Floral Resources Sustaining African Meliponine Bee Species (Hymenoptera: Meliponini) in a Fragile Habitat of Kenya

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Abstract

A vast majority of insects visit flowers for food, generally termed as floral rewards. Detailed insights on flowering phenology of plants could give a hint of habitat status and the extent to which such landscapes could support insect pollinators to render both direct and indirect ecosystem services. This study monitored flowering plants which could potentially provide both pollen and nectar sources to four African meliponine bee species (Apidae: Meliponini) naturally occurring in six diverse habitat gradients of the eastern arc mountains (Taita hills) of Kenya. Blooming sequences of identified flowering plants overlapped across seasons with approximately 80 different plant species belonging to 34 families recorded, with the highest proportions from Fabaceae and Asteraceae families dominating flowering plants that were visited (67% of the visits). A flowering calendar is presented to indicate the phenological pattern of all identified floral resources. Hypotrigona gribodoi being the most abundant species had the highest visitation rates on plants belonging to Fabaceae and Asteraceae families, followed by Meliponula ferruginea (black), Plebeina hildebrandti and Hypotrigona ruspolii. This indicates that such fragile habitat could invariably sustain nutritional requirements essential for the survival of insect pollinators such as native meliponine bee species, though bee abundance at flowers did not significantly correlate to food availability (expressed by flowering plant richness).

Keywords: floral sources, Afro- tropical meliponine bees, forest fragments, fragile habitats

1. Introduction

Pollinators are known to play key roles in delivering various forms of ecosystem services such as pollination and seed dispersal which benefits most plant populations (Ritchie, 1999). They also to a certain degree predict the community structure of plants in most habitats (Steffan-Dewenter and Tschamtke, 2002). A vast majority of angiosperms, including agricultural crops are insect pollinated (Kevan, 1999) with almost 25% of tropical crops depending mostly on bees for pollination (Heard, 1999). Insect groups such as moths, wasps, bees, beetles, butterflies and bats are essential for providing effective pollination of both cultivated and uncultivated plants (Free, 1993; Roubik, 1995). Symbiotic relationships are known to exist in plant communities between flowering plants and random visiting insects. These food resources (pollen and nectar) usually mediate mutualisms between flowers and potential visitors. As such, flowering plants benefit from the pollinator by being pollinated while the insect pollinator obtains floral rewards in return. Floral rewards are majorly of two forms: nectar rewards (as a source of sugar for energy) and pollen rewards (as a protein source for development). Pollen is a vital food and source of protein for a majority of insects, it contains essential amino acids and lipids which are known to be an essential resource for foraging bees and a vital component in plant reproduction and provides dual function interchangeably (Agostini et al., 2014), while nectar is a simple sugar solution consisting of a



variety of compounds suspended in aqueous solution (glucose, sucrose and fructose) to even more complex sugar solutions or mixtures of sugars, vitamins, lipids and other chemicals (Kevan, 1999).

The most abundant bees in the tropics are members of the diverse group of meliponine bees (Apidae, *Meliponini*) (Hubbell and Johnson, 1975). African meliponine bees (Hymenoptera: Apidae) belong to the tribe *Meliponini* of which more than 19 species are native to Africa (Eardley *et al.*, 2004), 14 of which are found in Kenya (Nkoba, 2012). Typically, a meliponine bee colony contains < 20,000 individuals, comprising of a single fertile queen, drones and workers. They pollinate > 90 crop species worldwide (Slaa *et al.*, 2006; Abramson *et al.*, 2007). They are important indicators of biodiversity as they have co-evolutionary relationships with plants and therefore their services are inevitable for the maintenance of the life cycles of many plant species (Sasidharan and Kunhikannan, 2007). It is widely accepted that habitat loss has negative effects on both flora and fauna biodiversity and that the amount of suitable habitat in any landscape influences species distribution of any organism(Frankie *et al.*, 1998; Wettstein and Schmid, 1999; Rickets *et al.*, 2008; Steffan-Dewanter and Tscharntke, 2000) and its abundance (Hargis *et al.*, 1999; Best *et al.*, 2001; Gibbs and Santon., 2001; Schuepp *et al.*, 2011).

The structure of bee populations is closely related to the floral communities they forage upon with several other key drivers such as floral diversity, floral abundance (Frankie *et al.*, 1998) and seasonal availability of these resources (Ricketts *et al.*, 2008) shaping their distribution and abundance (Gathmann and Tscharntke, 2002;Tepedino and Stanton, 1981). While foraged rewards provided by floral communities are generally accepted as the primary determinant of pollinator community structure(Thorp *et al.*, 1994), there is an increasing body of evidence suggesting that the extent to which a habitat has been disturbed may also play an important role for the occurrence of pollinators within any habitat (Westphal *et al.*, 2008). Previous studies have found that floral diversity to a certain degree can explain the degree of nest abundance, which is positively impacted by gradual improvements of both food and nesting resource availability in more simplified habitats (Roschewitz *et al.*, 2005; Tscharntke *et al.*, 2005).

Habitat fragmentation is one of the most evident forms of environmental degradation and a leading threat to pollinator survival and diversity. Increasing isolation from naturally ideal habitats can be associated with either a decline or an increase in species composition, richness and diversity (Ewers and Didham, 2006; Jauker *et al.*, 2009) which is yet to be determined in fragile habitats such as is found within Taita hills, a very likely place to suffer both plant and animal extinction due to drastic loss of its habitat. There is scarce information on the utilization of floral resources by meliponini colonies, particularly in vulnerable habitats such as taita hills. Meliponine bee species present immense pollination potential in relation to many native and cultivated plant species (Kevan, 1999). Information on resource diversity used, are essential in managing greenhouse and culture field colonies which makes it possible to determine the foraging area range and resource pattern (Ramalho *et al.*, 1991). The aim of this study was to describe the trophic niche breadth of Melipona bee species, as well as the kind of food resource that foragers of the studied species gather from flowers



visited in selected habitats while associating it with the natural occurrence of feral meliponine bee colonies. Here, we tested the hypothesis that the natural occurrence and abundance of African meliponine bee species is dependent on the available floral resources offering rewards at any given time. Additionally, we compared the abundance of such flowering plants to the levels of habitat disturbance in order to determine if this factor plays a vital role in predicting the natural occurrence of these bee species. These results are discussed in the context of understanding the influence of fragile habitats on meliponine bee's abundance, flower visitation, and overlap in use of pollen and nectar resources as current efforts to domesticate them are ongoing.

2. Materials and Methods

2.1 Study Site

Taita hills is the northernmost isolate of the Eastern Arc mountains (Pellikka *et al.*, 2013) and categorized into both highlands and lowlands respectively. The area has the status of a global biodiversity hot-spot (Adriaensen *et al.*, 2006). Taita hills lies in south- eastern Kenya at $03^{\circ}20$ S, $38^{\circ}15$ E, about 150km inland from the coast and covering an area of about 250km² (Brooks *et al.*, 1998) (**Fig 1**). The hills are isolated from other mountainous areas to the south-east (Shimba Hills), south (Usambara Mountains), south-west (Mt Kilimanjaro), west (Ngulia and Chyulu Hills) and north-west (Kenyan highlands) by the vast plains of Tsavo (Maeda *et al.*, 2010). Annual rainfall is received during two major seasons (March- May, September – October) and varies between 480 - 1200mm in the highlands (Reitalu *et al.*, 2012), but much less rain (~400mm) received on the surrounding plains of the lowlands (Pellikka *et al.*, 2005).

2.2 Lowlands

The lowlands are characterized by highly dispersed vegetation and fragmented patches of habitats dominated by grassland plains. Three different geographically detached communities (Msau, Mwatate and Mugama) make up a large percentage of the lowlands. Mean rainfall in the lowlands lands ranges around 400mm with annual rainfall peaks in April and November.

Vegetation is characterized by abundant *Commiphora myrrha* deciduous woodlands which are widely dispersed, but a considerable number of other deciduous tree species are persistently reduced to shrubs by extensive grazing and deforestation(Omoro *et al.*, 2010).

Common deciduous trees such as Albizia gummifera, Haplocoelum foliolosum, Comiphora schimperi, Balanites pedicellaris, Tamarindus indica, Sterculia africana, Ficus sycomorus, and Cordia sinensis are mainly found along streams (Pfeifer et al., 2012).

2.3 Highlands

A total of seven forest fragments are found in this region, and characterized by continuous forest landscapes. The highlands are composed of several communal forests which are considered as fertile areas suitable for agriculture; however, a very small area is available for agricultural purposes due to steep slopes and shallow soils occurring at high altitudes. Mwachora forest (03 25'S, 38 22'E) is an indigenous forest habitat situated at an altitude of



1,400 m measuring approximately 2 ha (Wilder *et al.*, 1998) and is regarded as part of remnants of the original afromontane forest, receiving 1700–2400 mm of annual precipitation. Tree species such as *Lobelia gibberoa*, *Phoenix sylvestis*, *Dracaena steudneri* and *Cyathea manniana* are characteristic to this forest. Chawia forest (03 28'S, 38 28'E) is a mixed forest habitat comprising of both indigenous and exotic tree species forming dense and continuous canopies, this forest has the status of being the most disturbed forest fragment out of the seven forest fragments found in Taita hills.

3. Sampling Procedure

3.1 Flowering Phenology and Floral Resource Abundance

Flowering phenology was monitored within each study site (25ha), twenty (20) linear transects measuring 250m x 20m each were established using a GPS to mark coordinates with relation to each habitat type. All flowering plants were sampled using the conventional belt transect method (direct observation of blooming flowers via visual census) (Potts et al., 2005). The time duration in which a relatively large number of flowers were in anthesis were regarded as the flowering peaks (Newstrom et al., 1994). The blooming duration of most flowering plant species were followed on a daily basis throughout the study period from May-December, 2014. Data on the type of flower reward obtained over months were recorded. Flowering stages in each species were classified into four groups: initial stage (when plants have started producing flower buds (Stage A); peak stage (when plants have opened flowers (stage B); late stage (when flowers retain their bloom after peak flowering (stage C) and (terminal stage) in which most flowers have passed blooming (stage D). For the purpose of this study, blooming periods have been defined as the time from actual senescence to the end of such bloom for every identified plant (stages A-D). Floral resources were expressed quantitatively based on the number of overlapping flowering species across both seasons (May-December), because major plant species flowering during this period largely represent the persistent plants in full bloom at any sampling period. To test the validity of using the number of overlapping flowering species as an index of floral resource level, the relationship between the number of flowering species and floral density was measured in all transects that were sampled from the lowlands (< 900m elevation) to the highlands (<1,400m elevation). Flowering plant species were counted on a daily basis throughout this period and floral density estimations were made based on the average number of open flowers within every measured transect. Samples of all flowering plants in the study area were collected and identified at the Kenyan museum botanical section.

3.2 Meliponine Bee Monitoring and Visitation Rates

Sampling of bees to determine fauna diversity, floral resource use and overlap was carried out using net-trapping and visual observations of bees at flowers which provided the main sources of data, feral nests of meliponine bee species were searched for within each linear transect from 8.00am- 17:00pm every day for possible nesting sites, by walking at a constant speed along each measured transect. The bees were sought on all flowering plants at reachable heights. When one was spotted, it was caught with an entomological net. The floral resource (pollen or nectar) collected by the bee was identified by observing pollen in the



corbicula. Visit frequency was recorded by counting the number of times foragers of any Meliponini bee species were seen on plants of each visited. A representative sample of approximately 5 bees was taken from each feral nest and deposited in the biosystematics unit of the international center for insect physiology and ecology (*icipe*), duduville campus (1° 17'S, 36°49'E), Nairobi Kenya. Observations were not conducted on rainy or cloudy days. Only data recorded in the measured transects were used for analysis in this study because the focus of the research is to monitor plant phenology and the occurrence of meliponine bee species.

4. Data Analysis

Flowering phenology of individual plant species were compared between habitats (fragmented and unfragmented) while the differences in resource availability (richness of flowering plants), and frequency of visits were evaluated by the chi-square test using the statistical software (Sigma plot v11.0). (Systat Software, San Jose CA, 2011). Spearman's correlation was used to determine if number of visits and richness of flowering plants correlated. Richness of the actual plant-species trophic niches was determined by recording both the number of visited and non-visited flowering species. Trophic niche breadth was calculated by using the Shannon-Wiener Diversity Index (Pielou, 1969). Nest abundance of feral colonies was compared in both sites by carrying out logarithmic transformation on the data and further subjecting it to a Pearson's correlation test throughout the entire sampling period using the statistical software Sigma plot V 11.0, (Systat Software, San Jose CA, 2011).





Figure 1. Map of Taita hills forests and surrounding areas.

5. Results

5.1 Flowering Phenology

A total of 80 plant species belonging to 34 families were found to be constantly flowering in both sites, with plants of the *Asteraceae* and *Fabaceae* families forming bulk of this proportion (80%) (**Table1**). Flowering commenced earlier in the lowlands (Msau, Mwatate and Mugama) at an altitude of < 900m than in the highlands (Mwachora forest, Chawia forest and Kisheyni) standing at an altitude peaking at 1,800m. Major periods (stages A-C) of flowering plants sampled in the lowlands lasted approximately ~240 days compared to the highlands which had a flowering period of ~ 190 days. All four species visited 54 species (48%) from 8 families. Thirty-six % of 192 visits were to twelve species of *Asteraceae* and ten species of *Fabaceae*. *Fabaceae* (40%) and *Asteraceae* (33%) were the most visited families. However, we found a high variation in the number of flowering plants belonging to both families during the study period ($\chi 2 = 67$; df = 17; P < 0.001). The highest numbers of flowering species were observed to bloom at the commencement of the short rain months



(September) (Fig. 2a). 78% of *H.gribodoi* bee species visits were to ten species of *Malvaceae*. Vernonia species and Bidens pilosa were the most visited species of Asteraceae and Fabaceae visited by Meliponula ferruginea (black) and Plebeina hildebrandti respectively. Peak flowering period expressed as flowering overlap of more than half of the identified plant species, occurred from May in the lowlands and sharply peaking in September, however low peak periods were observed from May - June in the highlands with further declines in the month of October (Fig 2a). During the monthly sampling of feral bee colonies, approximately three colonies could be found naturally occurring in each sampled transect of the lowlands while an estimated one colony would naturally occur in each habitat of the highlands. A total of 147 colonies was recorded, which comprises of four species namely; Hypotrigona gribodoi, Hypotrigona ruspolii, Plebeina hildebrandti and Meliponula *ferruginea* (black). The number of visited species significantly changed across both habitats during the study period ($\chi 2 = 92$; df = 17; P < 0.001). However, no correlation was found between monthly richness of flowering and visited plants. The Asteraceae, Malvaceae, Fabaceae, Meliaceae and Apocynaceae species were the main pollen sources, accounting for 32% of 71 visits. But the main floral resource collected was nectar, accounting for 66% of 121 visits, while pollen collection accounted for only 34%. (Table 1).



Figure 2a. Flowering abundance across months, comprising of the rainy and dry seasons.





Figure 2b. Mean nests abundance of meliponine bee colonies across two habitat types.

Plant species	Family	Form	Nectar source	Pollen source	High lands	Low lands	May	June	July	Aug	Sep	Oct	Nov	Dec
Helianthus annus	Asteraceae	Shrub					A-D							
Calendula spp	Asteraceae	Shrub					A-D							
Brideria micrantha	Phyllanthaceae	Shrub					A-D							
Bidens pilosa	Asteraceae	herb					A,B	A,B	В, С	С	C,D	D	D	
Vernonia brachycalyx	Asteraceae	Shrub					A	В						
Vernonia gamalensis	Asteraceae	Shrub							А	В	C-D			
Rhus natallensis	Anacardiaceace	Shrub					A-D				A-D			
Persea americana	Lauraceae	Tree					А	С						
Grewia bicolor	Malvaceae	Shrub					A-D							
Tamarindus indica	Fabaceae	Tree					A	В	С					
Carica papaya	Caricaceae	Tree					A-D							
Cajanus cajan	Fabaceae	Legume					A-D		A-D					
Lantana	Verbenaceae	Shrub					А	А	A,B	В	B,C	С	D	

Table 1. Flowering phenology of dominant plants found in habitats of Taita hills.



						_	_	_	_	_	_	
camara												
Theveta	Apocynaceae	Tree			А	В	C	D				[
thevetoides												
Melia volkensii	Meliaceae	Tree			А	В	B,C				A-D	
Albizia amara	Fabaceae	Tree			А		В					
Bougevillea spp	Nyctaginaceae	Shruby vine			А	В	C,D	C,D	D			
Alstonia boonei	Apocynaceae	Tree			А	В	С	C,D				
Gravilia	Proteaceae	Tree			A-D				A-D	A-D		
robusta												
Acacia	Fabaceae	Tree			A	B,C				А	В	C-D
mellifera												
Acacia tortilis	Fabaceae	Tree			А	B,C	B,C			А	B,C	- C-D
Acacia nilotica	Fabaceae	Tree			А	B,C	B,C			А	B,C	C,D
Acacia gerradii	Fabaceae	Tree			A	B,C	B,C			A-D	2,0	0,2
Acacia	Fabaceae	Tree			A	B	C-D			A-D		
mearnsii	Fubuceue	lice			~	Ь	C-D			A-D		
Cactus spp	Cactaceae	Shrub			А	В	С	D		А	В	C-D
Euphobia spp	Euphobiaceae	Shrub			A	В	c	C	С	D		CD
	^	Annual			A				L	1		
Ipomea batatas	Euphobiaceae	plant			А	B,C	С	D		A-D		
Tithonia	Asteraceae	Perennial			А	В	CD	D				
diversifolia	Asieraceae	herb			A	D	CD	D				
Acyranthes	Amaranthaceae	Perennial			А	BC	CD	D				
aspera	1 marannaceae	herb			~	be	CD	U				
Musa	Musaceae	Tree				A-D					-	
acuminata												
Fragaria	Rosaceae	Shrub			А	BC	CD		A-D			
anannassa							-					
Thurbegia	Acanthaceae	Shruby vine					A-D					
alata												
Commiphora	Burseraceae	Tree					AB	CD				
myrrha												
Erythrina	Fabaceae	Tree					А	BC	D			
abysinica												
Commelina	Commelinaceae	plant					AB	В	CD	D		
benghalensis												
Dalbergia	Fabaceae	Tree					А	B-D				
latifolia												
Mangifera	Anacardiaceae	Tree							А	BC	D	
indica												
Tagetes lucida	Asteraceae	Perennial					AB	С	D			
		herb								ļ		
Aspilia spp	Asteraceae	Semi-woody					A-D					
		herb										
Cesalpinia	Fabaceae	Shrub					A-D					
decapetala												
Ocimum	Lamiaceae	Shrub			А	В	С	CD	D			
gratissimum										ļ		
Piper capensis	Piperaceae	Shruby vine						A-D				



r		1	 -								
Culcasia	Araceae	Shruby vine					A-D				
scandens		<u></u>						~~			
Pentas	Rubiaceae	Shrub					AB	CD			
lanceolata		<u></u>									
Dombeya	Malvaceae	Shrub					A-D				
burgessiae						 					
Impatiens	Balsaminaceae	plant					A-D				
balsamina											
Pentaisia	Rubiaceae	Perennial					A-D				
angustifolia		herb				 					
Tarchonanthus	Asteraceae	Tree					A-D				
camphoratus											
Psycotia	Rubiaceae	Shrub			A-D		AB	CD			
domingensis											
Abutilon hirtum	Malvaceae	Shrub					A-D				
Lactuca	Compositae	Shrub					AB	CD			
innermis	compositue	Sindo					7.0	CD			
	Estración	Dlant				 					
Vigna	Fabaceae	Plant					A-D				
unguiculata						 		-			
Maerua kirkii	Capparaceae	Shrub					AB	С	CD		
Calotropis	Apocyanceae	Shrub					AB	CD			
procera											
Senna	Fabaceae	Shrub					AB	CD			
didymobotyra											
Psaidia	Asteraceae	Perennial					AB	CD			
punctulata	Asieruceue	herb					AD	CD			
^											
Crotolaria	Fabaceae	Shrub						A-D			
agatiflora	<i>a</i>										
Dodonea	Sapindaceae	Tree						A-D			
viscosa											
Aspilia	Asteraceae	plant						A-D			
mossambicensis						-					
Santalum	Santalaceae	Tree						A-D			
album							_	_			
Phytolacca	Phytolaccaceae	Trailing					А	BC	CD		
dodecandra		shrub									
Solanum	Solanaceae	Shrub					А	BC	CD		
incanum											
Tribulus	Zygophyllaceae	Annual						A-D			
terrstris		plant									
Plectranthus	Lamiaceae	Perennial						A-D			
amboinicus		plant									
Adenium	Apocynaceae	Perrenial						А	BC	С	CD
arabicum	просуписеие	plant						А	ыс	C	CD
Tridax	Asteraceae	Annual						AB	CD		
procumbens		plant									
Gardenia	Rubiaceae	Tree						A-D			
manni											
Brugmansia	Solanaceae	Shrub			A-D			AB	CD		
spp											
Lantana trifolia	Verbeniaceae	Shrub						A-D			
v	•	•	•							•	•



Phoenix dactylifera	Arecaceae	Tree						A-D		
Galinsoga	Asteraceae	Herbacious						A-D		
parviflora		plant								
Sanservieria	Asparagaceae	Perennial						A-D		
trifasciata		plant	 					-		
Megalochlamys violacea	Acanthaceae	Shrub						AB	CD	
Asystasia	Acanthaceae	Perennial						A-D		
gangetica		plant								
Acalypha	Euphobiaceae	Perennial					AB	CD		
indica	*	plant								
Rudbeckia	Asteraceae	Perennial						A-D		
fulgida		plant								
Ficus sur	Moraceae	Tree						A-D		
Ficus sycomorus	Moraceae	Tree						AB	CD	
Adansonia digitata	Malvaceae	Tree						A-D		
Aloe	Asphodelaceae	Annual				AB	BC	CD		
barbadensis	-	plant								
Capsicum	Solanaceae	Perennial						A-D		
annum		plant								

*: Initial stage (plant produce flower buds) Stage A; Peak stage (plant have opened flowers) Stage B; Late stage (plants retain their bloom after peak flowering) Stage C; terminal stage (flowers have passed blooming stage) Stage D.



Figure 3a. Adenium arabicum "desert rose" in full bloom in the lowland areas.





Figure 3b. "Unidentified plant" entering senescence in the lowland sites of Taita hills.

6. Discussion

In this vulnerable habitat, it was revealed that as many as 80 different plant species of 34 different families could still sequentially flower with overlapping blooming periods through the two seasons. Specific plant families including Asteraceae, phyllanthaceae, Anacardiaceae, Lauraceae, Malvaceae, Fabaceae, Cariacaceae, Verbenaceae, Apocynaceae, Moraceae, Meliaceae, Nyctaginaceae, Proteaceae, Cataceae, Euphobiaceae, Amaranthaceae, Musaceae, Rosaceae, Burseraceae, Arecaceae, Commelinaceae, Lamiaceae, Piperaceae, Rubiaceae, Balsaminaceae, Compositae, Capparaceae, Sapindaceae, Santalaceae, Phytolaccaceae, Solanaceae and Zygophyllaceae comprised of forest trees, shrubs, grasses and weeds. (Table1). However, only a small proportion of plants of the Verbenaceae, Apocynaceae, Proteaceae, Fabaceae, Euphorbiaceae, Asteraceae, Rosaceae and Commelineceae families were found to bloom at the same time in both highlands and lowlands sites. This study revealed that indigent pollinators such as African meliponine bee species can constantly visit different kind of flowers from these families, thereby benefiting from a diverse mix of resources of both pollen and nectar produced by flowers from these wide array of plants (Table 1). Despite harsh environmental conditions experienced in the lowlands, habitats could still support a wide range of plant species, but only within unfragmented and undisturbed sample sites (Fig 3a-b), with higher feral bee nesting abundance. This is in agreement with Tscharntke et al., (2005) who revealed that no clear ontogenetic sequence for floral resource availability is an indicator of ecological mutualisms (Tylianakis et al., 2008), where flowering resources through seasons functions to satisfy foraging requirements of pollinators, especially native bee species. It was revealed that contemporaneous floral resource availability in unfragmented habitats and phenological resources could interact to explain the higher mean nest abundance in unfragmented habitats.

We showed that blooming sequences overlapped sequentially in both habitats but plant composition differed over months as they represented different combinations of floral resources. Floral phenology in such habitats is largely determined by a combination of both



climatic factors and level of anthropogenic disturbance (Roubik & Wolda, 2001) which influences sequential flowering of available plants at any point in time (**Table 1**). We speculate that the context of flowering phenology available at a sampling time could impact on how bees may exploit available food resources for optimum survival.

At the individual scale, management and land-use practices determine the community composition of both pollinators and plants, and the extent to which biotic factors affect both groups (Kremen *et al.*, 2007). In relation to floral resources, it can be observed that flower abundance and species richness are positively associated (Wcislo and Cane, 1996; Steffan-Dewenter and Tscharnke, 2001; Potts *et al.*, 2003; Holzschuh *et al.*, 2007). Ultimately, increasing floral diversity provides a wider array of foraging niches for these bee species (Fenster *et al.*, 2004).

The availability of nesting resources could also play a key role in structuring native bee communities (Cane, 1991; Eltz et al., 2002; Potts et al., 2005) as seen in the case of meliponine bees naturally occurring in taita hills. In parallel with floral resources, the temporal and spatial distribution of nesting resources may determine natural occurring bee community composition in any given location. Eltz et al. (2002) found that the abundance, size and species of trees in tropical forests of Southeast Asia influenced the density of stingless bee nests. Similarly, in a diverse Mediterranean bee assemblage, the amount of exposed soil, number of sloped surfaces and number of cavities available as nest sites accounted for a high percentage of the variation in community composition (Potts et al., 2005). Pollinators (meliponine bee species) which are more generalized in their requirements for mutualistic relationships with plants could be highly successful in such fragile habitats, such as Taita hills of Kenya, but could still be affected by drastic environmental changes that could limit the availability and quality of nectar or pollen resources, thereby invariably altering pollinator foraging behaviour. Future studies are needed to investigate possible mechanisms driving these patterns for dispersal and foraging efficiency in these bee species, particularly, how they exploit food resources depending on the context of resource needs. Combinations of protected area networks and bee-friendly habitats within agriculture will become increasingly important for bee conservation as the impacts of global environmental change work in synergy with other contributing factors (Tylianakis et al., 2008). Currently, high quality habitats for bees may become unavailable as bee life cycles gradually shift with changing climatic conditions and/or as habitats become degraded.

7. Conclusion

It has been revealed that fragile habitats could modify microclimates and the availability of biotic resources, which may directly or indirectly change the patterns of plant reproduction and further altering floral resource availability for native pollinators (Holzschuh *et al.*, 2008; Kennedy *et al.*, 2013). In summary, in response to global environmental changes, adopting a wider landscape approach and linking up fragments of (semi-) natural landscapes possessing essential foraging and nesting features, such as hedgerows and field margins, will make it possible to increase landscape connectivity and allow bees to forage and disperse to more suitable areas (Gilbert *et al.*, 1998; Tewksbury *et al.*, 2002).



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References

Adriaensen, F., M. Githiru, J. Mwang'ombe, E. Matthysen, & L. Lens. (2006). Restoration and increase of connectivity among fragmented forest patches in the Taita Hills, Southeast Kenya: Report of Critical Ecosystem Partnership Fund project, v. 1095347968, p. 1–149.

Best, L. B., T. M. Bergin, & K. E. Freemark. (2001) Influence of landscape composition on bird use of rowcrop fields. *Journal of Wildlife Management*, 65(3), 442–449. https://doi.org/10.2307/3803096

Brooks, T., L. Lens, J. Barnes, R. Barnes, J. K. Kihuria, & C. Wilder. (1998). The conservation status of the forest birds of the Taita Hills, Kenya. *Bird Conservation International*, 8, 119–139. https://doi.org/10.1017/S0959270900003221

Colwell, R. K., X. M. Chang, & J. Chang. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, 85(10), 2717–2727. https://doi.org/10.1890/03-0557

Eardley, C. D. (2004). Taxonomic revision of the African stingless bees (Apoidea : Apidae : Apinae : Meliponini). *African Plant Protection*, *10*(2), 63–69.

Ewers, R. M., & R. K. Didham. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biological reviews of the Cambridge Philosophical Society*, *81*(1), 117–142. https://doi.org/10.1017/S1464793105006949

Frankie, G. W., R. W. Thorp, L. E. Newstrom-Lloyd, M. A. Rizzardi, J. F. Barthell, T. L. Griswold, J.-Y. Kim, & S. Kappagoda. (1998). Monitoring solitary bees in modified wildland habitats: Implications for bee ecology and conservation. *Environmental Entomology*, 27(5), 1137–1147. https://doi.org/10.1093/ee/27.5.1137

Gathmann, A., & T. Tscharntke. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, *71*(5), 757–764. https://doi.org/10.1046/j.1365-2656.2002.00641.x

Gibbs, J. P., & E. J. Stanton. (2001). Habitat fragmentation and arthropod community change: Carrion beetles, phoretic mites, and flies. *Ecological Applications*, *11*(1), 79–85. https://doi.org/10.1890/1051-0761(2001)011[0079:HFAACC]2.0.CO;2

Hargis, C. D., J. A. Bissonette, & D. L. Turner. (1999). The influence of forest fragmentation and landscape pattern on American martens. *Journal of Applied Ecology*, *36*(1), 157–172. https://doi.org/10.1046/j.1365-2664.1999.00377.x

Jauker, F., T. Diekäter, F. Schwarzbach, & V. Wolters. (2009). Pollinator dispersal in an



agricultural matrix: Opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology*, 24(4), 547–555. https://doi.org/10.1007/s10980-009-9331-2

Joseph K. Macharia, Suresh Kumar Raina, & E. M. M. (2010). STINGLESS BEEKEEPING: AN INCENTIVE FOR RAIN FOREST CONSERVATION IN KENYA. Ecosystem Based Management: Beyond Boundaries. Proceedings of the Sixth International Conference of Science and the Management of Protected Areas, 21–26 May 2007, Acadia University, Wolfville, Nova Scotia.: p. 514–518.

Kindt, R., & R. Coe. (2010, Tree diversity analysis. Training, 18, 18598–614.

Legendre, P., & E. D. Gallagher. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*(2), 271–280. https://doi.org/10.1007/s004420100716

Maeda, E. E., B. Clark, P. Pellikka, M. Siljander, & P. T. Vi. (2010). Driving forces of land-use change in the Taita Hills, Kenya. *International Journal*, no. Figure 1, 2–5.

Omoro, L. M. A., P. K. E. Pellikka, & P. C. Rogers. (2010). Tree species diversity, richness, and similarity between exotic and indigenous forests in the cloud forests of Eastern Arc Mountains, Taita Hills, Kenya. *Journal of Forestry Research*, 21(3), 255–264. https://doi.org/10.1007/s11676-010-0069-0

Pellikka, P. K. E., B. J. F. Clark, A. G. Gosa, N. Himberg, P. Hurskainen, E. Maeda, J. Mwang'ombe, L. M. A. Omoro, & M. Siljander. (2013). Agricultural Expansion and Its Consequences in the Taita Hills, Kenya. *Developments in Earth Surface Processes, 16*, 165–179. https://doi.org/10.1016/B978-0-444-59559-1.00013-X

Pellikka, P. K. E., B. J. F. Clark, T. Sirviö, & K. Masalin. (2005). Environmental change monitoring applying satellite and airborne remote sensing data in the Taita Hills, Kenya: Area, p. 223–232.

Pfeifer, M., N. D. Burgess, R. D. Swetnam, P. J. Platts, S. Willcock, & R. Marchant. (2012). Protected areas: Mixed success in conserving East Africa's evergreen forests. *PLoS ONE*, 7(6), 1–10. https://doi.org/10.1371/journal.pone.0039337

Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, & P. Willmer. (2005). Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, *30*(1), 78–85. https://doi.org/10.1111/j.0307-6946.2005.00662.x

Reitalu, T., O. Purschke, L. J. Johansson, K. Hall, M. T. Sykes, & H. C. Prentice. (2012). Responses of grassland species richness to local and landscape factors depend on spatial scale and habitat specialization. *Journal of Vegetation Science*, 23(1), 41–51. https://doi.org/10.1111/j.1654-1103.2011.01334.x

Ricketts, T. H. et al. (2008). Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters*, *11*(5), 499–515. https://doi.org/10.1111/j.1461-0248.2008.01157.x



Roubik, D. W. (2006). Review article stingless bee nesting biology. *Apidologie*, *37*, 124–143. https://doi.org/10.1051/apido:2006026

Sasidharan, K. R., & C. Kunhikannan. (2007). Role of bees as pollinators of tropical forest species and need for conserving their diversity. *Advances in pollen spore research, XXIV*, 79–91.

Schüepp, C., J. D. Herrmann, F. Herzog, & M. H. Schmidt-Entling. (2011). Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies. *Oecologia*, *165*(3), 713–721. https://doi.org/10.1007/s00442-010-1746-6

Steffan-Dewenter, I., & T. Tscharntke. (2000). Resource overlap and possible competition between honey bees and wild bees in central Europe: p. 288–296. https://doi.org/10.1007/s004420050034

Tepedino, V. J., & N. L. Stanton. (1981). Diversity and Competition in Bee-Plant Communities on Short-Grass Prairie. *Oikos, 36*(1), 35–44. https://doi.org/10.2307/3544376

Táhm ér ész, B. (1995). Comparison of different methods for diversity ordering. *Journal of Vegetation Science*, 6(2), 283–290. https://doi.org/10.2307/3236223

Ugland, K. I., J. S. Gray, & K. E. Ellingsen. (2003). The species-accumulation curve and estimation of species richness: p. 888–897.

Westphal, C. et al. (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, 78(4), 653–671. https://doi.org/10.1890/07-1292.1

Wettstein, W., & B. Schmid. (1999). Conservation of arthropod diversity in montane wetlands:Effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers.JournalofAppliedEcology,36(3),363–373.https://doi.org/10.1046/j.1365-2664.1999.00404.x

Wilder, C., T. Brooks, & L. Lens. (1998). Vegetation Structure and Composition of the Taita Hills Forests. *Journal of East African Natural History*, 87(1), 181–187. https://doi.org/10.2982/0012-8317(1998)87[181:VSACOT]2.0.CO;2

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