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Diversity of Life-History Traits, Functional Groups and Indicator Species of Bee Communities from Farmlands of Central Uganda

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Abstract

Bees are keystone organisms that sustain human life on earth through their pollination services. However, very little is known about functional groups and indicator species of bee communities from agricultural landscapes in Sub-Saharan Africa and Uganda. Responses to anthropogenic disturbances and the quality of pollination services delivered by different bee species are often associated with bee life-history traits. Diverse bee functional groups have different pollination service impacts on wild and cultivated plants. Efficient bee species are often good indicator species belonging to the same functional group. To provide baseline data on functional traits of bee communities in agricultural landscapes, a study was conducted in 2006 at 26 sites with varying local and landscape characteristics in central Uganda. Bees were sampled using colored pantraps, hand nets and line transect counts. The farmland bee community was characterized by a diversity of functional traits and guilds. Most of the bee species and individuals collected by the three sampling methods applied were solitary (37-70%), ground-nesting (41-65%), polylectic (74-91%), long-tongued (73-87%) and of small (<5.5mm) to medium (5.5-10.5mm) body sizes (18-37%). Using Indicator value method (*IndVal*), more than 17 species were recorded as indicator species or "species characteristics of the farmland habitats". Indicator species are generally ubiquitous species potentially delivering pollination services of high quality to cultivated and wild plants in farmland environments. They were recommended by to monitoring programs aiming at detecting the status and trends in Apoidea communities in central Uganda. To prevent future decline in the functional diversity, it is important to develop strategies to conserve landscape and habitats as reservoirs of different functional groups of bees. This will greatly contribute to the spatio-temporal stability of yield of pollinator-dependent crops that are pollinated by different pollinator groups. Monitoring programs aiming at detecting changes in bee faunas in farmlands of central Uganda may focus on the 17 indicator species identified by this study.

keywords: Functional groups, life history-traits, coffee-banana agroforests, functional group conservation, crop yield stability, Central Uganda.

1. Introduction

Pioneering works have highlighted the fact that bees are by far the most important providers of biotic pollination services in the world (Roubik, 1995; Dag, 2009). As the world's primary pollinators, bees constitute a critically important functional group. Although other taxa including butterflies, flies, beetles, wasps, bats, birds, lizards, and mammals may be important pollinators in certain habitats, none achieves high functional role of fidelity to particular plant species as key pollinators as bees (Munyuli, 2010 ; Ollerton *et al.*, 2011).The likely reason for this is that unlike other taxa, bees are obligate florivores throughout their life cycle, with both adults and larvae dependent on floral products, primarily pollen and nectar (Ollerton *et al.*, 2011).

With an estimated 20,000-30,000 species worldwide; bees are also a useful group for the study of biodiversity in farmland habitats. Currently, it is well established that bees are the world's dominant and vital pollinator taxa (Liow*et al.,* 2001; Fontaine *et al*., 2006) of most crop species: bees are essential for the productivity of many agricultural crops worldwide. Scientific studies state that a great proportion of the economic value of crop production is attributed to the free services ("public good") of pollinating services provided by a diversity of functional groups of bees (Klein *et al.*, 2007; Morandin *et al*., 2007). Bees are therefore keystone organisms that sustain human life on earth, through their irreplaceable pollination services (Munyuli, 2011a). Overall, bees play key roles in the maintenance of a diversity of wild plant communities (Bawa, 1990).They also provide pollination services of high economic values (Steffan-Dewenter and Westphal, 2008; Olschewski *et al.*, 2007). Some calculations are available for European Union and North America. For example, honey bees (*Apis mellifera* L.) are the main crop pollinator in the USA, contributing annually to estimate $1.6- $14.6 billion in pollination services (Southwick and

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Southwick, 1992; Chamberlain and Schlisin, 2008). The economics gains from non-managed wild bees are estimated to be of US$3.07 billion per annum in USA alone (Slaa, *et al.*, 2006; Losey and Vaughan, 2006). The ecological, agricultural and economic importance of pollinators is immense (Munyuli, 2011b). The value of pollination to agricultural production worldwide is currently estimated to be worth US$226 billion (€153 billion) (Klein *et al.*, 2007; Morandin *et al.*, 2007; Gallai *et al.*, 2009). In Uganda, the economic value of pollinating services delivered to the crop production sector is on average of 0.52 billion per annum (Munyuli, 2010). Despite the vital role played by bee communities in traditional agro-ecosystems, the ecological and economic importance of these organisms (Martins, 2004), the diversity of functional groups remain largely unknown and un-surveyed (Eardley *et al.*, 2009; Gordon *et al.*, 2004) in Uganda.

There is a need to understand functional groups and indicator species of farmland bee faunas since these two types of bio-indicators can be used to monitor trends, predict and prevent degradation of bee biodiversity pollination services needed by a high number of pollinator-dependent wild and cultivated plants found in rural landscapes of Uganda and in East Africa. Also, the knowledge of the diversity of functional groups is important to acquire since responses to anthropogenic disturbances and the quality of pollination services delivered by different bee species are often associated with life-history traits. Diverse functional groups of bees have different pollination service impacts on wild and cultivated plants. Efficient bee species often belong to the same functional group. Some wild and cultivated plant species are pollinated by bee species in the same functional group such as sharp decline in these bee groups may lead to the disappearance of plant species in strong linkage and interactions with them. For example, in Uganda, efficient pollinators of cucurbits are often solitary bees in the Halictini (Halictidae). Thus, cultivation of cucurbits in environments that have low Halictid bee diversity may lead to high pollination limitation and to drastic reduction of the yield (Munyuli, 2010).

The diversity and incidence of different bee traits varies from a region to another. Within a region, bee species may also differ in their degree of voltinism (number of generations produced within a single growing) and in their flight season (period when the bee start being active and period when it ends or cease being actively seen foraging on different flowering plant species). Generally dietary specialization is associated with a higher extinction rate and/or with sensitivity to disturbance for a variety of bee taxa and functional groups. Oligolectic bee species are species known to gather pollen from a small number of related flower species, whereas polylectic bees are pollen generalists. Oligolectic species probably account for a large fraction of global bee diversity, since they constitute about 30% of species in temperate communities and up to 60% of species in the more species-rich desert (Moretti *et al.*, 2008). Cleptoparasitic bees are morphologically highly divergent from other bees. They are often heavily armored and lack pollen-collecting structures. Cleptoparasitic species are widespread in Apidae, Megachilidae, and Halictidae (Michener, 2007). There are only a few species of cleptoparasitic Colletidae. Overall, no cleptoparasites have been reported from Melittidae, Andrenidae and Stenotritidae bee families worldwide. Cleptoparasitism in Uganda remains largely un-documented. It is important to know how many bee species are parasitic in a given habitat to better plan the conservation of pollination services delivered by non-parasitic bee species.

In most European countries, 89% of bee species are known to be bees with narrow habitat range; whereas 10% have wide habitat range. More than 65% of European bees are univoltine (one generations per year) and less than 35% of them are multivoltine (species having several generations per year) (Bismeijer *et al.*, 2006 a and b). The degree of voltinism for afrotropical bees remains largely undescribed. Approximately, 80% of the European bee species are oligolectic bees and less than 20 % are polylectic. In the European countries, 70% of bee species are long-tongued bees and only 30% are short-tongued bees (Biesmeijer *et al.*, 2006; Westphal *et al.*, 2008). The proportion of long-tongued bees in Uganda remains undescribed.

The ability to predict the responses of ecological communities and individual species to human-induced environmental change remains a key issue for ecologists and conservation managers alike (Williams *et al.*, 2010). Apoidea fauna with shared life-history and ecological traits can present variability in responses to different drivers within the same environment (Williams et *al.*, 2010). Therefore, knowledge of range of life-history and ecological traits of bee community can be used to predict bee responses to a change in a variety of disturbance types (agriculture intensification, cropping intensification, proportion of semi-natural habitats, distance to natural habitats, pesticide use, distance to natural habitats or habitat isolation, climatic factors, farm management system, grazing intensity, fire regimes, deforestation rate, etc) or drivers from a given farm-landscape. Understanding the diversity of functional traits can also help in better planning conservation strategies for the protection of bees to guarantee spatio-temporal delivery of pollination services to crops and wild plants. Ensuring spatio-temporal delivery of pollination services to crops is very critical for Ugandan agriculture since 78% of crop species and varieties grown by farmers in Uganda are pollinator-dependent (Munyuli, 2011a and b).

Monitoring changes in bee populations and functional traits in relationship to changes in drivers is another important step to build good conservation strategies that can reduce or prevent decline in bee species and populations. Overall, understanding how diverse bee traits are can also help in predicting the vulnerability of plant-pollinator interactions to global environmental change, to land-use (land-cover) changes and to various other drivers and pressures including climate change. Such knowledge can also help in better managing pollination services to meet the requirements of different plant /crop species. Some plant species can only be pollinated by certain group of bee species. The absence of such functional groups of bees may lead to decline or disappearance of such specialized plant / crop species.

Functional traits can be used to predict the response of bee species to various drivers. Functional traits can therefore be used in monitoring programs to detect trends and status of species and population in a habitat subjected to pressures of different types. Indicator species can also be used to monitor the status of a bee community in a given habitat / landscape. If time and resource allow, monitoring the overall status of bee communities in a landscape / habitat can simultaneously be conducted using functional traits and or indicator species information. Policy measures and conservation strategies based on both indicator species and bee functional traits are likely to be useful in the protection of most species in a landscape/habitat (Munyuli, 2010). In addition, indicator species can help in developing effective monitoring plans of bee communities in farmland habitats of central Uganda. Challenges related to monitoring and conservation of bee faunas in farmlands of Uganda include the absence of basic knowledge about their natural history, abundance, diversity, functional traits and in their spatio-temporal distribution in agricultural landscapes.

The objective of this study was to identify the different functional groups and indicator species of bee communities found in agricultural landscapes in central Uganda.

In this study, it was hypothesized that farmland bee communities are not diverse in functional groups and indicator species because agriculture intensification may cause the disappearance of specialized bee groups and may tend to favor few common groups. In general farmland habitats are expected to support poor rich bee communities because they subjected to constant disturbances (e g crop production intensification) although studies from Kakamega Forest in Kenya (Gikungu 2006) showed that bees can be more diverse in farmland matrix habitats.

2. Material and Methods

2.1. Study area

This study was conducted in the banana-coffee system of Lake Victoria Arc zone, central Uganda (Fig. 1). The study zone belongs to the Lake Victoria phytochorion with shrubs of *Acacia* spp, legume trees, melliferous plant species, *Papyrus* and palms ranging from 2 to 15m high dominating the remnant secondary vegetation. Several oily, food and cash crops are grown, mainly cassava (*Manihot esculentum* L.), Sweetpotato, (*Ipomoea batatus*, L.), maize (*Zea mays*), beans (*Phaseolus vulgarus* L.), groundnut (*Arachis hypogea* L.); tomato (*Lycopersicon esculentum*), watermelon (*Citrullus lanatus*), pumpkin (*Cucurbita moschata*), cucumber (*Cucumis sativus*), melon (*Cucumis melo*); chilies (*Capsicum* spp.); and several other fruits, vegetables and horticultural crops (cabbage, onion, egg plants, sim-sim, etc). The majority of these crops require different functional groups of bees to provide pollination services of high quality.

This study was conducted in 26 sites selected to represent a range of habitats types with varying degrees of anthropogenic disturbances and management intensities. Selected study sites were grouped into clusters using human population density as a surrogate measure of agricultural intensity (Bolwig *et al.*, 2006) and anthropogenic disturbances. Each cluster comprised of 2 to 4 similar sites. Detailed environmental and landscape vegetation characteristics of the 26 sites and clusters are presented in Munyuli (2011c).

2.2. Bee sampling design

In each study site (1 km^2), five linear transects of 1000 x 200 m each were set using a GPS and a tape measure. Bees were sampled on one central line transect (1000m x 20m) visited on each round of data collection to obtain replicable results. Bees were sampled using three complementary methods: transect walk-and-counts (direct observations of foraging activities on flowers: visual censuses), capture using a handnet and colored pantraps following approaches described by previous workers (Potts *et al*, 2005; Cane,2000; Wilson *et al.*, 2009; Banaszak and Manole, 1987, 1994; Roulston *et al*., 2007; Droege *et al.*, 2010; Aizen and Feinsinger, 1994)

Bee specimens were sorted out and processed at Makerere University (Zoology Department Museum). All bee species were washed in 70% alcohol solution prior to pinning activities. Specimens were pinned, mounted and sun-dried for three days. Preliminary identification of the bees to the family or genus level was conducted in the laboratory at Makerere University, using published dichotomous keys (Michener, 2007) and the online keys available through www.discoverlife.org (Ascher *et al.*, 2008). Bee identifications up to species levels were further conducted at bio-systematic division of the Plant Protection Research Institute (ARC-Pretoria, South Africa), at the Natural History Museum, London (UK) and at the University of Reading (UK). Another set of bee specimens (stingless bees) were sent to STRI (Smithsonian Tropical Research Institute) in Panama. The identification of bees at ARC-Pretoria was conducted under guidance of Dr Connal Eardley. The identification of bee specimens at Smithsonian Tropical Research Institute was done by Dr David Roubik. The identification of bees at the natural history museum- London was conducted by Dr David Notton. A reference collection of bees of Uganda was established and is currently housed at Makerere University Zoology Museum.

2.3. Data analyses.

2.3.1. Classification of bee species per functional traits and ecological characteristics

Attempts were made to group all bee species recorded in this study into different functional categories in order to examine relative importance of each functional group (Moretti *et al*., 2009). Bee species were grouped according to taxonomic affinity and body size (Biesmeijer *et al.*, 2006; Fontaine *et al.*, 2006). Functional traits were obtained from the literature (Michner, 2007; Eardley and Urban, 2010**;** Eardley *et al.*, 2010; Eardley and Urban, 2010; Roubik,1995), where available.

In case, there is no information in the literature and no particular observation was conducted in the field, the trait attributes of different species were obtained from taxonomists, with experience on African bee fauna. Species which had no information on their functional traits were put in the unknown category. Overall, dietary breadth and nesting habits were determined for most species by reference to previous studies.

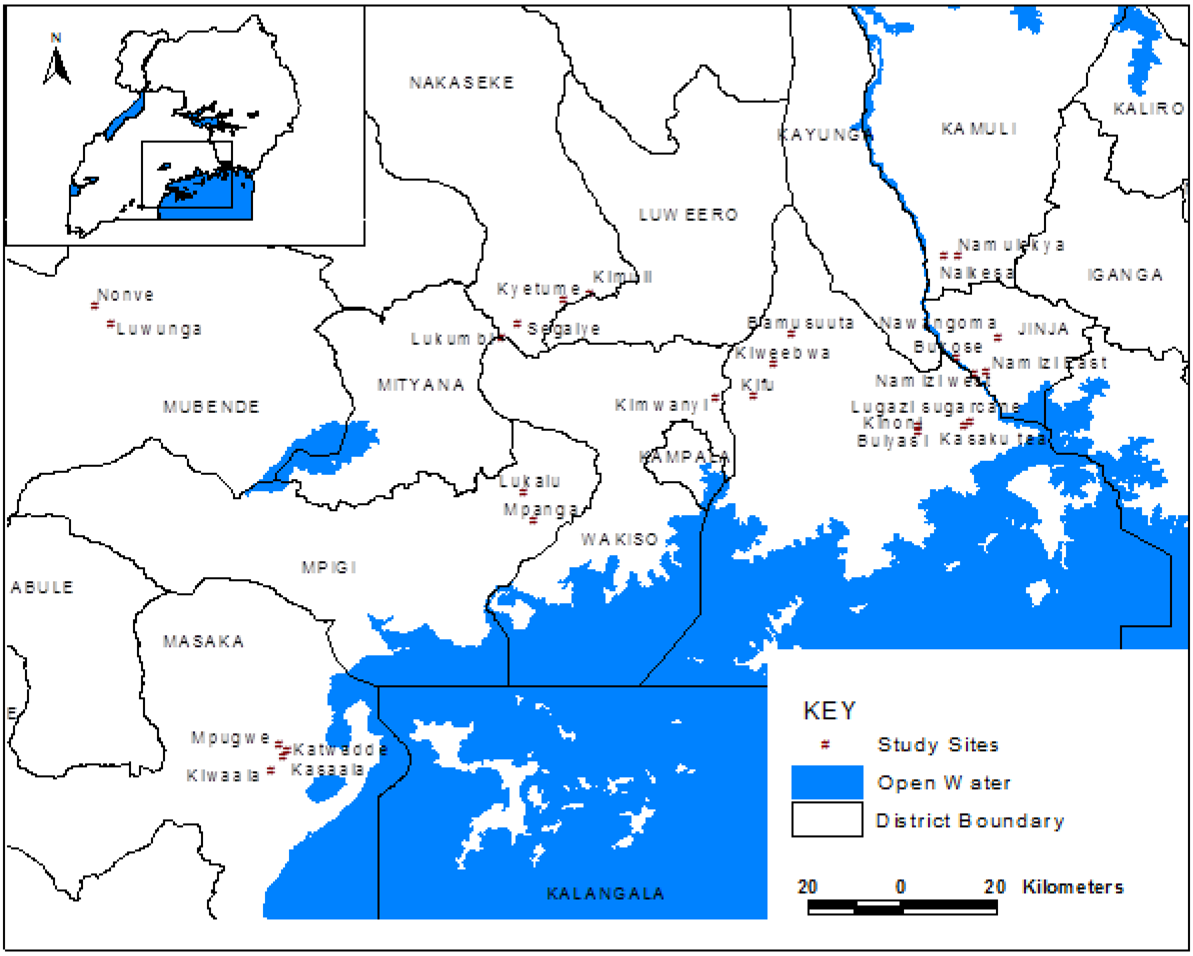

Figure1. Location of study sites in which the survey was conducted in the banana-coffee growing area around Lake Victoria in Uganda.

Nesting habits of bee species for which published records were not available were inferred if all other members of the same genus or subgenus used the same nesting substrate (e.g., all nest in the ground). Only two species represented by two individuals remained ambiguous for their nesting habits and were excluded from analyses as recommended (Cane *et al.*, 2006).

The traits to which each species was categorized included:

(i) *Feeding specialization*: (1) No lectic status (having no pollen collecting requirements; i.e. cleptoparasite), (2) Polylectic (pollen collecting on a number of species from different plant families), (3) Oligolectic (pollen collecting restricted to plants within the same plant family), (4) Monolectic (pollen collecting at a single species).

(ii) *Tongue length /length of the glossa /mouthparts length):* (1) short tongue (2) long tongue (3) medium-tongue. (1) Short tongue (<3mm); (2) intermediate or medium tongue (3-7mm); (3) long tongue (7-12mm); very long (>12-15mm) (Yanagizawa & Maimoni-Rodella, 2007).

(iii) *Nesting specializations* (*breeding strategies*)*:* (1) no nest building, (2) excavator in the ground (miner), (3) nests in termite mounds and other ground nesters, (4) carpenter: excavator in woody substrate , (5) renter of pre-existing nest and holes above the ground (cavity nesters), (6) live tree/stamp (dead wood), (7) house walls, (8) hives and (9) building nest with mud (mason bees).

(iv) *Parasitic status*: (1) cleptoparasitic (i.e. solitary parasitic bee), (2) social parasitic, (3) non parasitic;

(v)*Sociality status*/degree: (1) solitary: solitary, communal and semi-social; (2) social: colony founded by single individual on annual cycle (primitive eusocial) or a year-round colony (advanced eusocial); (3) variables: species is either solitary or social depending upon locality / environmental conditions (vi) *Bee body length* or *Bee body size* (*mm*)*:* (1) small (<5.5mm), (2) medium (5.5-10.5mm), (3) large (15.5-2.5mm), (4), very large (>21mm).

The analysis of the different traits was limited to the determination of the importance (%) of each group using data from the count of number of species and individuals that fall under a given trait category.

2.3.2. Species constancy and indicative value

The species constancy is the proportion of sites where a given species occur permanently across sampling seasons (rounds). The species constancy provides indications about most common species in the farm-landscape habitats.

Indicator species are “ecological characteristic species” of bee communities inhabiting certain type of habitats of a given landscape. It is important to know indicator species, particularly when interested at assessing the strength and reliability of association between individual bee species and particular study sites characterized by certain land-use, habitat, biotopes and vegetation types. Indicator species are also important and effective pollinator species of many crops and wild plant species in agricultural landscapes

(Munyuli, 2010) of Uganda. The usefulness of indicator species is that these species are easy to monitor and to sample. Indicator species are also species likely to deliver pollination services of high quality with high spatio-temporal stability (Munyuli, 2010) particularly in sub-Saharan tropical environments and in Uganda.

In this study, species constancy was calculated following the approach previously described by Banaszak (2000), d´Avila & Marchini (2008) and Silva-Pereira and Santos (2006) and Lee (2002). To determine reliable and stable "indicator species" or "characteristic species" in farmland habitats of central Uganda, the indicator (*IndVal*) method of Dufrêne & Legendre (1997) was adopted and used in this study in a modified form as recommended by Banaszak (2000) and Munyuli (2010) to identify indicator species of pollinator communities.

2.4. Statistical analysis

2.4.1. Variation in abundance and species richness among bee taxonomic groups.

The number of bee species and individuals of different taxa were measured during the determination of the bee community structure. Statistical analyses were conducted to determine the importance of some taxa relative to others. To explore whether there were statistically significant differences in occurrences or proportional abundance / species richness between different taxonomic groups (genera, families, etc), chi-square tests in Minitab release version 15 were applied.

2.4.2. Indicator species identification.

Significance of the indicator value for the site with the highest indicator value was evaluated by a Chi-square test comparing the observed indicator value for a site to indicator values calculated each of the five sampling rounds conducted. Hence, Chi-square testing in Minitab 15 was applied to determine the significance of the indicative value of each species across the five rounds of data collection as recommended (Banaszak, 2000; Munyuli 2010).

3. Results

3.1. Bee biodiversity structures and composition

Overall 80,883 individuals representing 652 native bee species from 6 families, 14 sub-families, 34 tribes and 79 genera were captured (see species list in Munyuli, 2010; Munyuli 2011c). Up to 645 species were new records for Uganda from the overall bee fauna diversity. There were variations in effectiveness of different sampling methods used. There was a significant ($P<0.001$) difference in the number of species captured using the three sampling methods. Significantly [$\chi^2_{(2,\ n=932)} = 402.414$; $P<0.0001$] higher number of bee species were captured using handnet (559 species) than when using transect count (59 bee species) and pantrap (314 be species) methods. Most bees were recorded through line transect counts (85% of total individuals) and very few individual bees were captured by handnet (8%) and pantraps (7%).

3.2. Functional traits characterization of bee fauna

Functional traits characterization of pantrapped bee community

A great variation in the abundances and species richness of different functional groups of bees attracted to different colors was detected (P<0.0001). Bee families differed significantly in species richness (χ^2 5df = 56.1, P<0.001) and in abundance (χ^2 5df = 75.87, P<0.0001). Apidae was the most species-rich (41.38% of species recorded in pantraps) followed by Halictidae (30.09%), Megachilidae (15.99%) and Colletidae (6.02%). Similarly, the bee family with the highest number of individuals was Apidae (46.5% of total bee individuals recorded) followed by Halictidae (38.52%), Andrenidae (5.82%) and Colletidae (4.13%).The most species-rich bee genus captured by pantraps was Halictus followed by Lipotriches and Patellapis, Ceratina, Allodapula and Braunsapis.

The species richness (χ^2 1df =69.886, P<0.001) and the abundance (χ^2 1df = 79.92, P<0.001) of non-parasitic bees were significantly higher compared to the abundance and species richness of parasitic bees captured in pan traps. In fact, 91.8% of 314 species registered and 94.7% of 5672 individuals recorded in pantraps belonged to non-parasitic bee species category compared to parasitic (cleptoparasitic) bees that accounted for only 5.3% of the total bee individuals recorded in five rounds of data collection across 26 study sites.

Bees of different breeding strategies occurred in pantraps; but overall, the bee fauna was composed of a significantly (χ^2 2df = 99.9397, P<0.0001) greater proportion of solitary bee species (96.25% of total number of bee species recorded) than of social bee species richness (3.75%).

3.3. Functional traits of transect-recorded bee fauna

Social status and breeding strategy

There was a significant difference among the different sociality (breeding strategy) categories in species richness (χ^2 3df =114.92, P<0.0001) and proportion of bee individuals (χ^2 3df =151.7351, P<0.0001). Solitary bees were the most species rich bee category (Fig.3), although social-bees were more abundant than other bee categories (Fig.3).Very few bee species and individuals were parasitic (cleptoparasitic). Except for bees in the cleptoparasitic genera (e.g., Thyreus, Cleptotrigona), most bee species recorded are potential efficient and good pollinator species of many entomophilous crop species.

3.4. Diversity of nesting specialization habits

There were significant differences in species richness (χ^2 5df = 189.86, $P<0.0001$) and abundance (χ^2 5df =74.081, $P<0.0001$) among the 6 different nesting-guild categories found in the bee fauna inhabiting farmlands of central Uganda. Ground-nesters were the most species-rich followed by wood/tree/pith nesters and cavity-nesters (Fig.4). House-wall nesters and beehives were the least species rich nesting categories recorded (Fig.4). Ground nesters (soil nesters, termite mound nesters) that were the most species-rich were also the most abundant bees. Wood or pith nesters were the second most species-rich and abundant, followed by hive, house wall and cavity nesters (Fig.4).

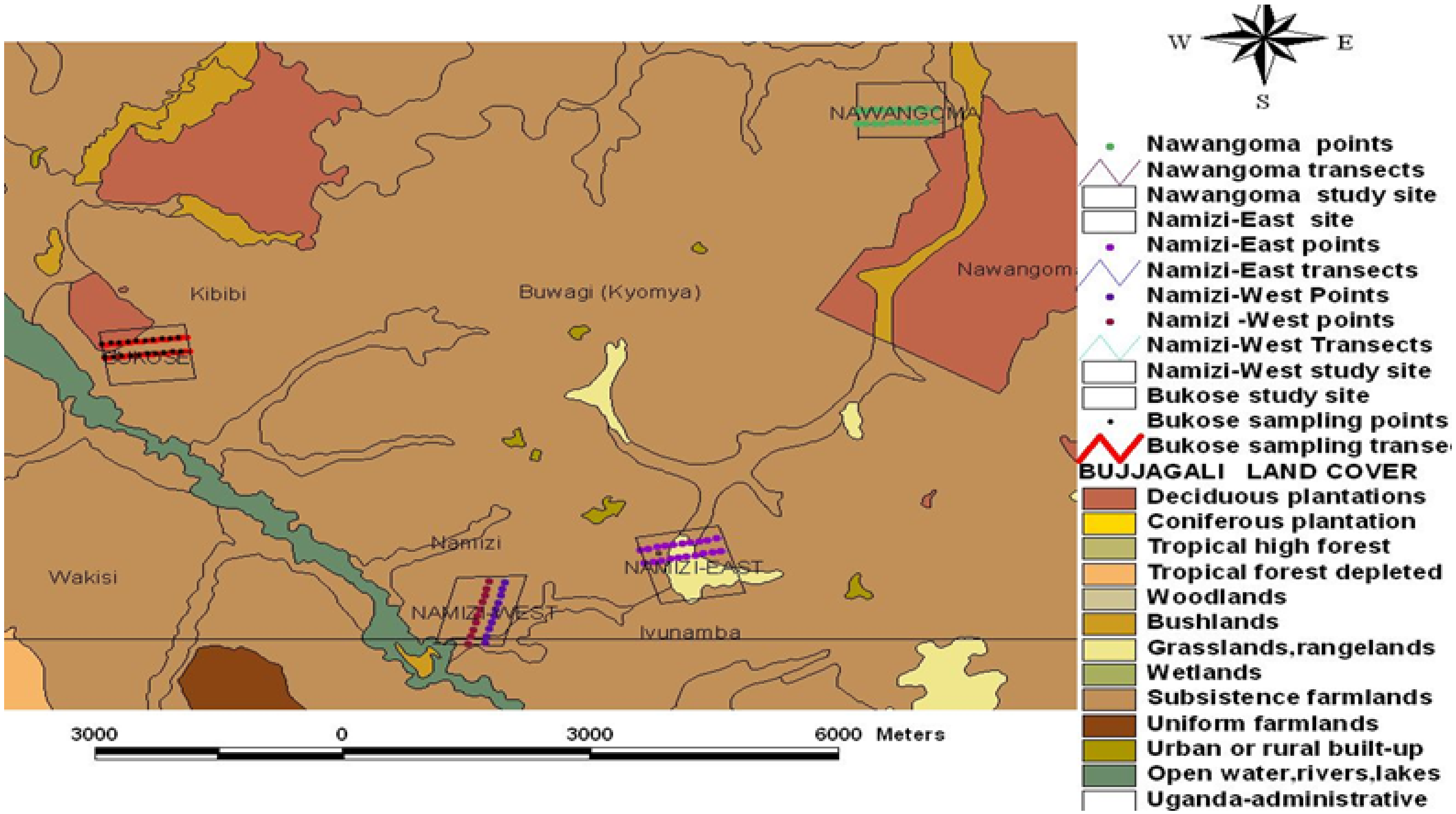

Figure 2. Location of Bukose, Namizi-East, Namizi-West and Nawangona study sites in Jinja district

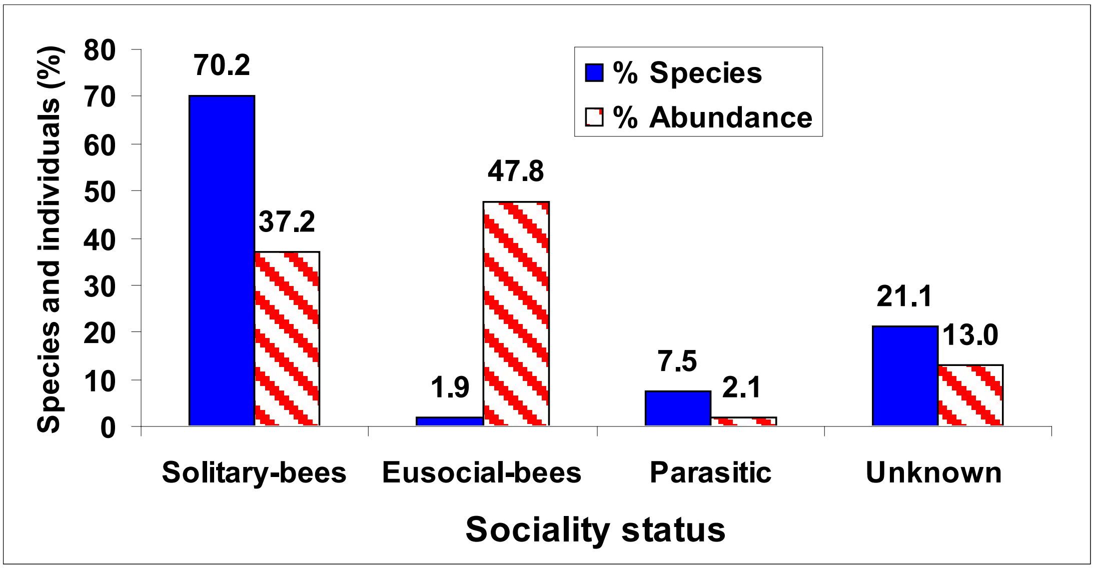

Figure 3. Percent (%) of species and individuals with respect to sociality/breeding strategy of different bee species collected from agricultural landscapes of central Uganda in 2006. *(N for bee species=602; N for bee individuals= 75221)*

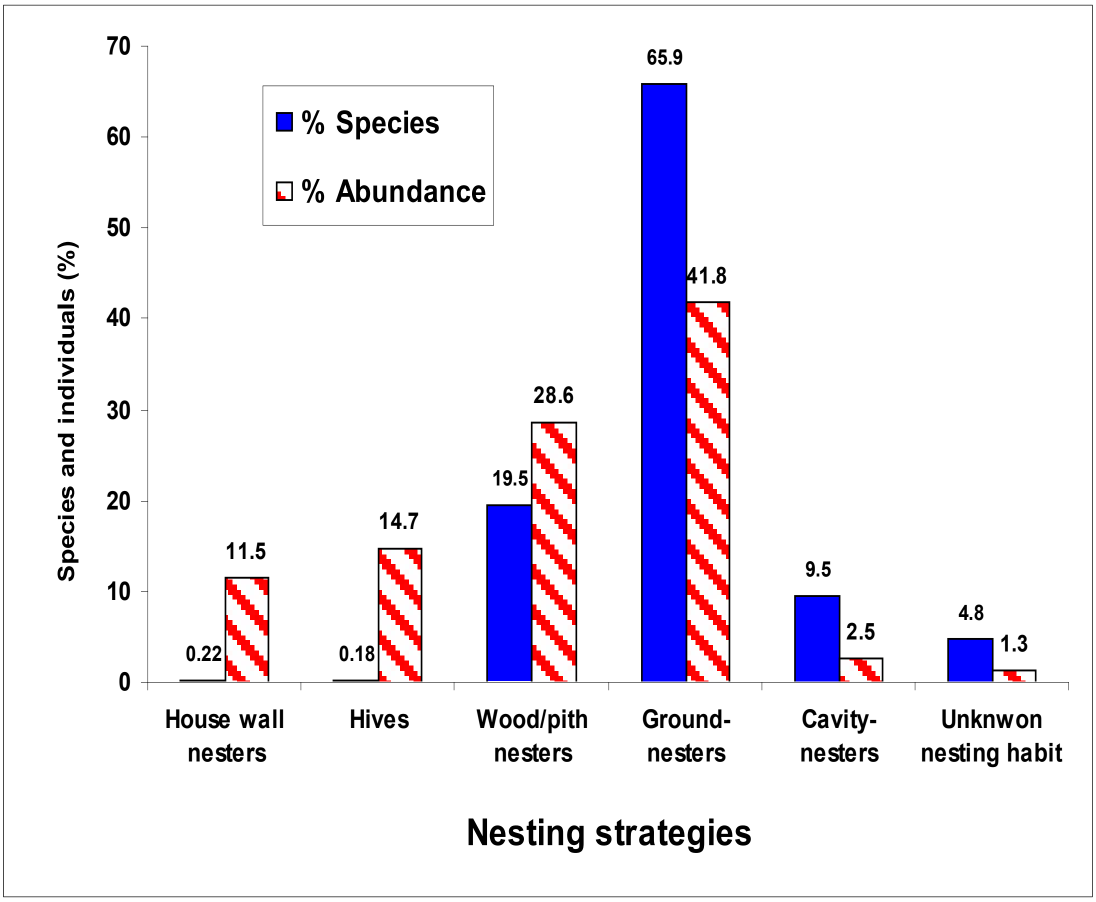

Figure 4. Proportion (%) of species and individuals with respect to nesting strategies of different bee species collected from agricultural landscapes of central Uganda in 2006. *(N for bee species=602; N for bee individuals= 75221)*

avity nesters were third most species-rich compared to house-wall nesters and hive users (honeybees) but the abundance of hive users and that of house wall nesters were greater than that of the cavity nesters (Fig.4). The nesting strategies of 4.8% of the bee species and 1.3% of total individuals encountered were unknown.

3.5. Feeding specialization and tongue length

Bee individuals recorded in farmlands of central Uganda included both oligolectic (characterized by flower constancy) and polylectic bees. Fewer specialist bees (oligolectic) occurred in farmlands of central Uganda compared to generalist bees (polylectic bees) (Fig.5A). Monolectic species were not recorded in this study.

Four tongue-length categories characterized the farmland bee community: long-tongue, short-tongue, and medium-tongue and uncertain tongue length class. There were significant differences among the tongue categories in species-rich (χ^2 3df = 130.559, *P*<0.0001) and abundance (χ^2 3df = 209.943, *P*<0.0001). The most species-rich and abundant category was long-tongued bees. Medium-tongued- bee group was the least species rich comprised only 1.9% of total bee individuals recorded (Fig.5B).

3.6. Body size (length)

Significant differences in bee species richness (χ^2-test: χ^2 5df = 45.06, *P*<0.0001) and in bee abundances (χ^2 5df = 217.7, *P*<0.0001) among the 6 bee-body length classes were detected. Medium sized bees formed the richest class followed by small, very small and large bees (Fig-6). Contrastingly, very small-bodied bees (34.3% of individuals) were the most abundant category followed by medium sized and small-sized classes (Fig. 6).

3.7. Species constancy and Indicator species of bee assemblages

The results of the analysis of the species constancy indicated that 16 species could be classified as highly constant species (C>70-100%).Fewer species (14 species) were found to be constant species (C>50-70%).The rest of the species encountered (622 species) were considered as occasional or accidental species (species with constancy values of C=0-49%) visiting or inhabiting coffee-banana systems of central Uganda (Table-1). *Apis mellifera adansonii* had maximum species constancy values (100%), indicating that the species occurred with maximum prevalence in all farmland locations/sites (Table.1).

Overall 17 bee species scored significantly (P<0.05, df=4, χ^2-test) high indicative values (*IndVal*>12%; Table.1). The "indicator species" were considered as the most ecologically important species and characteristic of bee assemblages inhabiting coffee-banana system(a system characterized by high level of habitat disturbance due to farming activities) (Table.1).These characteristic species had also high constancy value (>50%).

These 17 species are also the most common bee species among wild bees; they are also very plastic, both in respect of their range forage plants (polylectic), and in selection of nesting sites (they can nest in various substrates (in wooden materials, human buildings, underground soils, hollow dry stems, etc). However, these species are characterized by unstable abundances over different seasons of the year (occurring with high abundance in rainy seasons and represented by few individuals in dry seasons).These few species that dominated the bee fauna and that were well-represented in different study sites were also the most frequent species characterized by a high constancy. Thus they seem having lower environmental requirements (they are not specialized) because they were also found on more than 50% of studied sites; so they can be regarded as characteristic species to be considered for further monitoring program in farmlands of central Uganda.

4. Discussion

4.1. Patterns of indicator species

In this study, 17 species were identified as indicator species of farmland bee communities. Compared to the large number of bee species recorded in this study, only few species could occur as "characteristics" of farmlands habitats in Uganda for years 2006-2008 when the study was carried out. Although few species occurred as indicator species, this information may be of relevance to long-term ecological monitoring programs of species, populations and activities particularly when interested at detecting and predicting changes in the composition and structure of the entire bee community from the landscape/habitat. Based on predictions of the entire bee community, it is believed that sound measures for the protection of pollinators can be outlined in relationship to mitigation of potential drivers of changes in species occurrence.

A high diversity of bees was recorded in farmlands of central Uganda. Similarly, Gikungu (2006) highlighted a high diversity of bees in an agricultural matrix in Kakamega region (western of Kenya). In both cases (Uganda and Kenya), a few numbers of species (<20 species) are common species were recorded. These can be used as indicator species of the entire bee communities when interested at monitoring the status of bee assemblages in rural landscapes in East Africa.

For the case of central Uganda, monitoring 17 species may help in the future to provide an indication on of trends and patterns in the most common and constant species. The 17 species appeared to be relevant in the coffee-banana farming system of central Uganda. However, it is possible that a high number of species may be recorded in other sub-Sahara African countries.

In the future, a simple guide of identification of these indicator species should be produced and distributed to bee biodiversity planners in order to facilitate their work and alert regularly other stakeholders on probable future decline of bees while highlighting the drivers and mitigation measures.

4.2. Patterns of functional traits and ecological groups

The relevance of identifying bee functional traits composition (dominant traits and functional diversity) is that traits can be used to predict the functional responses of bee communities to local, regional and global environmental changes in habitats of conservation importance in different regions with distinct disturbance regimes (Moretti *et al.*, 2009). Functional traits can be used as indicators of pollinator biodiversity response to land-use changes across ecosystems and climatic regions.

The exploration of different functional traits of bees can be also conducted to identify functional groups that are probably delivering pollination services of high quality to crops and wild plants in farmland habitats such as the banana-coffee system in Uganda.

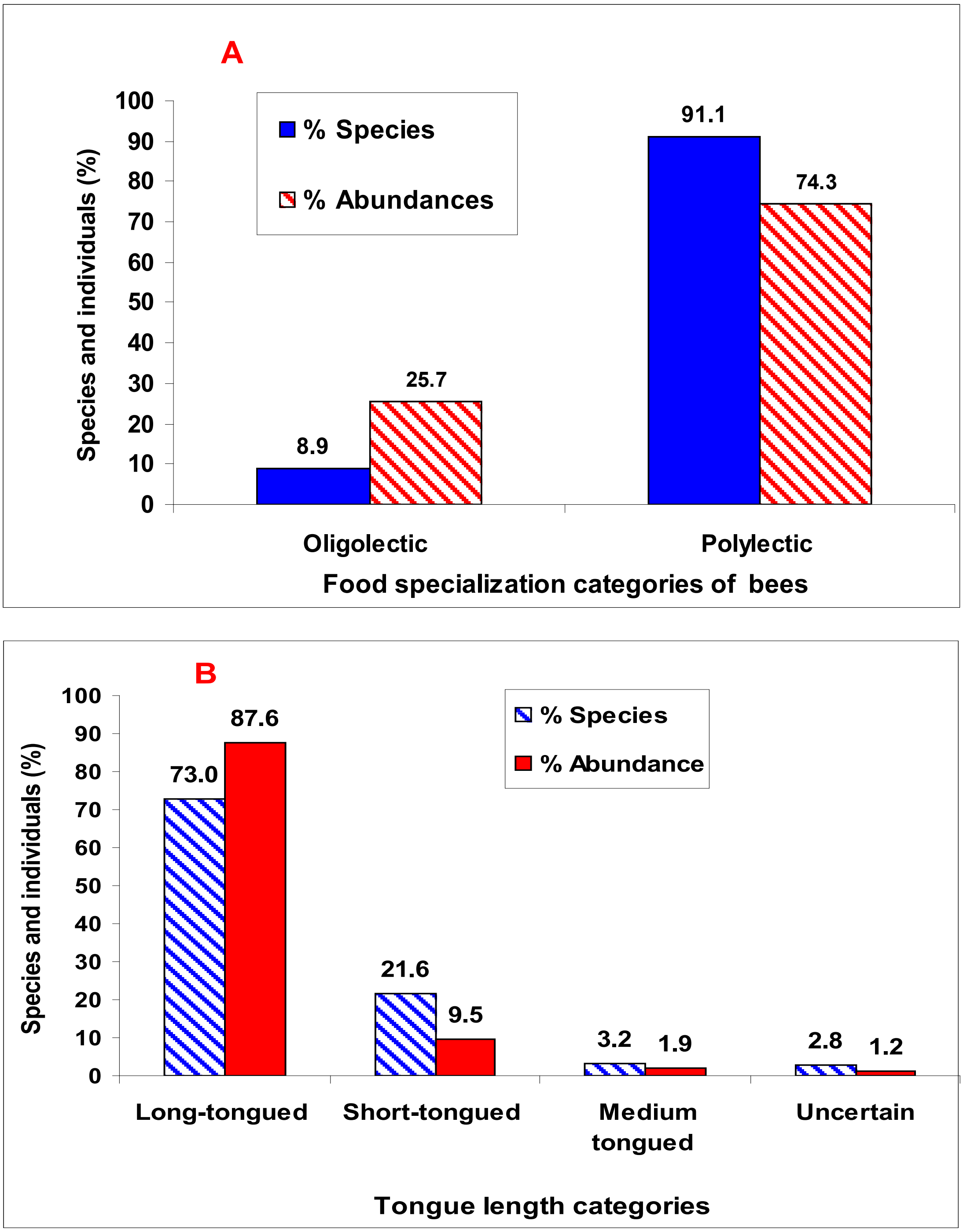

Figure 5. Percentage (%) of bee species and individuals captured in agricultural landscapes of central Uganda with respect to (A) floral specificity (oligolectic: pollen-gather specialists, polylectic: pollen-gather generalists) and (B) proboscis or tongue length (feeding strategy= feeding ability index) of bees collected in farmlands of central Uganda in 2006. N for bee species=602; N for bee individuals= 75221.

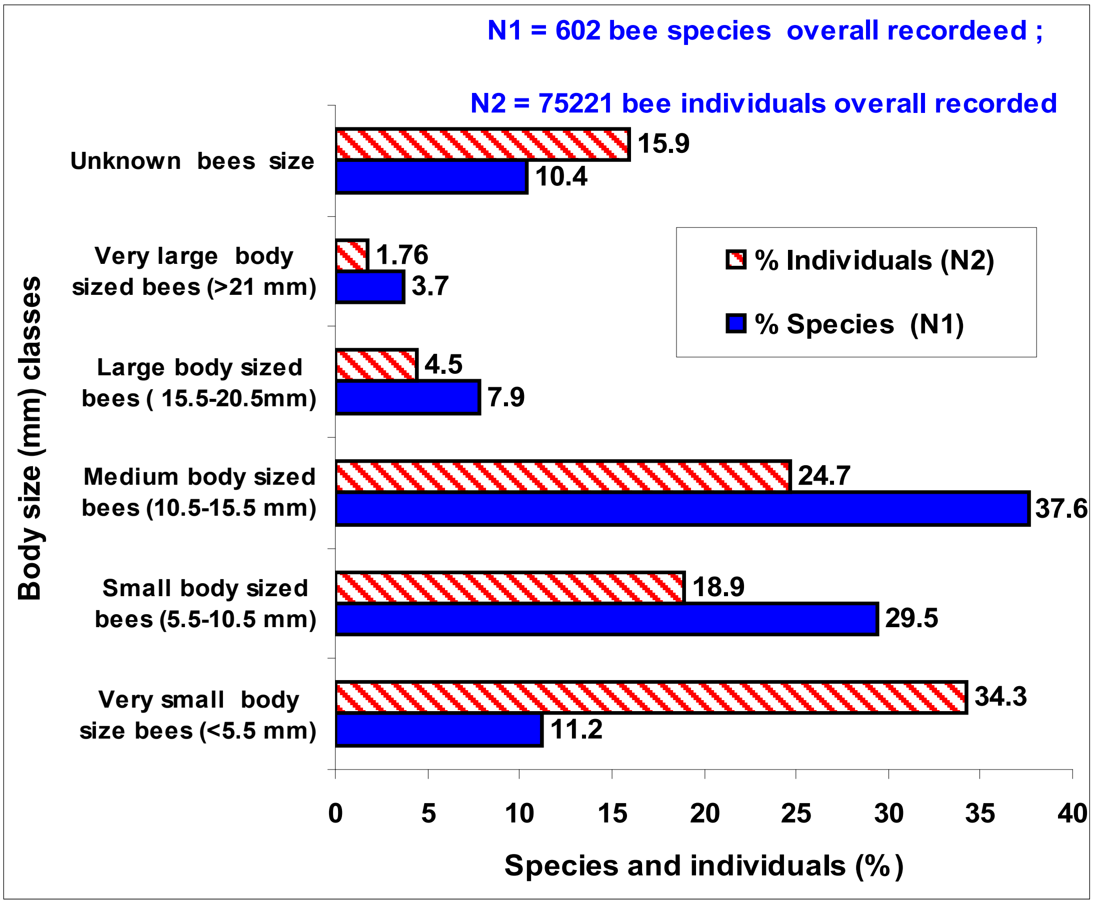

Figure 6. Percentage of bee species and individuals in different body size classes captured on agricultural landscapes of central Uganda in 2006.

Ecological grouping of different bee species can also generally be conducted to identify functional groups of bees from farmlands that are likely to be more susceptible (or resist, tolerate or adapt) to various climatic, pressures and anthropogenic changes; as the degree of susceptibility vary from a group to another one.

Overall, it has been shown that knowledge of range of life-history and ecological traits of bee communities can be used to predict bee responses to a change in a variety of environmental disturbance types (agriculture intensification, cropping intensification, proportion of semi-natural habitats, distance to natural habitats, pesticide use, distance to natural habitats or habitat isolation, climatic factors, farm management system, grazing intensity, fire regimes, deforestation rate, etc) or drivers from a given farm-landscape (Williams et *al.*, 2010).For example, species that nest above ground, and species that use previously established nest cavities may be more sensitive to various disturbance regimes than species that nest in the ground or excavate their own nests.

In this study, it was found that the majority of bee species and individuals recorded were solitary, long-tongued, polylectic and of small to medium body sizes. From 181 bee species recorded in total during a faunistic survey conducted in "Cerradão" area in Brazil, 30.8% and 69.2% of them were classified as sociable and as solitary respectively (d´Avila and Marchini, 2008). Similarly to observation made in farmland of central Uganda where it was found that farmland bee fauna was dominated by long-tongued bees followed by short tongued bees species; in coastal sand dune of northeastern of Brazil, very long to long-tongued (>7-12mm) solitary bee species (best represented by Anthophorinae) were the dominant bee categories followed by bees of intermediate glossa (3-6.9mm) and by the category of short tongued bees or bees with short bilobate (<3mm) from Apinae, Halictidae, Megachilidae and Colletidae bees (Viana and Kleinert,2005).

Worldwide, relatively small proportions (~6%) of all bees are eusocial bees (Michener, 2007). Even in the coffee-banana farming system of central Uganda, only 3.25% of bee species occur as eusocial bee species. Globally, an estimated 20% of all bee species are cleptoparasites (cuckoo parasites) that lay their eggs in the nests of other bees (Michener, 2007). Parasitic bee species comprised <10 % (64 species) of the total bee species that visit flowers of various crop/plant species but do not collect pollen in central Uganda. Cleptoparasitic species are among the poorly known bees in the world and in Uganda. Less than 10% of species were identified as cleptoparastic bees in farmlands of central Uganda.

Among non-parasitic species recorded from central Uganda, more than 65% of them were found to be ground-nesting and approximately 20% were wood-nesting bee species. Nesting-sites preference of different farmland bee species differed between the study sites, and the results suggested that differentiation in the distribution of farmland bee fauna from central Uganda is mostly related to food resources availability and to differences in farming practices and regimes (Munyuli, 2010).

Table-1: Sites of permanent occurrence (SPO), species constancy (SC) and species indicative value (IDV) of bee community, from the coffee-banana-farmlands of central Uganda during year **2006.**

Bee species	SPO	SC(%)	MIDV(%)	Bee species	SPO	SC(%)	MIDV(%)	Bee species	SPO	SC(%)	MIDV(%)
Apis mellifera adansonii	26	100	96.25 *	*Meliponula bocandei*	4	15.4	0.17 ns	*Pachymelus sp.*	2	7.9	0.034 ns
Hypotrigona gribodoi	22	84.6	81.42 **	*Nomia scutellaris*	7	26.9	0.28 ns	*Pasites jenseni*	2	7.7	0.033 ns
Axestotrigona ferruginea	22	84.6	70.92 **	*Patellapis albofasciata*	8	30.8	0.03 ns	*Liotrigona sp.*	4	15.4	0.028 ns
Lasioglossum sp.1	17	65.4	44.51 **	*Ceratina rufigastra*	15	57.7	0.10 ns	*Ctenoplectra* sp.2	10	38.5	0.024 ns
Halictus sp.1	26	100	42.71 **	*Pachyanthidium bicolor*	9	34.6	0.03 ns	*Coelioxys torridula*	4	15.4	0.023 ns
Apis mellifera scutellata	22	84.6	40.19 **	*Ceratina lineola*	20	76.9	2.51 ns	*Cleptotrigona cubiceps*	6	23.1	0.023 ns
Lipotriches sp.1	25	96.2	23.78 *	*Patellapis (Zonalictus)* sp.1	13	50.0	0.08 ns	*Tetraloniella sp.*	3	11.5	0.020 ns
Lasioglossum kampalense	24	92.3	17.92 *	*Lasioglossum(Ctenonomia) duponti*	6	23.1	0.02 ns	*Scrapter nitidus*	8	30.8	0.020 ns
Ceratina sp.1	22	84.6	14.39 *	*Megachile gratiosa*	7	26.9	0.02 ns	*Colletes* sp.1	4	15.4	0.020 ns
Braunsapis angolensis	21	80.8	12.87 *	*Melitturga penirithorum*	12	46.2	1.29 ns	*Lithurge sp.*	3	11.5	0.019 ns
Heriades sp.1	23	88.5	12.49 *	*Hylaeus braunsi*	11	42.3	0.10 ns	*Lasioglossum* sp.3	4	15.4	0.018 ns
Allodapula sp.	22	84.6	8.19 ns	*Braunsapis* sp.	2	7.7	0.10 ns	*Lipotriches dominarum*	9	34.6	0.018 ns
Halictus jucundus	24	92.3	17.51 *	*Halictus frontalis*	8	30.8	0.09 ns	*Amegilla acraensis*	7	26.9	0.018 ns
Allodape sp.	23	88.5	14.66 *	*Compsomelissa nigrinervis*	16	61.5	1.49 ns	*Anthidium strigatum*	2	7.7	0.016 ns
Lasioglossum sp.2	23	88.5	13.85 *	*Nomia granulata*	4	15.4	0.09 ns	*Lasioglossum* sp.4	7	26.9	0.015 ns
Meliturgula sp.	22	84.6	2.57 ns	*Pachymelus* sp.1	7	26.9	1.85 ns	*Dactylurina schmidti*	6	23.1	0.015 ns
Plebeina hildebrandti	8	30.8	2.19 ns	*Halictus* sp.2	21	80.8	0.43 ns	*Melitta arrogans*	2	7.7	0.015 ns
Ctenoplectra sp.1	13	50.0	1.52 ns	*Anthophora sp.*	11	42.3	0.07 ns	*Ctenoplectra politula*	4	15.4	0.015 ns
Apotrigona nebulata	20	76.9	15.54 *	*Scrapter flavostictus*	2	7.7	0.07 ns	*Megachile* sp.2	7	26.9	0.014 ns
Ceratina sp.2	15	57.7	1.42 ns	*Othinosmia globicola*	12	46.2	0.06 ns	*Xylocopa inconstans*	18	69.2	0.012 ns
Lipotriches sp.1	12	46.2	1.12 ns	*Halterpis nigrinervis*	11	42.3	0.06 ns	*Andrena* sp.	4	15.4	0.012 ns
Plebeilla lendliana	9	34.6	1.12 ns	*Patellapis* sp.1	3	11.5	0.05 ns	*Hylaeus ugandicus*	5	19.2	0.011 ns
Nomia atripes	24	92.3	13.13 *	*Patellapis dispostia*	2	7.7	0.05 ns	*Megachile fimbriata*	2	7.7	0.011 ns
Ceratina tanganyicensis	15	57.7	12.99 *	*Braunsapis fascialis*	7	26.9	0.05 ns	*Braunsapis bouyssoui*	5	19.2	0.011 ns
Allodapula acutigera	18	69.0	16.89 *	*Ctenoplectra polita*	9	34.6	0.04 ns	*Thyreus* sp.	2	7.7	0.006 ns
Xylocopa caffra	17	65.4	0.35 ns	*Coelioxys natalensis*	6	23.1	0.03 ns	*Hoplitis sp.*	3	11.5	0.006 ns
Lipotriches sp.3	14	53.8	0.23 ns	*Pseudanthidium sp.*	10	38.5	0.03 ns	*Tetralonia (Eucara) sp.*	2	7.7	0.007 ns

Significant:* =P<0.05; ** =P<0.001; ns=not significant, $\chi2$-test (n=5). Chi-square test done based on IDV values of each species in the five rounds of data collection.SPO= represent the number of sites where the species was frequently recorded each round of data collection.SC (%) = represent the proportional number of sites where a species occur permanently in 26 farmland sites studied. MIDV(%) = is the mean species indicative value=Relative abundance X Relative frequency X 100 of the species in sites where it occurs permanently.

The response of different functional groups of bees to farming practices, land-use and environmental variables are presented in a different manuscript submitted elsewhere.

Few oligolectic species were recorded in this study and this was expected since the study was conducted in disturbed habitats (farmlands) compared to less disturbed habitats (where oligolectic foraging strategies are expected to dominate given higher floral diversity) (Schlindwein, 1998).

In central Uganda, polylectic bee species (generalist foragers :> 90% of species recorded) dominated in farmlands of central Uganda. Similarly, the dominance of polylectic bee species was recently reported in USA (Norden, 2008) and in Poland (Moroń *et al.*, 2008). However, findings from this study do not concur with the results of Minckley (2008) who stated that areas where bee species richness is greatest have a greater proportion of oligolectic bee species compared to polylectic bee species. On the contrast, farmlands of central Uganda were found to be species-rich with dominance of polylectic bee species. Oligolectic bees are rarer than diet generalists (Grundel *et al.*, 2010); they are generally well associated with linear and non linear semi-natural habitat and natural habitat features; hence their populations may be especially affected by degradation of natural and semi-natural habitats in the farm landscape.

Oligolecty is a significant predictor of bee species' decline over time in northwestern Europe, and of sensitivity to fragmentation in desert ecosystems. For example, among European *Bombus*, all of which are polylectic, species with more specialized diets show greater population declines over time. Presumably the risk of decline is heightened by being more reliant on a smaller number of food sources. In addition, oligolectic bees have more genetically isolated populations and lower genetic diversity which further increases their susceptibility to decline (Winfree, personal communication). As part of the dietary specialization, oligolectic species are able to time their emergence to the bloom of their host plant species better than polylectic species. Because both polylectic and oligolectic bees play distinct important roles in the maintenance of wild and cultivated plant species in Sub-Sahara Africa (Munyuli, 2010); hence they are irreplaceable by generalist bees in some countries in Sub-Sahara Africa and in neotropical regions like in Brazil. The conservation of oligolectic in landscape may therefore appear imperative (Buschini *et al.*, 2009) particularly in sites where they are the leading pollinators of some plants and crops.

In farmlands of central Uganda, two bee body size classes dominated the bee community: the class of 5-10mm followed by that of 10-15mm body size. Similarly, in an agricultural landscape in the state of São Paulo (Brazil), it was observed that 5-10mm (49%) body size and 10-15mm (35%) body size classes dominated the farmland bee communities (Souza and Campos, 2008**).** Generally, there is a strong linkage between bee body size (mm) and their foraging distance and bee foraging distance affects agricultural production (Greenleaf *et al.*, 2007). Foraging distance determines the spatial scale at which different group of wild bees can provide pollination services to crops. Animal pollination is required to produce 30% of the world foods (Klein *et al.*, 2007; Greenleaf *et al.*, 2007). It can be expected that functional groups of wild bees that pollinate crops nest in natural habitats and forage on crops within their daily travel distance that is related to their body size (Greenleaf *et al.*, 2007).

In addition larger species travel over larger distances (>2000-3000m) than do smaller species (250-1000m) for the spatial exploitation of food resources available at different scales of the landscape (Westphal *et al.*, 2008). Although small and medium sized bee species dominated central Uganda farmland bee community; unfortunately, the majority of crop species grown are pollinated by tiny, small and medium bees (Munyuli, 2011c). Hence, the need of growing pollinator-dependent crop species in the foraging range of their pollinators, or alternatively managing conservation of habitats nearby farms to attract effective pollinators to nest in the vicinity of fields.

Much as it is not always easy to predict extinction risk and sensitivity to disturbance of different bee species based on body size data; landscape-wide availability of different resources (mass flowering crops and semi-natural habitats) should be considered by farms and landscape managers to maintain a variety of functional groups of bees in the proximity of cultivated crop species.

5. Conclusion and Recommendations

In this study, it was found that farmlands support a rich bee fauna comprising of over 600 species belonging to several tribes, families, genera and functional guilds. The study highlighted species that should be currently characterize the bee fauna pollinating crops in central Uganda and could be monitored to detect potential decline in bee species in the farmland of Uganda when aiming at preventing total loss of species due to anthropogenic factors. Strategies to prevent future decline (driven by anthropogenic and climate change factors) in species richness and in different functional traits are therefore outlined below. Making farmland more suitable for different functional groups of bees can benefits both agriculture and nature conservation (Carvalheiro *et al.*, 2010). In Sub-Sahara and in East Africa, there exist few studies of bee communities in rural landscapes (Gikungu, 2006; Kajobe, 2008).

This study focused on the characterization of agricultural bee fauna (functional groups) in central Uganda. This is the first solid contribution to the study of bee faunas from farmlands in Uganda. There has been no previous extensive study highlighting the diversity of bee functional traits occurring in the region. It is therefore believed that this study will form a basis for further studies in other countries of Sub-Sahara Africa with similar environmental characteristics in order to develop and set proper monitoring and conservation strategies of pollination services delivered by functionally diverse bee communities.

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