis rank sum test at 95% confidence level was applied to analyze differences in diversity among the sites and post hoc contrasts were conducted using pairwise Wilcoxon's rank sum test for multiple comparisons.

#### *Beta diversity*

To evaluate beta diversity of pollen across the study sites, the non-metric dimensional scaling (NMDS) technique was adopted, whereby after several iterations, $k = 4$ dimensions produced the lowest stress value ($< 0.2$) (Taguchi & Oono, 2005). The Bray-Curtis distance matrix was used to create a dissimilarity matrix, while NMDS ordination was used for visualization. We used a permutational multivariate analysis of variance (PERMANOVA) to test the ability of geographical site to explain variation in the NMDS plot (Oksanen, 2017). A Shephard's diagram was produced to demonstrate the goodness of fit for each pollen sample. Subsequently, a pairwise similarity percentage (SIMPER) test was carried out to assess which pollen taxa were responsible for the observed differences among the pollen samples (CLARKE, 1993). The SIMPER test was carried out between four pairs of sites, which demonstrated the largest separation on the NMDS plot.

#### *Protein data analysis*

For the analysis of crude protein in pollen, we carried out the Kruskal–Wallis rank sum test at 95% confidence level to analyze the differences in crude protein concentration in pollen across the six study sites and across the months (seasons) of the year. The 'Devtools' and 'dplyr' packages in R (Wickham et al., 2020) were used for this exercise.

## Results

### *Pollen identification*

A total of 124 plant species belonging to 57 families were identified across all 6 sites (reference to appendix). A Pareto chart showing their combined distribution across the six sites is shown in Figure 3. For the combined distribution, a threshold was determined based on the pareto chart, whereby those species whose numbers did not contribute to the cumulative 100% were excluded. Further, Figure 4 shows plant composition at the family level in a stacked chart for each of the six sites in order of their degradation levels.

Species accumulation curves showed that overall species richness as a function of the sampling effort was satisfactory, based on the shape of the curve asymptote. However, individual rarefaction curves indicated that Kasanga and Itiva sites were more exhaustively sampled than others (Figure 5).

The most abundant plant families were the Capparaceae (15.9%), Combretaceae (14.1%) and Asteraceae (13.6%), all with individual pollen counts $>$ 3000, across all the sites (Appendix B).

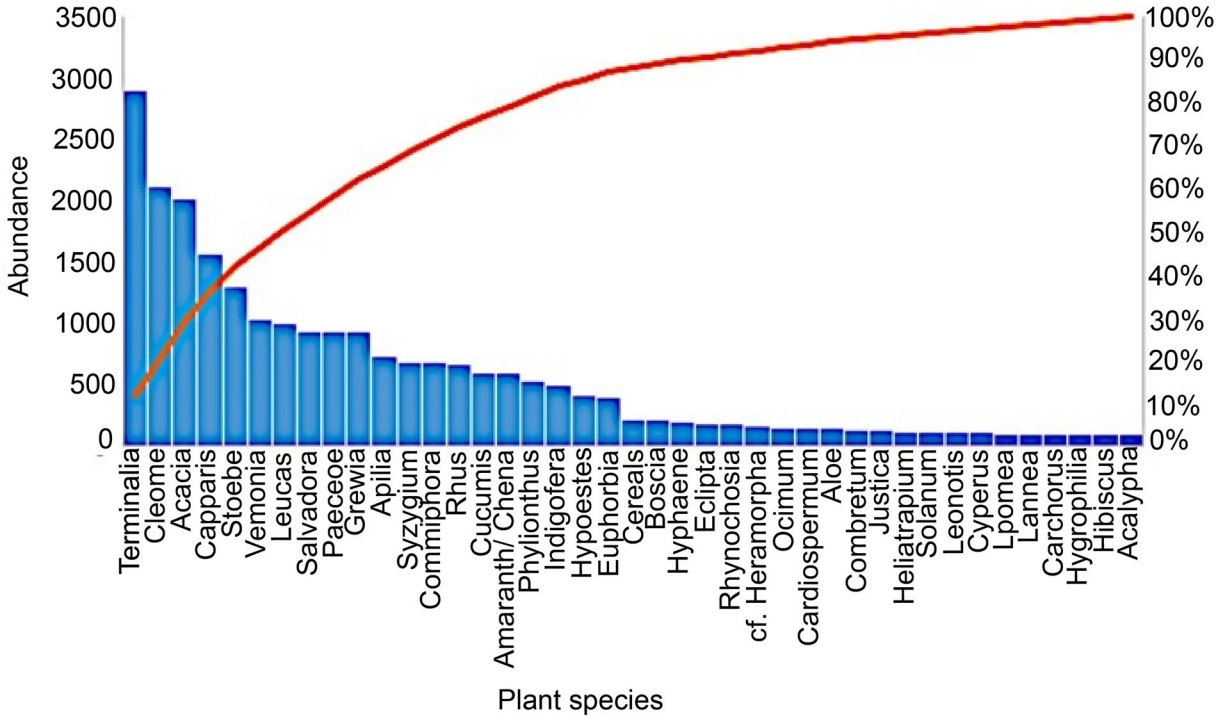


Figure 3. Plant species abundance and cumulative values in all the six study sites. The bars represent the species occurrence in descending order while the line represents the cumulative percentage of species. The *Terminalia* spp., *Cleome* spp. and *Acacia* spp., were the most abundant species overall.

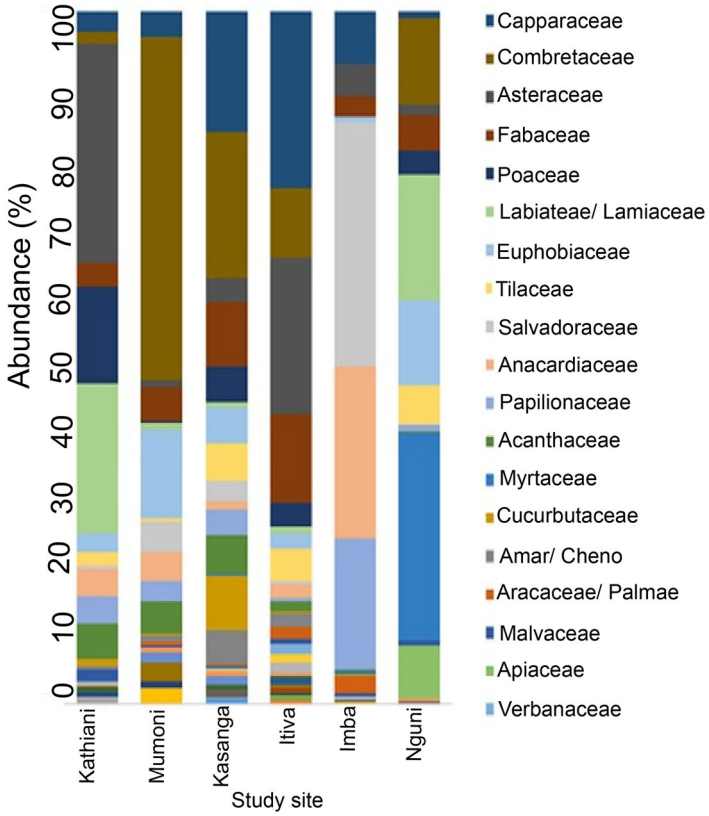


Figure 4. Stacked bars show plant composition at family level according to the bee bread diversity scores in the six sites presented in the following order: Least degraded (Kathiani, Mumoni), moderately degraded (Kasanga, Itiva) and highly degraded (Imba, Nguni).

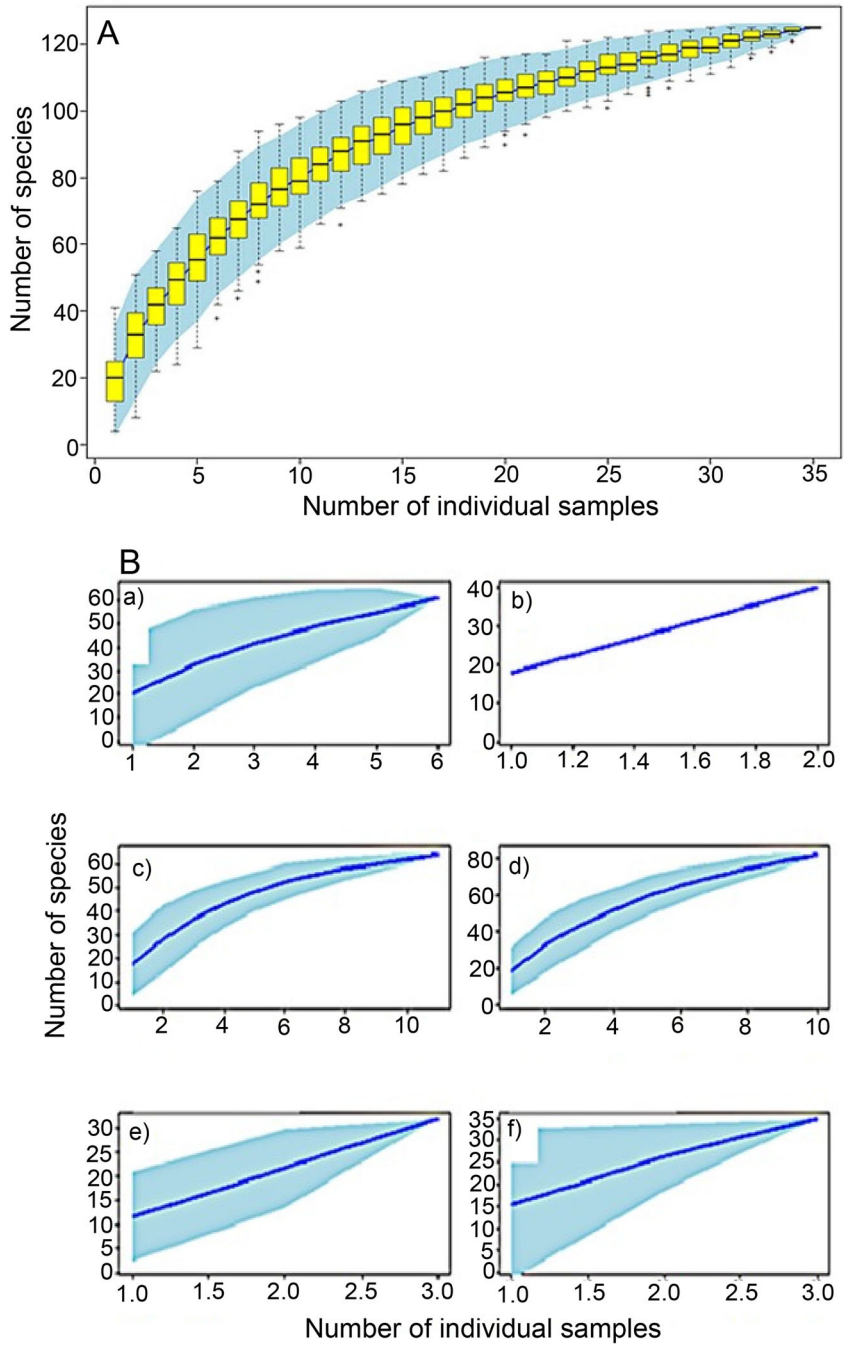


Figure 5. **A:** Species accumulation curve (Mao Tau's sample rarefaction) showing the total number of pollen samples versus the sampling effort that was required to observe them. The asymptote of the curve demonstrates that overall, the pollen samples were suitably sampled. **B**: Individual rarefaction curves showing the total number of plant species (y-axis) versus the number of samples that were acquired at individual sites. The panels are arranged in the following order: a = Kathiani, b = Mumoni, c = Kasanga, d = Itiva, e = Imba, f = Nguni. Light blue shading around the blue line represents bootstrapped 95% confidence intervals.

### *Pollen diversity*

*Alpha diversity*

Figure 6 shows the results of the selected RAD models with the lowest AIC for each site. The steepest gradients are seen in the high degradation sites (panels 5 and 6), showing lower species evenness in these sites.

Additionally, Renyi diversities for the six sites showed the lowest diversity values for the highly degraded sites (mean = 1.87) and highest diversity values for the moderately degraded sites (mean = 2.61). Average diversity of the least degraded sites was 2.05, averaged for the $\alpha$-values (total richness, Shannon-Wiener, Simpson-Yule and Berger-Parker).

Further, a statistically significant difference was observed in diversity across the sites (Kruskal–Wallis chi-squared = 14.732; $p$-value = 0.01) using Renyi diversity metrics (Figure 7).

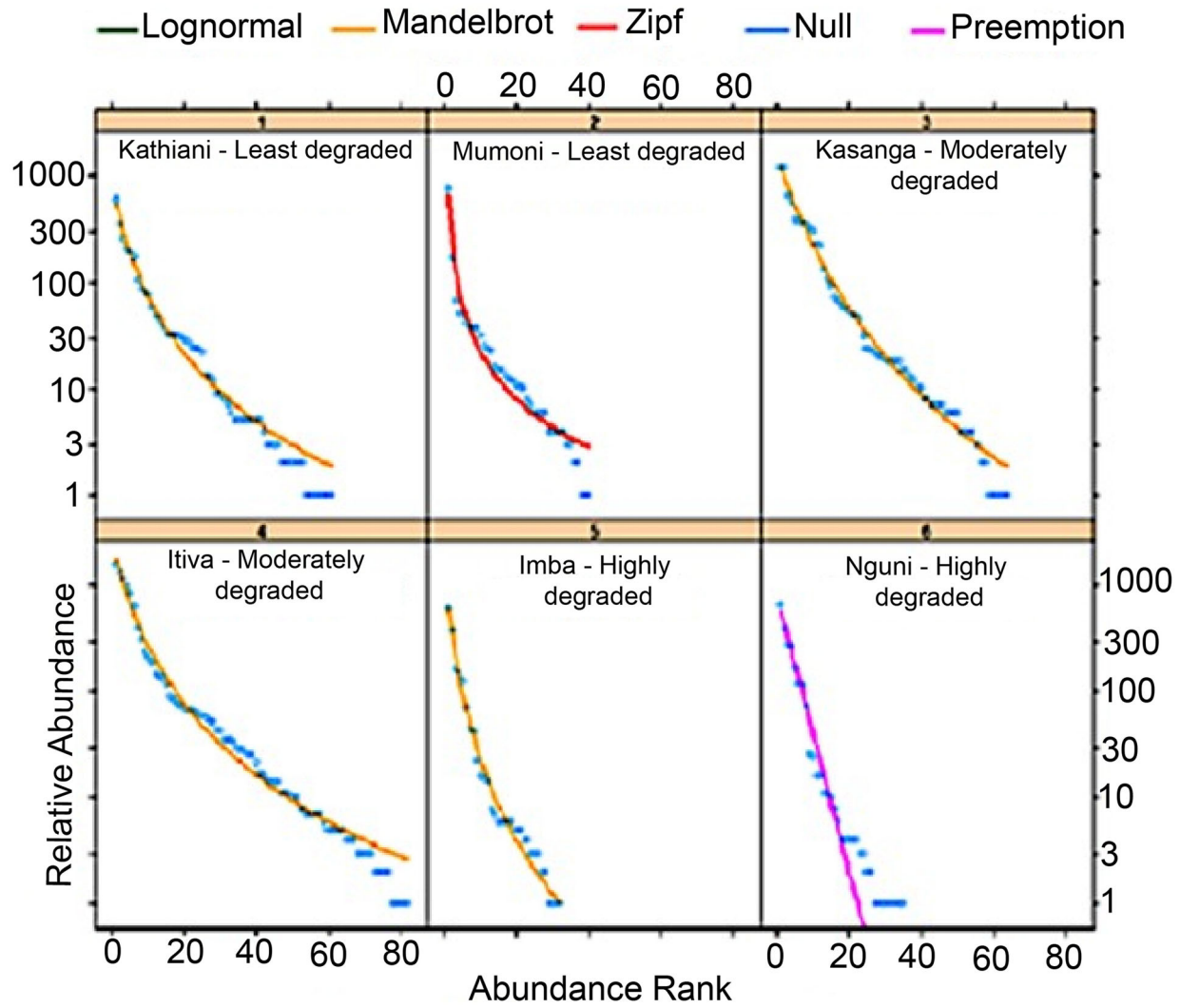


Figure 6. RAD models for the six study sites, falling within various land degradation levels. Individual panels show the RAD model with the lowest AIC. A steeper gradient demonstrates low evenness while a shallow gradient demonstrates high species evenness.

*Beta diversity*

Pollen composition between the six sites displayed overlaps and the overall dissimilarity was insignificant as shown by the results from PERMANOVA: F-value = 1.19; *p*-value = 0.07; Stress = 0.12, non-metric $R^2$ = 0.985; Linear $R^2$ = 0.843; k = 4. However, pairwise results from PERMANOVA showed significant dissimilarities between Itiva and Nguni only, with p-value = 0.04 PERMANOVA, *F*-value = 1.19; *p*-value = 0.07; Stress = 0.12, non-metric $R^2$ = 0.985; Linear $R^2$ = 0.843; k = 4. The NMDS diagram and a Shepherd's diagram, with correlation statistics demonstrating the goodness of fit of the pollen samples from the NMDS analysis are shown in Appendix D.

Furthermore, Appendix E shows SIMPER test results that had significant dissimilarities from the PERMANOVA test, i.e., Itiva versus Nguni (*p*-value = 0.04) and three other pairs of sites which showed separation on the NMDS plot i.e., Imba versus Kathiani, (*p*-value = 0.09); Imba versus Kasanga (*p*-value = 0.09); and Imba versus Nguni (*p*-value = 0.09); showed the plant species contributing to the separation between the sites. The plant species *Salvadora* spp., *Rhus* spp., *Leucas* spp. and *Syzygium* spp. had the strongest contribution in separating these four pairs of sites.

### *Pollen protein analysis*

Crude protein concentration of pollen showed no significant differences across the six sites (Kruskal–Wallis chi-squared = 3.9114, *df* = 5, *p*-value = 0.56) as seen in Appendix F. In contrast, crude protein concentration across the different data collection months (May 2017, January 2018, June 2018, and November 2018) showed significant differences (Kruskal–Wallis chi-squared = 10.532, *df* = 3, *p*-value = 0.014), (Figure 8). The rainfall months of May and November showed high amounts of protein concentration while the dry months of January and June showed lower amounts of protein concentration.

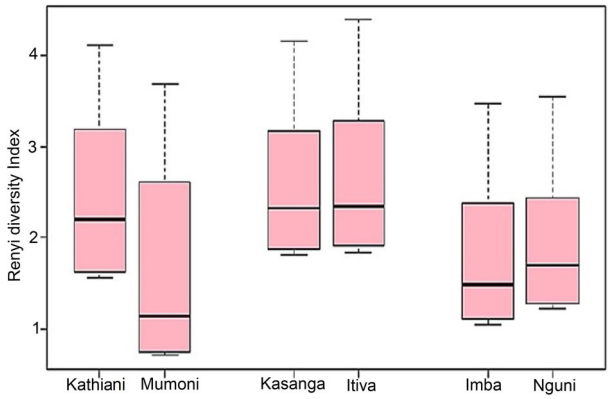


Figure 7. A comparison of the Renyi diversity indices for pollen samples from all six sites. The boxplots show the distribution of $\alpha$ values across all samples. Pairwise comparisons are shown in Appendix C (a). Within the box plots, the thick line indicates the median, the box shows the interquartile range (IQR) between the 1st and 3rd quartile, and the whiskers indicate the 10th and 90th percentiles.

## Discussion

This study involved pollen identification, diversity and protein analysis conducted on 35 bee bread samples across five seasons and in six study sites. Pollen collected from moderately degraded landscapes displayed the highest pollen diversity compared to the least degraded landscapes. This result is similar to several findings which indicated that landscape heterogeneity and diversity are positively associated with higher floral resource availability and richness (Burnett et al., 1998; Honnay et al., 2003; Statzner & Moss, 2004). Likewise, landscape heterogeneity at multiple spatial scales has been positively correlated with plant species richness (Costanza et al., 2011). This association between floral variety and landscape diversity can be explained by the habitat diversity hypothesis proposed by Shmida & Wilson (1985), whereby heterogeneous landscapes encompass additional accessible habitats and, consequently, contain more species (Meltsov et al., 2013). Furthermore, it has been shown that greater landscape variety results in higher species richness (Reitalu et al., 2012). This was noted to be the case in the present study as the RAD curves indicated that low species evenness corresponded to low species diversity as demonstrated by the Renyi diversity index. Similarly, the variety of pollen in these areas suggests floral diversity which can result in disparities in pollen quality (Di Pasquale et al., 2013; Hulsmann et al., 2015) which are fundamental requirements for strong honey bee colonies.

The higher diversity of plant species in the moderately degraded areas may provide more balanced nutrition than those from areas with fewer plant species as shown by Blüthgen & Klein (2011), therefore resulting in stronger colonies. However, recent studies have indicated that a simple increase in plant diversity is insufficient to improve the nutritional health of bees, because specific key pollen host plants may play an important role in balancing bee diets than other less important plant species. Therefore, both pollen diversity and adequate pollen species composition is needed to support bee populations (Filipiak, 2018; 2019; Filipiak et al., 2017). This can also be supported by the finding in the study, whereby only four plant species contributed greatly to the total number of species identified in the study. Additionally, landscapes consisting of greater proportions of non-forested areas have exhibited higher floral richness than those consisting of totally closed natural/semi-natural landscapes as well as those whose composition consisted of very little semi-natural landscapes (Billeter et al., 2007).

Landscape configurational heterogeneity originating from small-scale agriculture has also been shown to contribute strongly to the maintenance of pollinator communities in Europe due to the possible availing of flowering weeds from croplands (Hass et al., 2018). These weeds could be advantageous for the bees since different crops would produce different flowering weeds at various times of the year depending on crop growing seasons within the locality (Bretagnolle & Gaba, 2015), in addition to the flowering from the semi-natural habitats (Wratten et al., 2012). Hence, contributing to all year long forage availability. Moreover, plant species richness has also been shown to increase with landscape heterogeneity at the farm scale due to the presence of a variety of habitats such as arable land, open pastures and semi-natural vegetation (Weibull et al., 2003). The present study's results indicate that stronger honey bee colonies would be better supported in heterogeneous landscapes since a variety of pollen are able to provide continuous supply of forage throughout the year unlike in areas with higher plant homogeneity. In addition, we postulate that for honey bees, floral resources are more important than nesting structures since the hive is already provided by the beekeeper. Potentially therefore they would thrive more in pollen-rich heterogeneous areas which are similar to areas that are moderately degraded. This is in contrast to wild bees which require nesting structures from semi-natural areas which would be more abundant in the low

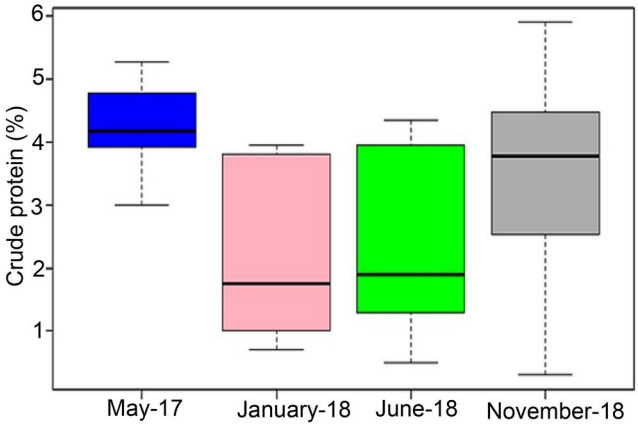


Figure 8. Total crude protein concentration (%) across the different months. May and November are typically the rainy seasons while January and June are dry months. Kruskal–Wallis chi-squared = 9.83 $df = 3$, $p$-value = 0.02. Pairwise comparisons are shown in Appendix C (b). Within the box plots, the thick line indicates the median, the box shows the interquartile range (IQR) between the 1st and 3rd quartile, and the whiskers indicate the 10th and 90th percentiles.

degraded landscapes (Winfree et al., 2007). However, in this study, individual rarefaction curves indicated that some sites were better sampled than others. Colony absconding occurred frequently in some of the six sites (Mumoni, Kathiani and Nguni) and this could explain why the inidividual rarefaction curves show lower sampling effort in some sites as compared to others, and which could also contribute to the low pollen diversity seen in these areas.

Only four plant species i.e., *Terminalia* spp., *Cleome* spp., *Acacia* spp. and *Capparis* spp. contributed to at least 50% of the cumulative number of the identified 124 plant species in the current study. This is despite observations that abundant flowering plants like the *Bougainvillea glabra* were located near the hives yet did not feature prominently amongst abundant pollen. Further, the study determined that the most abundant plants at the family level were the Capparaceae, Combretaceae and Asteraceae plants. This is partially in agreement with the findings of Onyango et al. (2019) who in a study in a mountainous region of Kenya, found that the Asteraceae was amongst the melliferous plant families most preferred by the honey bee. The family Fabaceae also occurred quite frequently in our study similar to findings by Moh' et al. (2015) who carried out a study to document important pollenifarous and nectarifarous plant species in Palestine. In a similar study in Northeastern Nigeria, Dukku (2013) found that the families Fabaceae and Combretaceae recorded the highest abundances among the plant families visited by the honey bee. Lau et al. (2019) and Brodschneider et al. (2019) also found a predominance of the families Fabaceae and Asteraceae in studies carried out in the United States of America and Austria, respectively. These findings points towards honey bees having pollen preferences also shown by Visscher and Seeley (1982) who found that pollen foragers showed distinct pollen preferences and targeted only a few of the available resources in their foraging vicinity. Olsen et al. (1979) also demonstrated that honey bees disregarded pollen from cucumbers and cotton fields despite their proximity to these plants. Moreover, the large overlaps which we observed in pollen composition across the six sites as represented by the NMDS results, further reinforces that there were possibly pollen preferences by the bees, leading to similarities in collected pollen across the sites. Furthermore, pollen yielded by different plant species have displayed considerable variation regarding their protein and mineral content and these variations may contribute to the pollen preferences of honey bees (Keller et al., 2005). Such qualitative differences might have a strong impact on the foraging decisions of honey bees and could possibly explain preferences for certain pollen types. Nonetheless, further experimental studies are required for this conclusion to be made (Keller et al., 2005b).

On the other hand, analysis of the crude protein percentages in pollen at both the spatial and temporal levels indicated that protein content did not vary significantly by geographical location but varied by time of collection (month). Higher protein percentages were observed in pollen during the long rainy seasons of May and November, as opposed to the dry seasons in January and June. This finding may be linked to the main honey bee colony reproductive seasons in the study area, which follow the same bimodal rainfall pattern. This is similar to findings by DeGrandi-Hoffman et al. (2018) who showed that pollen harvested in spring had higher concentrations of amino acids, which support brood production. Further, this outcome is analogous to that of de Sá-Otero et al. (2009) who found that some pollen taxa harvested by honey bees had varying amounts of protein at different dates. Steffan-Dewenter et al. (2017) also found that amount and diversity of pollen were influenced mainly by season and not by geographical location. However, these studies did not specifically analyse protein content in the pollen. This variation in protein content of bee bread by season may

be due to the different plant species available during various seasons which affects the nutritional composition of the pollen and may also be linked to pollen preferences (Keller et al., 2005b), although more studies are required to establish this.

This study raises some fundamental questions about the sustainable management of ecosystems. It is postulated that high plant diversity benefits beekeeping activities (i.e. maintenance of honey bee colonies for pollination and collection of hive products), which are optimal in moderately disturbed areas (Mensah et al., 2017). In other parts of the world, the intensive management of a few pollinator species is seen as a threat to overall pollinator biodiversity (Garibaldi et al., 2013). Here it is shown that beekeepers should avoid completely undisturbed areas as well as highly disturbed environments, due to poorer availability of pollen resources. It has been shown that conservation of pollinator biodiversity and pollination services are commonly not compatible (Kleijn et al., 2016), with common bee species mostly performing most of the pollination service. Given that beekeeping is less productive in areas with minor disturbance, these areas should be seen as protecting wild pollinators. On the other hand, habitats with heterogenous plant diversity are ideal for beekeeping activities and will likely also benefit other common bee species which can provide a pollination ecosystem service. In contrast, highly degraded environments that are of limited conservation and beekeeping value should employ initiatives to improve plant diversity and vegetation cover.

However, it is essential to take caution when scaling out these results to other regions given the relatively low number of study sites per landscape degradation area. Further studies with larger numbers of sites are required in order to further verify the effect that floral variety and landscape structure exhibits on pollen diversity in various biomes.

## Conclusions

Pollen diversity was highest in moderately degraded landscapes which comprised proportions of woody vegetation, grasslands and hedges versus proportions of croplands in almost equal measure. This indicates that honey bees are likely to have stronger colonies in these sites due to the presence of varied pollen which has been shown to improve honey bee strength. Furthemore, it was also found that seasonality rather than location affected crude protein content in pollen whereby higher protein content, which has previously been shown to be important for colony development and maintenance, was found during the rainy seasons. We therefore suggest that beekeepers should select apiary locations within moderately degraded areas and manage their colonies to maximise hive productivity during the wet season due to higher protein content in pollen. However, caution must be taken with regard to broadly extrapolating our results due to the limited number of sites used in this study.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

## Supplementary material

Supplementary appendices are available via the 'Supplementary' tab on the article's online page (https://doi.org/10.1080/10.1080/00218839.2021.1899656).

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**Appendix A**

RAD models, their formulae and use. The formulae in each RAD model shows how the abundance of species at rank r ($a_r$) is calculated. Descriptions are derived from Gardener (2014).

| **RAD model** | **Formulae** | **Use** |
|---|---|---|
| Broken Stick Model | $a_r = J/S\ \Sigma(1/x)$ | *J* is the number of individuals, and *S* is the number of species in the community |
| Lognormal model | $a_r = \exp(\log(\mu) + \log(\sigma) \times N)$ | *N* is the normal deviate and μ and σ are the mean and standard deviation of the distribution |
| Mandelbrot model | $a_r = Jc\ (r + \beta)\ \gamma$ | *J* is the number of individuals, γ is a decay coefficient. The addition of the β parameter leads to the $P_1$ part of the Zipf model becoming a scaling constant, *c*. |
| Preemption model | $a_r = J\alpha\ (1 - \alpha)\ (r - 1)$<br>In | *J* is the number of individuals and the parameter α is a decay rate of abundance with rank. |
| Zipf model | $a_r = J \times P_1 \times r\gamma$ | *J* is the number of individuals, $P_1$ is the proportion of the most abundant species and γ is a decay coefficient |

**Appendix A continued**

Table showing AIC values and matching model names for each study site following the radfit() function in vegan package.

| | Kathiani | Mumoni | Kasanga | Itiva | Imba | Nguni |
|---|---|---|---|---|---|---|
| Null | 1790.22 | 1728.98 | 4902.03 | 8445.82 | 1518.54 | 1939.6 |
| Preemption | 608.9 | 1223.05 | 891.75 | 2066.45 | 360.01 | 261.96 |
| Lognormal | 373.24 | 389.74 | 1246.64 | 1672.69 | 255.39 | 464.33 |
| Zipf | 667.63 | 298.44 | 2334.03 | 2877.14 | 346.76 | 713.07 |
| Mandelbrot | 330.57 | 300.44 | 564.06 | 694.12 | 176.2 | 265.96 |

**Appendix B**

Plant species for pollen collected from six study sites in Mwingi, eastern Kenya. Samples were collected from honeybee hives in during the period May 2017 to November 2018.

| Species/sample# | Family | Kathiani | Mumoni | Kasanga | Itiva | Imba | Nguni |
|---|---|---|---|---|---|---|---|
| *Acanthaceae indet.* | Acanthaceae | 13 | 0 | 0 | 0 | 3 | 0 |
| *Blepharis* | Acanthaceae | 1 | 0 | 0 | 0 | 0 | 0 |
| *Hypoestes* | Acanthaceae | 3 | 23 | 335 | 56 | 1 | 1 |
| *Penstrophe* | Acanthaceae | 2 | 0 | 13 | 0 | 2 | 0 |
| *Achyranthes* | Acanthaceae | 88 | 0 | 0 | 0 | 0 | 0 |
| *Justicia* | Acanthaceae | 25 | 4 | 22 | 70 | 5 | 8 |
| *Hygrophilia* | Acanthaceae | 12 | 44 | 43 | 0 | 0 | 3 |
| *Trianthera* | Aizoaceae | 0 | 0 | 0 | 3 | 0 | 0 |
| *Aloe* | Aloeceae | 0 | 19 | 1 | 129 | 1 | 1 |
| *Aerva* | Amar/Cheno | 2 | 0 | 0 | 0 | 0 | 0 |
| *Amaranth/Cheno* | Amar/Cheno | 7 | 16 | 369 | 174 | 0 | 32 |
| *Lannea* | Anacardiaceae | 5 | 60 | 0 | 0 | 46 | 0 |
| *Rhus* | Anacardiaceae | 107 | 0 | 0 | 117 | 444 | 0 |
| *Sclerocarya* | Anacardiaceae | 0 | 11 | 72 | 0 | 1 | 0 |
| *cf. Heromorpha* | Apiaceae | 0 | 0 | 0 | 0 | 0 | 167 |
| *Adenium* | Apocynaceae | 0 | 0 | 7 | 32 | 0 | 0 |
| *Hyphaene* | Aracaceae/Palmae | 0 | 11 | 0 | 15 | 42 | 131 |
| *Asclepidiaceae* | Asclepidiaceae | 0 | 0 | 1 | 0 | 0 | 0 |
| *Ageratum* | Asteraceae | 2 | 3 | 0 | 0 | 2 | 0 |
| *Asteraceae Indet* | Asteraceae | 5 | 0 | 7 | 0 | 0 | 0 |
| *Apilia* | Asteraceae | 361 | 24 | 116 | 41 | 195 | 8 |
| *Eclipta* | Asteraceae | 194 | 0 | 0 | 0 | 0 | 0 |
| *Elephantopus* | Asteraceae | 0 | 0 | 0 | 0 | 1 | 0 |
| *Sphaelanthus* | Asteraceae | 32 | 0 | 0 | 0 | 0 | 0 |
| *Stoebe* | Asteraceae | 0 | 0 | 0 | 1179 | 0 | 125 |
| *Tagetes* | Asteraceae | 34 | 0 | 0 | 0 | 0 | 0 |

**Appendix B continued**

| Species/sample# | Family | Kathiani | Mumoni | Kasanga | Itiva | Imba | Nguni |
|---|---|---|---|---|---|---|---|
| *Tarchonanthus* | Asteraceae | 0 | 0 | 2 | 0 | 71 | 0 |
| *Vernonia* | Asteraceae | 255 | 5 | 108 | 5 | 473 | 199 |
| *Balanites* | Balanitaceae | 0 | 0 | 0 | 21 | 7 | 0 |
| *Bombax* | Bombacaceae | 0 | 0 | 0 | 6 | 0 | 0 |
| *Cordia* | Boraginaceae | 1 | 0 | 3 | 14 | 2 | 0 |
| *Heliotropium* | Boraginaceae | 3 | 3 | 0 | 58 | 8 | 55 |
| *Brassicaceae* | Brassicaceae | 0 | 0 | 7 | 3 | 0 | 4 |
| *Boswellia* | Burseraceae | 0 | 0 | 0 | 0 | 4 | 1 |
| *Boscia* | Capparaceae | 0 | 33 | 13 | 33 | 126 | 10 |
| *Capparaceae indet* | Capparaceae | 2 | 0 | 0 | 25 | 0 | 1 |
| *Capparis* | Capparaceae | 0 | 0 | 0 | 1225 | 346 | 0 |
| *Cleome* | Capparaceae | 24 | 51 | 1188 | 831 | 8 | 11 |
| *Leonotis* | Capparaceae | 60 | 0 | 50 | 0 | 6 | 2 |
| *Maerua* | Capparaceae | 1 | 12 | 0 | 0 | 0 | 0 |
| *Parinari* | Chrysobalanceae | 0 | 0 | 0 | 0 | 0 | 15 |
| *Commiphora* | Combretaceae | 46 | 0 | 355 | 7 | 2 | 275 |
| *Terminalia* | Combretaceae | 0 | 1942 | 0 | 596 | 355 | 2 |
| *Commelina* | Commelinaceae | 0 | 7 | 11 | 0 | 0 | 0 |
| *Ipomea* | Convulvulaceae | 22 | 0 | 54 | 26 | 0 | 9 |
| *Cucumis* | Cucurbutaceae | 31 | 6 | 567 | 0 | 0 | 2 |
| *Momordica* | Cucurbutaceae | 0 | 0 | 0 | 4 | 6 | 0 |
| *Cyperus* | Cyperaceae | 0 | 110 | 6 | 0 | 0 | 0 |
| *Dracaena* | Dracenaceae | 0 | 0 | 0 | 0 | 0 | 5 |
| *Acalypha* | Euphorbiaceae | 2 | 7 | 21 | 6 | 64 | 0 |
| *Alchornea* | Euphorbiaceae | 0 | 2 | 0 | 0 | 5 | 14 |
| *Croton* | Euphorbiaceae | 3 | 15 | 1 | 13 | 13 | 1 |

**Appendix B continued**

| Species/sample# | Family | Kathiani | Mumoni | Kasanga | Itiva | Imba | Nguni |
|---|---|---|---|---|---|---|---|
| *Euphorbia* | Euphorbiaceae | 33 | 10 | 23 | 32 | 28 | 280 |
| *Phyllanthus* | Euphorbiaceae | 40 | 174 | 300 | 15 | 10 | 0 |
| *Ricinus* | Euphorbiaceae | 0 | 15 | 5 | 10 | 0 | 0 |
| *Acacia* | Fabaceae | 84 | 44 | 634 | 166 | 50 | 1046 |
| *Albizia* | Fabaceae | 9 | 0 | 0 | 5 | 0 | 0 |
| *Combretum* | Fabaceae | 0 | 56 | 12 | 52 | 24 | 0 |
| *Delonix* | Fabaceae | 0 | 0 | 1 | 33 | 14 | 2 |
| *cf. Hypericum* | Hypericaceae/Guttiferae | 8 | 0 | 0 | 0 | 0 | 0 |
| *Indet* | Indet | 0 | 0 | 0 | 2 | 0 | 0 |
| *Basilicum* | Labiateae/Lamiaceae | 0 | 0 | 0 | 8 | 0 | 0 |
| *Leucas* | Labiateae/Lamiaceae | 595 | 0 | 6 | 5 | 5 | 397 |
| *Ocimum* | Labiateae/Lamiaceae | 5 | 13 | 60 | 78 | 0 | 2 |
| *Chlorophytum* | Liliaceae | 0 | 0 | 0 | 6 | 0 | 61 |
| *Loranthus* | Loranthaceae | 0 | 0 | 1 | 0 | 0 | 26 |
| *Ammania* | Lythraceae | 0 | 39 | 0 | 43 | 0 | 0 |
| *Abutilon* | Malvaceae | 0 | 0 | 0 | 53 | 0 | 0 |
| *Hibiscus* | Malvaceae | 49 | 6 | 20 | 2 | 7 | 16 |
| *Pavonia* | Malvaceae | 0 | 0 | 0 | 0 | 1 | 16 |
| *Sida* | Malvaceae | 0 | 0 | 0 | 1 | 0 | 0 |
| *Melia* | Meliaceae | 0 | 0 | 0 | 0 | 6 | 0 |
| *Melia* | Meliaceae | 0 | 38 | 15 | 0 | 0 | 0 |
| *Mimosa* | Mimosaceae | 0 | 0 | 0 | 0 | 4 | 0 |
| *Bosquea/Trilepisium* | Moraceae | 5 | 0 | 0 | 0 | 0 | 0 |
| *Ficus* | Moraceae | 1 | 0 | 3 | 0 | 0 | 0 |
| *Maesa* | Myrsinaceae | 0 | 0 | 1 | 0 | 0 | 0 |
| *Syzygium/Eucalyptus* | Myrtaceae | 0 | 7 | 11 | 4 | 6 | 658 |

**Appendix B continued**

| Species/sample# | Family | Kathiani | Mumoni | Kasanga | Itiva | Imba | Nguni |
|---|---|---|---|---|---|---|---|
| *Boerhavia* | Nyctaginaceae | 0 | 0 | 4 | 1 | 4 | 6 |
| *Boungainvillea* | Nyctaginaceae | 1 | 0 | 0 | 0 | 0 | 0 |
| *Ximenia* | Olacaceae | 0 | 0 | 0 | 0 | 3 | 0 |
| *Olea* | Oleaceae | 13 | 18 | 5 | 28 | 0 | 0 |
| *Crotaralia* | Papilionaceae | 24 | 0 | 0 | 11 | 0 | 1 |
| *Indigofera* | Papilionaceae | 75 | 41 | 231 | 10 | 148 | 0 |
| *Legume indet* | Papilionaceae | 2 | 1 | 18 | 0 | 15 | 3 |
| *Rhynochosia* | Papilionaceae | 2 | 8 | 6 | 8 | 169 | 0 |
| *Sesbania* | Papilionaceae | 5 | 0 | 15 | 7 | 0 | 0 |
| *Tamaridus* | Papilionaceae | 0 | 0 | 0 | 0 | 5 | 0 |
| *Tephrosia* | Papilionaceae | 0 | 0 | 4 | 3 | 0 | 16 |
| *Vigna* | Papilionaceae | 1 | 0 | 0 | 0 | 0 | 0 |
| *Pittosporum* | Pittosporaceae | 0 | 0 | 0 | 0 | 0 | 1 |
| *Cereals (Millet/sorghum)* | Poaceae | 209 | 0 | 0 | 0 | 14 | 0 |
| *Poaceae* | Poaceae | 177 | 1 | 375 | 55 | 162 | 168 |
| *Zea Mays* | Poaceae | 6 | 4 | 0 | 0 | 0 | 4 |
| *Polygonum* | Polygonaceae | 1 | 0 | 1 | 6 | 19 | 0 |
| *Rumex* | Polygonaceae | 0 | 0 | 0 | 0 | 3 | 1 |
| *Protea* | Proteaceae | 0 | 1 | 0 | 0 | 0 | 0 |
| *Ziziphus* | Rhamnaceae | 0 | 61 | 0 | 0 | 0 | 0 |
| *Juniperus* | Rosaceae | 0 | 0 | 6 | 0 | 0 | 0 |
| *Anthocleista* | Rubiaceae | 0 | 0 | 0 | 0 | 0 | 61 |
| *Anthospermum* | Rubiaceae | 0 | 0 | 12 | 3 | 0 | 0 |
| *Canthium* | Rubiaceae | 0 | 3 | 0 | 1 | 0 | 1 |
| *Lepidangathus* | Rubiaceae | 1 | 0 | 0 | 0 | 0 | 0 |
| *Psychotria* | Rubiaceae | 0 | 12 | 4 | 7 | 0 | 0 |

**Appendix B continued**

| Species/sample# | Family | Kathiani | Mumoni | Kasanga | Itiva | Imba | Nguni |
|---|---|---|---|---|---|---|---|
| *Rubiaceae indet* | Rubiaceae | 0 | 0 | 0 | 8 | 5 | 0 |
| *Rutaceae* | Rutaceae | 33 | 0 | 0 | 7 | 0 | 0 |
| *Vepris* | Rutaceae | 0 | 0 | 0 | 4 | 0 | 0 |
| *Salvadora* | Salvadoraceae | 9 | 67 | 221 | 12 | 632 | 0 |
| *Allophyllus* | Sapidaceae | 0 | 0 | 0 | 0 | 0 | 4 |
| *Sapindaceae* | Sapidaceae | 0 | 0 | 65 | 0 | 0 | 4 |
| *Stemodia* | Schlorophulaceae | 5 | 0 | 0 | 1 | 0 | 89 |
| *Stemodia* | Schlorophulaceae | 0 | 1 | 0 | 0 | 3 | 0 |
| *Striga* | Schlorophulaceae | 0 | 0 | 0 | 0 | 1 | 0 |
| *Tragia* | Schlorophulaceae | 3 | 0 | 0 | 0 | 0 | 0 |
| *Solanum* | Solanaceae | 5 | 24 | 33 | 26 | 3 | 34 |
| *Steculia* | Steculiaceae | 0 | 0 | 0 | 1 | 0 | 0 |
| *Corchorus* | Tiliaceae | 29 | 1 | 0 | 0 | 68 | 7 |
| *Grewia* | Tiliaceae | 28 | 54 | 338 | 255 | 128 | 133 |
| *Typha* | Typhaceae | 0 | 0 | 0 | 0 | 0 | 1 |
| *Celtis* | Ulmaceae | 0 | 0 | 4 | 27 | 0 | 37 |
| *Unknown* | Unknown | 0 | 1 | 5 | 0 | 0 | 4 |
| *Cardiospermum* | Verbanaceae | 5 | 6 | 4 | 0 | 0 | 140 |
| *Cassia* | Verbanaceae | 4 | 0 | 0 | 0 | 0 | 1 |
| *Cissus* | Verbanaceae | 0 | 0 | 0 | 0 | 0 | 5 |
| *Tribulus* | Zygophyliaceae | 0 | 0 | 0 | 0 | 7 | 0 |

**Appendix C (a)**

Pairwise comparisons (p-values) of Renyi diversities carried out using the Wilcoxon Rank Sum Test

| | **Imba** | **Itiva** | **Kasanga** | **Kathiani** | **Mumoni** | **Nguni** |
|---|---|---|---|---|---|---|
| **Imba** | 1 | 0.01* | 0.02* | $0.08^{NS}$ | $0.32^{NS}$ | $0.32^{NS}$ |
| **Itiva** | 0.01* | 1 | $0.71^{NS}$ | $0.32^{NS}$ | 0.02* | 0.03* |
| **Kasanga** | 0.02* | $0.71^{NS}$ | 1 | $0.44^{NS}$ | 0.03* | $0.05^{NS}$ |
| **Kathiani** | $0.08^{NS}$ | $0.32^{NS}$ | $0.44^{NS}$ | 1 | $0.05^{NS}$ | $0.11^{NS}$ |
| **Mumoni** | $0.32^{NS}$ | 0.02* | 0.03* | $0.05^{NS}$ | 1 | $0.27^{NS}$ |
| **Nguni** | $0.32^{NS}$ | 0.03* | $0.05^{NS}$ | $0.11^{NS}$ | $0.27^{NS}$ | 1 |

Significance codes: ≤ 0.05 '*' ≥ 0.05 '$^{NS}$';NS = Not significant

**Appendix C (b)**

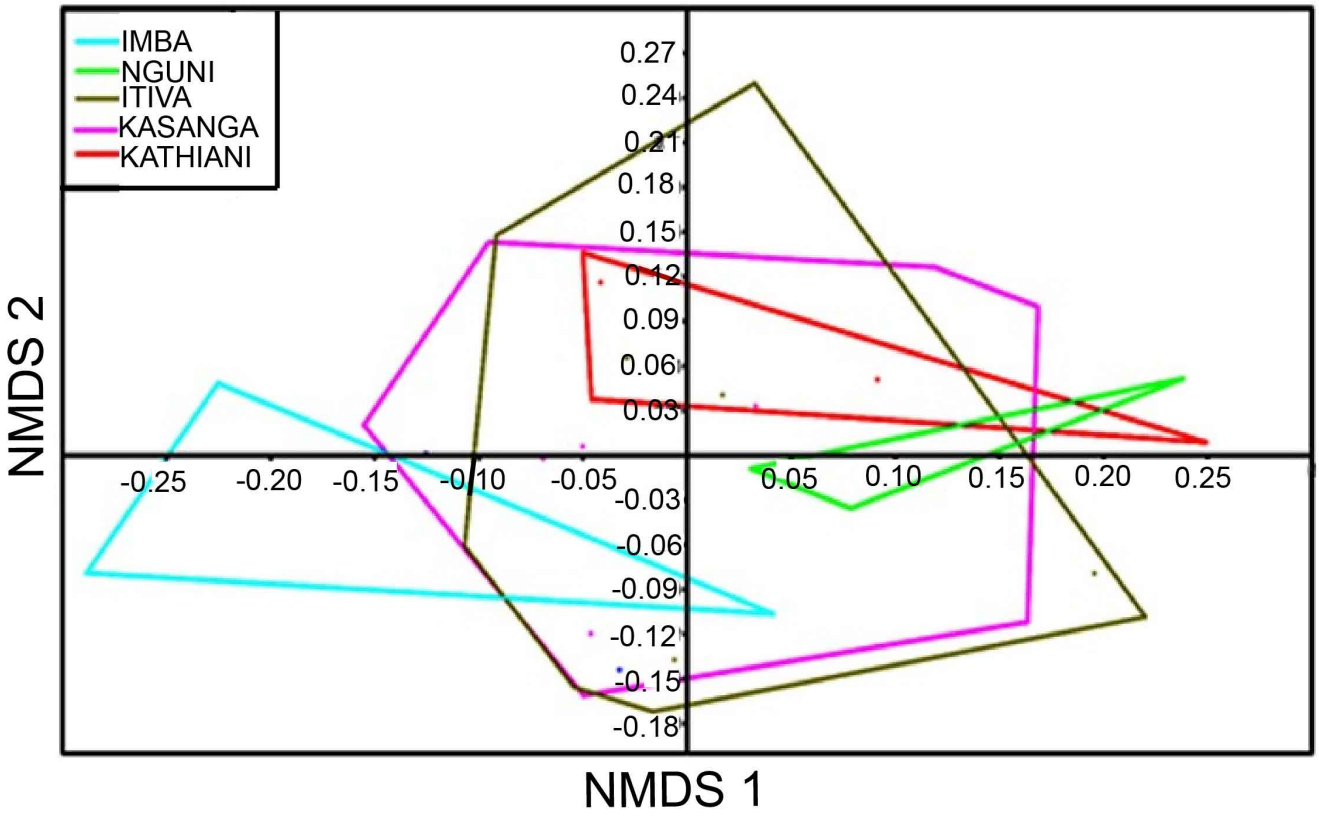
Pairwise comparisons (p-values) of crude protein concentration (%) across seasons carried out using the Wilcoxon Rank Sum Test

| | **May** | **January** | **June** | **November** |
|---|---|---|---|---|
| **May** | 1 | 0.00* | 0.02* | $0.15^{NS}$ |
| **January** | 0.00* | 1 | $0.87^{NS}$ | $0.15^{NS}$ |
| **June** | 0.02* | $0.87^{NS}$ | 1 | $0.24^{NS}$ |
| **November** | $0.15^{NS}$ | $0.15^{NS}$ | $0.24^{NS}$ | 1 |

Significance codes: ≤ 0.05 '*' ≥ 0.05 '$^{NS}$';NS = Not significant

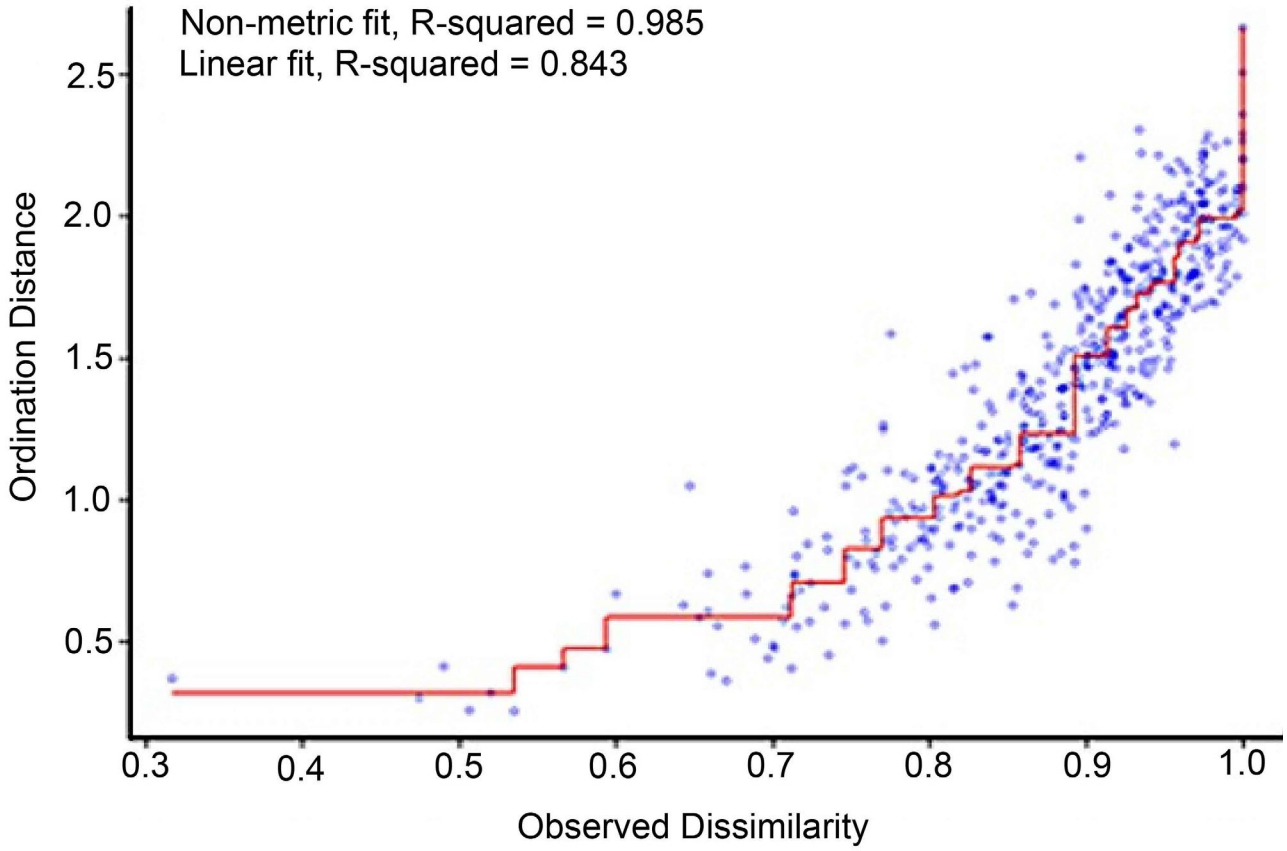
**Appendix D (a)**

The diagram shows NMDS ordination based on Bray–Curtis dissimilarities (k = 4) in pollen samples in the six study sites. The samples are distinguished and colored by site as indicated on the figure legend.



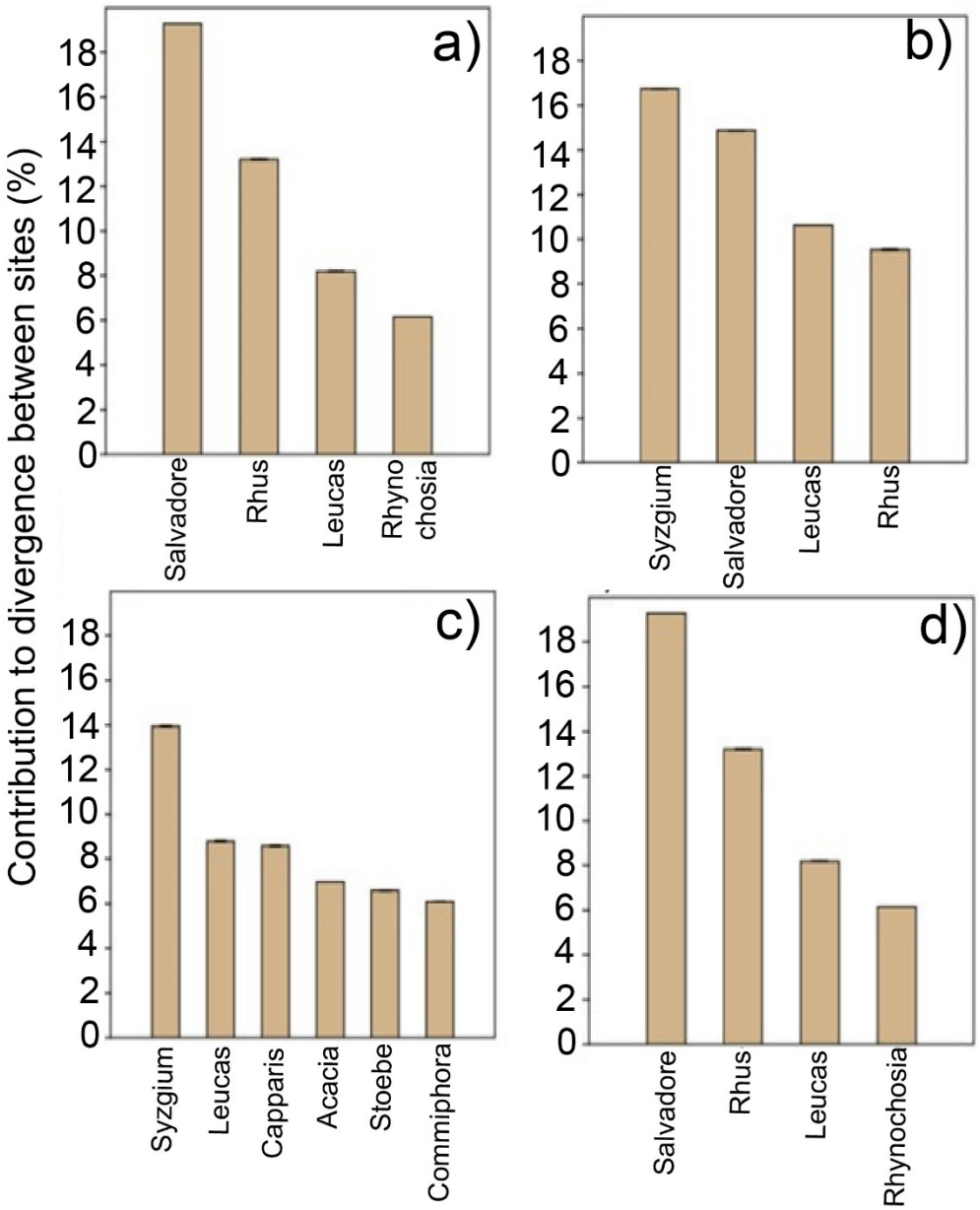
**Appendix D (b)**

Shepherd's diagram, with correlation statistics demonstrating the goodness of fit of the pollen samples from the NMDS analysis. The X-axis corresponds to the input dissimilarities while the Y-axis corresponds to their MDS reconstruction. The red line denotes the disparities while each of the blue dots corresponds to the distance between each pair of plant communities.



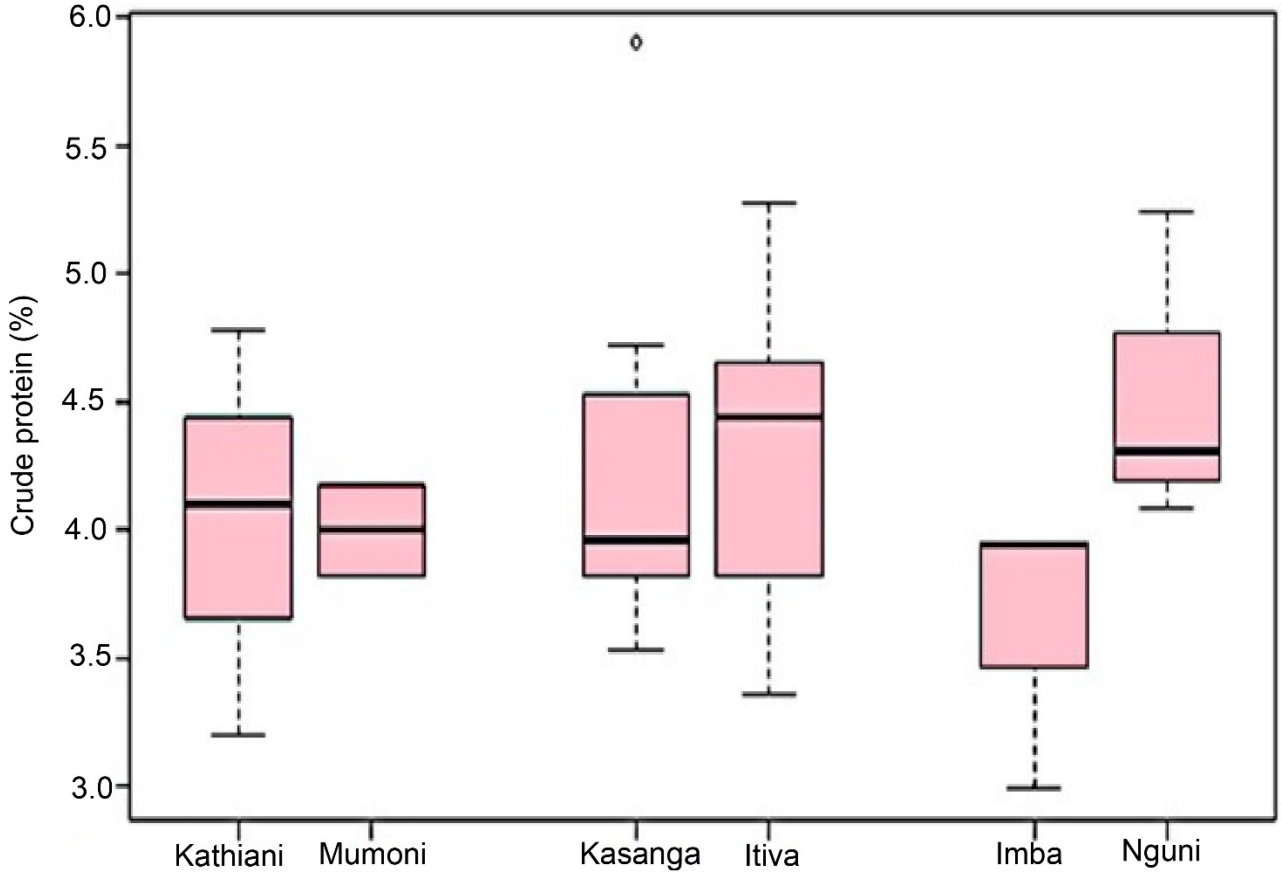
**Appendix E**

Pairwise SIMPER with Bray-Curtis similarity test results for the four most separated pairs of sites as derived from the NMDS ordination graph. a) Imba versus Kathiani b) Itiva versus Nguni c) Imba versus Kasanga and d) Imba versus Nguni (Plant species which are primarily responsible for the perceived difference between the sites (up to approximately 50% contribution) are shown in the graphs.



**Appendix F**

Total crude protein concentration (%) across the six study sites, grouped from left to right as: least degraded, moderately degraded, and highly degraded. Within the box plots, the border of the box adjacent to zero signifies the 25th percentile, the black line inside the box indicates the median, and the boundary of the box farthest away from zero indicates the 75th percentile. Whiskers above and below the box signify the 10th and 90th percentiles.




Kruskal-Wallis chi-squared = 3.9114, df = 5, p-value = 0.56