Forest Fragmentation Shapes Resource Partitioning for Endemic Pollinators (*Hymenoptera*: *Meliponini*)

Bobadoye Bridget. O[1, 2, *]

[1]International Centre of Insect Physiology and Ecology (*icipe*), P.O. Box 30772-00100 Nairobi, Kenya.

[2]Federal College of Forestry (FCF), P.M.B 5087, Ibadan, Oyo State, Nigeria.

Abstract

A field study was undertaken along six diverse habitat gradients of Kenya to evaluate the occurrence and underlining drivers that shape meliponine bee species diversity. These gradients ranged from continuous forest habitats (Indigenous forests, mixed forests and exotic forest patch) representing unfragmented habitats to dispersed habitats (Mixed deciduous woodlands, Grasslands dominated by perennial grasses such as *Cenchrus ciliaris*, *Chloris roxburghiana* and Acacia dominated bush lands) representing fragmented habitats respectively.

A total of four different species of meliponine bees were encountered with *Hypotrigona gribodoi* being the most abundant species, followed by *Meliponula ferruginea* (black), *Plebeina hildebrandti* and *Hypotrigona ruspolii* in descending order. Occurrence and diversity of *Hypotrigona gribodoi*, *Melipona ferruginea (*black), *Plebeina hildebrandti* and *Hypotrigona ruspolii* was significantly influenced by the degree of fragmentation (vegetation type) and floral diversity (P = 0.0056); the mean number of colonies recorded per study site ranged from 2.3 in dispersed habitats in the lowlands to 1.0 in continuous forest landscapes in the highlands, whereas the mean population density ranged from 2.0 to 172 colonies/25 ha-transects.

The results provide substantial support to better understand interactions between habitat structure and the degree of fragmentation in linking species diversity to habitat loss.

Introduction

Insect pollinators are the most important providers of ecosystem services globally [16] with an estimated 20,000-30,000 species worldwide; as they are also important indicators of biodiversity. They have co-evolutionary relationships with plants and therefore their services are inevitable for the maintenance of the life cycles of many plant species [17].

The structure of bee communities is closely related to the floral communities they forage upon with several key characters already identified, including floral diversity (Tepedino and Stanton, 1981; Gathmann and Tscharntke, 2002)[18], floral abundance [6] and seasonal availability of these resources [15]. Up until recently, some studies have attempted to quantify the combined effect of other structuring agents to the diversity of pollinators within a specified habitat [13]. Such drivers have been identified to impact directly upon insect pollinator communities, while others impact indirectly through the modification and compositioning of floral communities or other forms of habitat structure. Bees are known to exhibit a diverse array of nesting strategies with respect to the type of habitat they are naturally occuring in, type of nesting substrate used, and the materials required for nest construction making them easily partitioned into several exclusive guilds on the basis of their nesting habitats [13].

While forage rewards provided by floral communities are generally accepted as the primary determinant of pollinator community structure, there is an increasing body of evidence suggesting that habitat structure may also play an important role in the occurrence of endemic pollinators such as meliponine bee diversity within any habitat [21].

It is widely acknowledged that habitat loss has negative effects on biodiversity and that the quality of suitable habitat in any landscape enhances species diversity. The effect of habitat fragmentation and isolation ranges on diversity of insect pollinators is less clear. Increasing isolation from naturally ideal habitats can be associated with either a decline or an increase in species composition, richness and diversity.

Material and Methods

Site Description

The Eastern Arc mountains has the status of a global biodiversity hot-spot (Pellikka *et al.*, 2013; Adriaensen *et al.*, 2006)[1] and it lies in south-eastern Kenya at 03°20 S, 38°15 E, about 150 km inland from the coast and covering an area of about 250 km^2[2] (**Fig 1**). The hills are isolated from other mountainous areas *viz* the south-east (Shimba Hills), south (Usambara Mountains), south-west (Mt Kilimanjaro), west (Ngulia and Chyulu Hills) and the north-west (Kenyan highlands) by the vast plains of Tsavo [9]. The annual rainfall is characterized by two rainy seasons (March- May, September – October) and varies between 480 and 1200 mm in the highlands [14], but much less rainfall (250 mm) (**Fig 2**) is observed on the surrounding plains of the sparse lowlands [11].

Habitat Features

Sparse Lands

The eastern arc mountains are characterized by highly dispersed vegetation and fragmented habitats dominated by dry grassland plains (**Table 1**). The mean rainfall in the lowlands ranges around 400 mm with peaks in April and November every year.

Vegetation is characterized by mixed commiphora deciduous woodlands in Msau, which are widely dispersed, but a considerable number of mature deciduous trees have been reduced to shrubs by extensive grazing and deforestation. Common deciduous trees such as *Albizia gummifera G., Haplocoelum foliolosum Terminalia sinensis* H., *Terminalia sinensis L., Comiphora schimperi O., Balanites pedicelaris* Mildbr.*, Tamarindus indica* L.*, Sterculia Africana* (Liour.), *Ficus sycomorus* L.*, and Cordia sinensis* Lam. are majorly found along streams. [12].

The grasslands consisting mainly of perennial grasses such as *Chloris roxburghiana* Scult, *Cenchrus ciliaris, Erythrococca bongensis* Pax, *Pennisetum menzianum* Lee and also *Setaria sphacelata* (Schumach.) Common shrubs included *Croton dichogamous* Pax, *Ocimum kilimadischaricum* Guerke. Undergrowth is minimal with bare soil surface exposure clearly evident. With increased regional slope, large gully systems are rapidly formed and have rendered the land
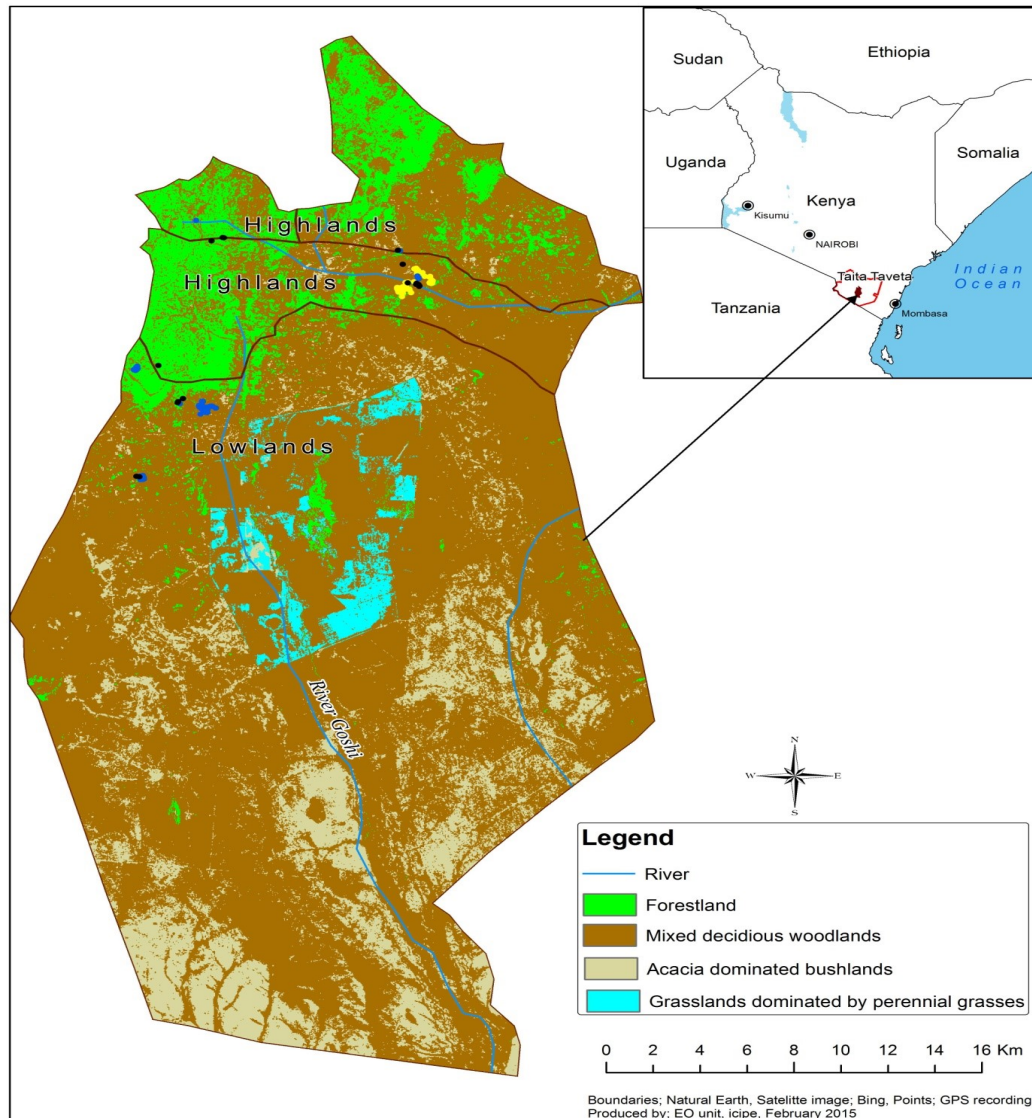
Figure 1. Map of Taita hills forests and surrounding area showing the data collection sites.

Table 1. Summary of site locations and habitat area.

Site code	Coordinates	Ecological zone	Location
MDW	3.26086°S/38.26525°E	Woodlands	Lowlands
GL	3.46000°S/38.36528°E	Grasslands	Lowlands
ADBL	3.37269°S/38.42814°E	Bush lands	Lowlands
IMF	3.41875°S/38.36939°E	Indigenous forest	Highlands
EFP	3.36208°S/38.33072°E	Exotic forest	Highlands
HCH	3.46612°S/38.35899°E	Mixed forest	Highlands
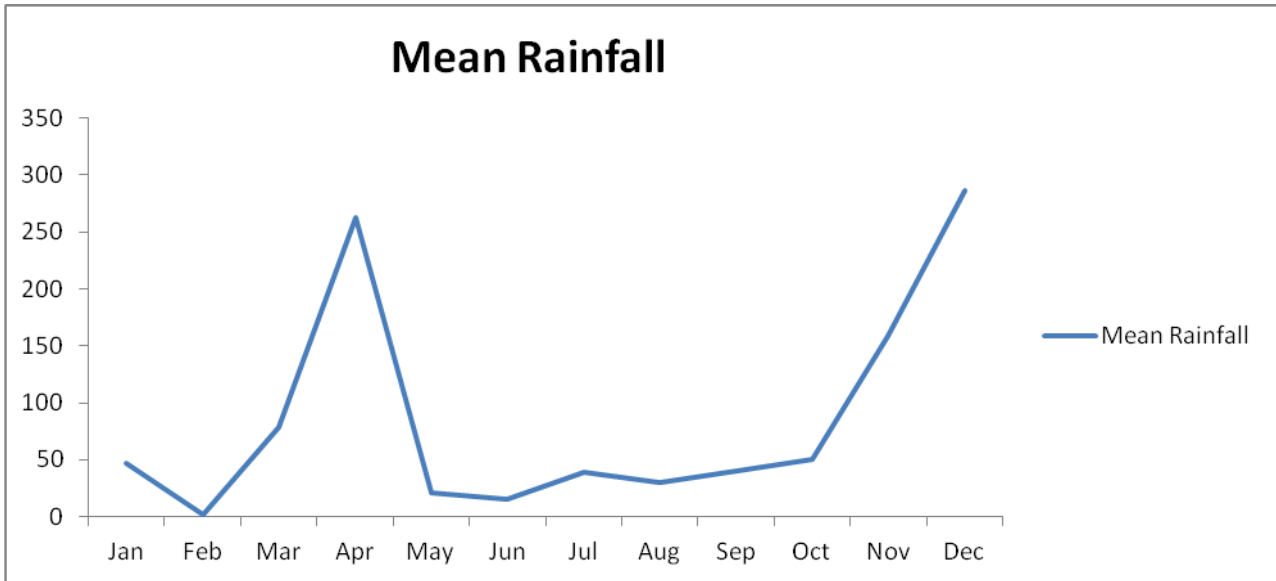
Mean Rainfall

Figure 2. Mean rainfall in the eastern arc mountains.
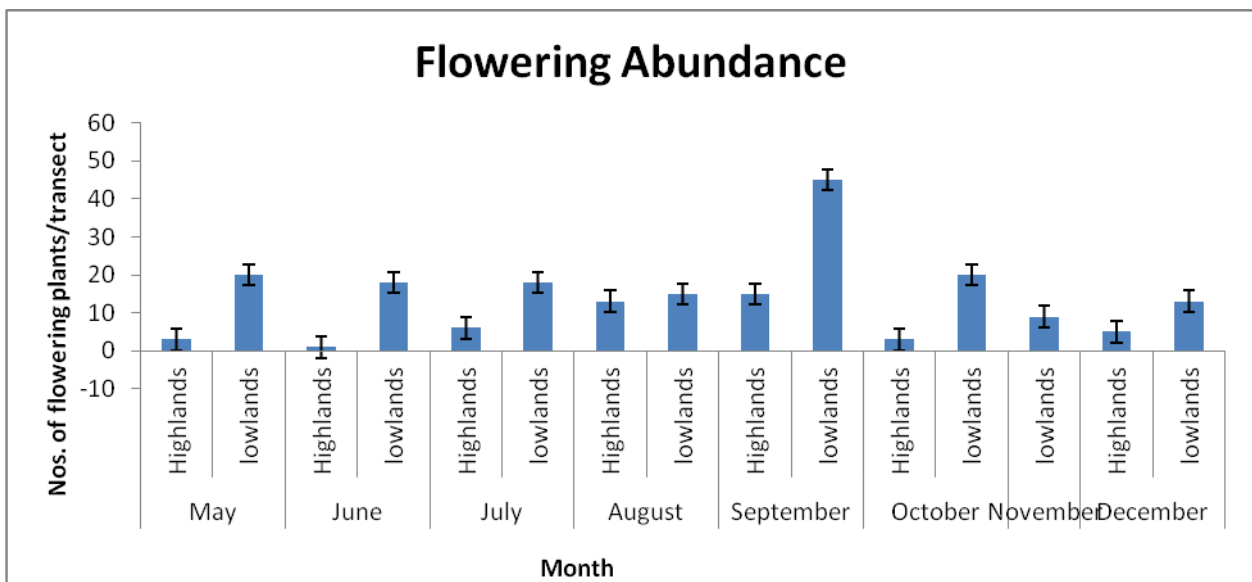
Flowering Abundance

Figure 3. Abundance per transect across major flowering seasons.

unproductive for agriculture.

The *Acacia* dominated bush lands is characterized by very poor vegetation cover with overgrazing causing the removal of topsoil and leading to intense red patches and silting of local water supplies. Rocky outcrops were observed to be quite common. *Acacia* tree species interspersed with perennial grasses dominated this habitat. *Acacia geradii* Benth was more dominant and closely associated with *A. nilotica*, and *A. tortilis*. Grasses predominant in this area included *Digitaria macrobrephara* Hack, *Cynodon dactylon* Pers., *Themeda triandra* Forsk, *Cenchrus ciliaris* L, *Chloris roxburghiana* Schult. *Setaria pyramidilis Beauv.* and *Pennisetum. Menzianum Leeke*.[10].

Highlands

The highlands are considered as high potential agricultural areas which are suitable for agriculture. However, a very small area is available for agricultural purposes due to steep slopes and shallow soils. A total of seven [7] forest fragments are found in this region, and characterized by continuous forest landscapes. Most forests (03°25'S, 38°22'E) are indigenous habitat situated at an altitude of 1,400 m measuring approximately 2 ha [22] and is regarded as part of remnants of the original montane forest, receiving 1700–2400 mm of annual precipitation. Tree species such as *Lobelia gibberoa* Hemsl, *Phoenix sylvestris* Sylvestris, *Dracaena steudneri* Engl*.* and *Cyathea manniana* L. are characteristic to this forest. Some isolated forests (03°28'S, 38°28'E) are mixed forest habitats comprising both indigenous and exotic tree species forming dense and continuous canopies, which has a reputation of being the most disturbed forest fragment out of most forest fragments. Tree species predominantly found in the highlands are cypress (*Cupressus lusitanica*), eucalyptus (*Eucalyptus saligna*), pines (*Pinus caribea*, *P. patula*), *Maesopsis eminii* and grevillea (*Grevillea robusta*) and *Acacia mearnsii*.

Sampling Procedure

In each study site (25 ha), twenty [20] linear transects of 250 m x 20 m each were established using a GPS to mark coordinates with relation to habitat type and altitude. Transects were used as a basic sampling unit for all bees and vegetation data. In addition, the central line transect method was used to represent different habitats of the entire study area and also increase the chances of sampling nesting sites and vegetation types that dominate all study sites.

In order to obtain quantitatively reliable data, each line transect (250m) was divided into five separate sections of 50m x 20m each. The starting point for bee sampling was rotated (starting from the first point and ending at fifth point, then beginning at point 5 during the next sampling round) between the end points of the transects to randomize sample collections thus reducing bias in data collection. Surveys were carried out along four successive different habitats (forest, grassland, bush lands and woodlands); the sites were chosen due to the dissimilarity in habitat structure with key factors such as isolation, geographic location and micro-climates taken into consideration.

Insect Pollinators Sampling Method

Meliponine bees were specifically sampled using the conventional complementary method, belt transect (direct observation of nesting colonies: visual census). Belt transect counts are the traditional (with standardized protocols) methods of sampling bees from existing vegetation [13].

The belt transect method was used to sample foraging bees within a transect of 250 m x 20 m at each site, a total of six (6) sites were sampled. While walking in each transect at a slow speed, nest colonies of meliponine bees were observed on both living and dead substrates. Each sampling day, observations were made from 8:00 hr to 5:00 hrs (9 hours) to encompass the main flowering periods (**Fig 3**) and peak foraging hours. Observations were made under conditions favorable for bee flights, characterized by sunny weather, weak wind and maximum temperature from 9: 00 hr to 5: 00 hrs.

Statistical Analysis

Analysis of variance via R statistical package was used to compute the significant effect of habitat type on species abundance. A non-linear regression model such as the species accumulation curve was used to estimate the number of meliponine bee species represented in the whole surveyed area [20]. The species accumulation curves was used to estimate species richness and rank abundance of meliponine bee

species across varying habitats types [3]. Biodiversity indices (species richness, abundance and Shannon index) were computed using the R statistical package called Biodiversity R [8]. Species richness, species diversity (using Shannon index and Renyi diversity profiles), and the proportion of habitat type with most abundant meliponine bee species were computed using Renyi diversity profiles [19]. Renyi diversity profiles are curves that provide information on richness and evenness, similar to rank abundance curves. Renyi diversity profiles however have the advantage over rank abundance curves because of easy rank ordering from lowest to highest diversity. For this reason, a Renyi diversity profiles was used in this instance [19].

Results

Meliponine Species Composition

A total of four (4) different meliponine bee species were identified on the basis of morphological differences in the field (**Table 2**). The four species were determined at species level based on the descriptions from literature of African meliponine bee species [4]. All the four species were recorded in all the habitats sampled in the lowlands. (**Table 2**). *Hypotrigona gribodoi* was the most dominant species across the two study sites (58.3%) of all recorded nests, followed by *Meliponula ferruginea* (32.0%). The proportion of *Plebeina hildebranti* (7.4%) and *Hypotrigona ruspolii* (2.3%) species revealed that they were the least distributed species. This indicates that all the four (4) species were highly dispersed in distribution across the three habitats (Mixed deciduous woodlands, grasslands and Acacia dominated bush lands) in lowlands sites. The species showed a rank abundance of 1 for *Hypotrigona gribodoi,* (2) for *Melipona ferruginea,* (3) for *Plebeina hildebrandti and* (4) for *Hypotrigona ruspolii* respectively.

Meliponine Species Nest Abundance

Data analysis was illustrated by box plots which showed varying distribution ranges of meliponine bee nest species within the four habitat types (forests, grasslands, woodlands and bush lands) (**Fig 4).** Species nest abundance was skewed to the left particularly in dispersed habitats of the lowlands characterized by mixed deciduous tree woodlands (**MDW**), Acacia dominated bush lands (**ADBL**) and grasslands (**GL**),

signifying a normal distribution. The range of nest abundance was wide in habitats characterized by **ADBL**, **GR** and **MDW**. Site type (fragmented and unfragmented sites) had significant effect on nest abundance (P = 0.003) (**Fig 5**), thus revealing a distinct preference between the two main site types.

Meliponine Bee Species Richness and Diversity

According to the Renyi diversity profile, a total of four species was recorded across the four main habitat types sampled and further extrapolation with Shannon evenness index also predicted a total species richness of 4.24 (**Table 3**). The species accumulation curve reached a plateau with about four species at exactly 80 sampling points (**Fig 6**). A comparison of species richness for individual habitats showed no significant difference in species richness (p = 0.08). The profiles indicate that **MDW** habitat was more diverse than **ADB**, **GL**, **EFP** and **IF** habitats in descending order. The **EFP** and **IMF** could not be adequately ordered, as the profile curves overlapped. At the α = 0 scale, **IMF** habitat overlapped **EFP** habitat, at the α = 1 (Shannon index), species diversity was ranked in sequential order **MDW**>**GL**>**ADB**> **EFP**>**IMF**, at the α=2 (Simpson index) species diversity showed the same pattern for the three (3) dispersed habitats in the lowlands. Shannon diversity extrapolation for each habitat predicted more species in mixed deciduous woodlands and grasslands than for other habitats.

Discussion

Meliponine Bee Species Composition.

Species number recorded in all sampled sites indicates the composition of meliponine bee species within this hotspot, though this is comparatively less than the species recorded in Kakamega, it unmistakably signifies the effects of habitat fragmentation in determining species composition within an ecosystem[5]. The majority of *H. gribodoi* species was more dominant and featured in all habitat types but at variable proportions, which may be attributed to its plasticity in nesting in varying habitat types.

Meliponine Bee Species Richness and Diversity.

The four species recorded directly from sampling are close to the J Evenness extrapolated predicted value of 4.24. The species accumulation curve indicated
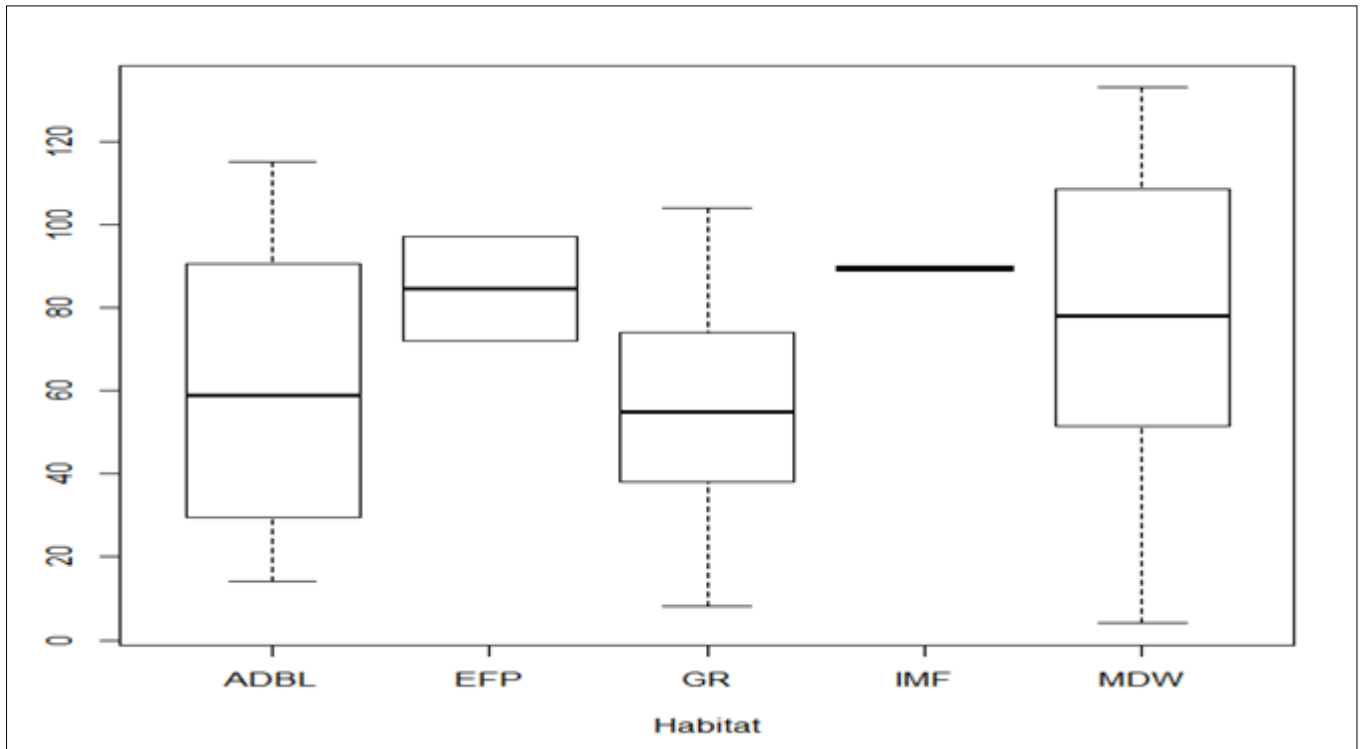
Figure 4. Range of Nest abundance within specific habitats. Note**: IMF**=Indigenous mist forest (**H**), **ADBL**=Acacia dominated bush lands (**L**), **EFP**=Exotic Forest Patches (**H**), **GR**=Grasslands (**L**), **MDW**=Mixed deciduous woodlands (**L**).

Figure 5a. Mean nests abundance in four habitat types. Note**: IMF**=Indigenous mist forest (**H**), **ADBL**=Acacia dominated bush lands (**L**), **EFP**=Exotic Forest Patches (**H**), **GR**=Grasslands (**L**), **MDW**=Mixed deciduous woodlands (**L**).
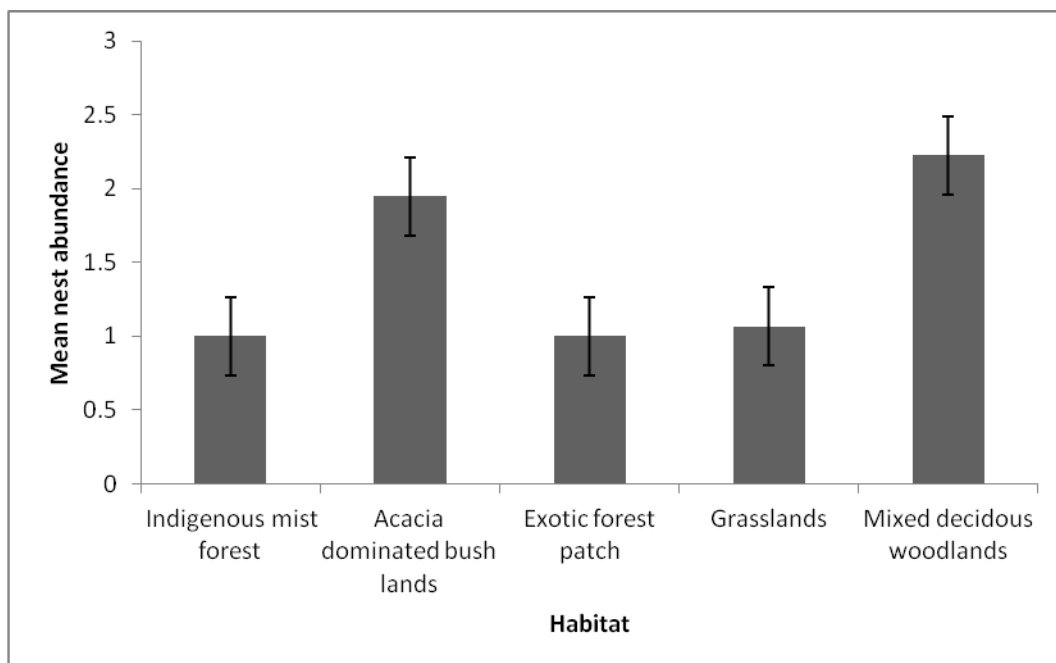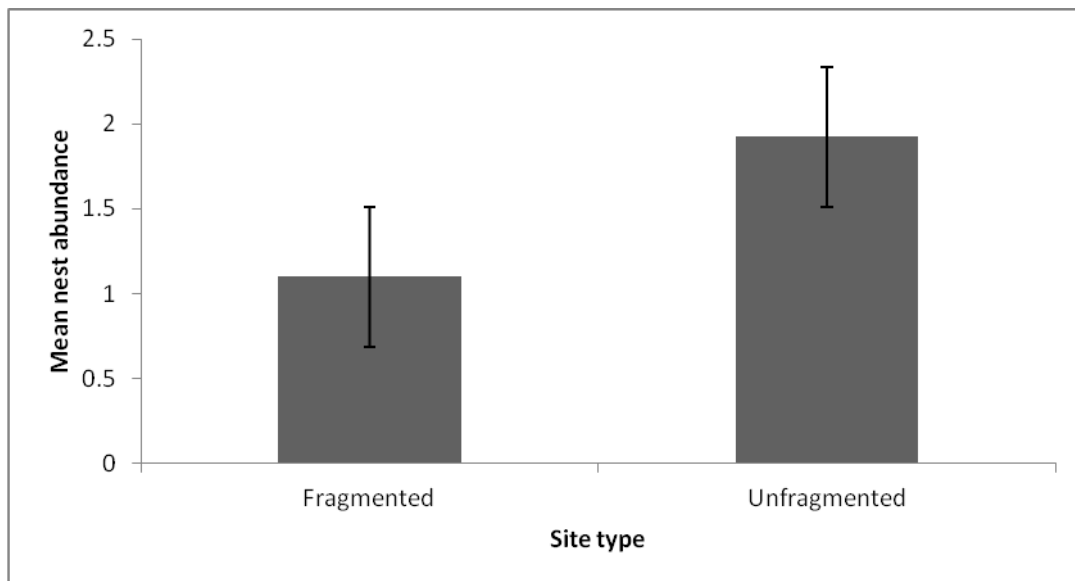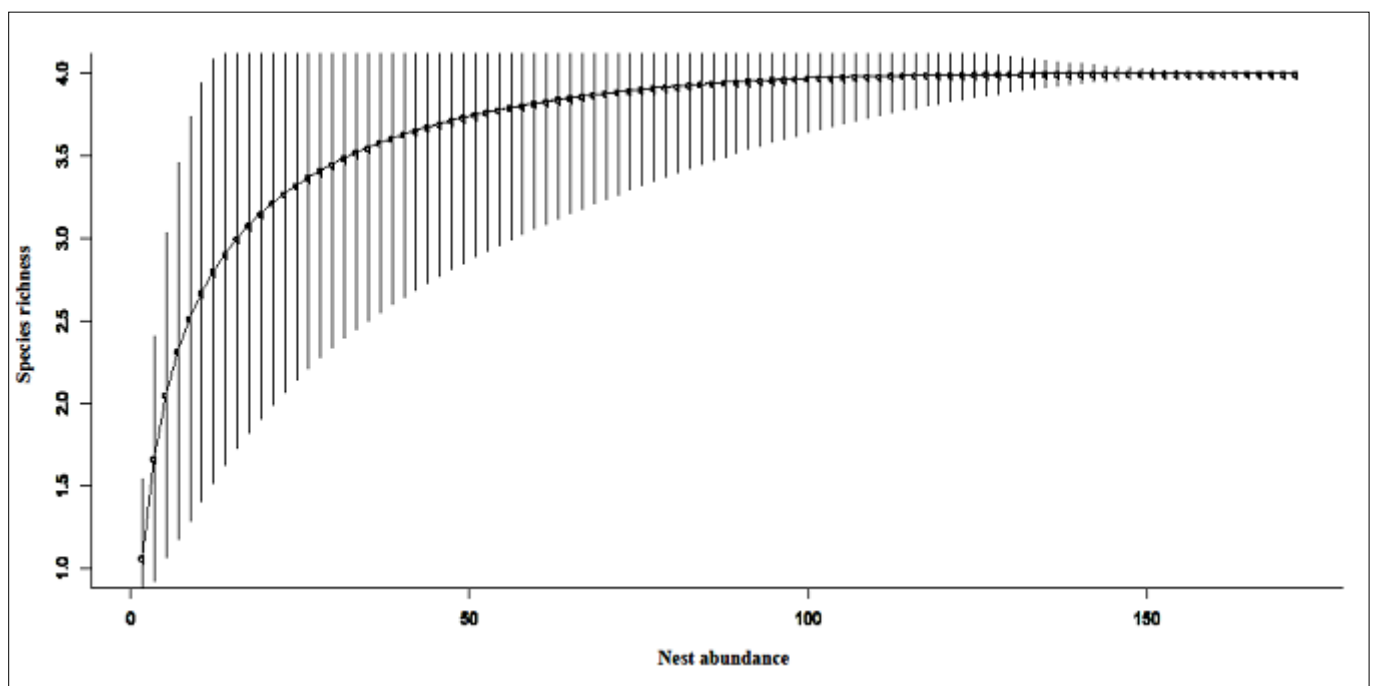
Figure 5b. Mean nests abundance across the two site types.

Figure 6. Species accumulation curve for meliponine bee species.

Table 2. Rank of total bee species observed within Taita hills.

Species	Rank	Total abundance	Proportion
Hypotrigona gribodoi	1	102	58.3
Meliponula ferruginea	2	56	32.0
Plebeina hildebrandti	3	13	7.4
Hypotrigona ruspolii	4	4	2.3

Table 3. Diversity indices for each habitat in the study site

| Habitat | Sampled points | Diversity index | | | | |
		Total Richness	Shannon diversity	Total Abundance	Evenness	J Evenness
IMF	2	1	0	2	1	NaN
ADBL	19	3	0.723	32	0.687	0.658
EFP	2	1	0	4	1	NaN
GR	31	3	0.965	41	0.875	0.879
MDW	44	4	1.010	96	0.686	0.728

Note**: IMF**=Indigenous mist forest (**H**), **ADBL**=Acacia dominated bush lands (**L**), **EFP**=Exotic Forest Patches (**H**) **GR**=Grasslands (**L**), **MDW**=Mixed deciduous woodlands (**L**) * (H): Highlands; (L): Low

approximately 80 sampling points as adequate to recover at least four species.

Conclusion

The species accumulation curve clearly distinguished habitat types that share similarity in species diversity. The habitat types with **IMF** and **EFP** were in the same group, while **MDW** and **GR** formed a divergent group from **ADBL**, both indicating similarities and close proximity to each other for habitats (dispersed habitats in lowlands) in the same group. Similar trends were noted in box plots with respect to habitat type (Dispersed lowland habitats) showing higher variation than continuous forested landscapes of the highlands, implying greater heterogeneity in dispersed vegetation in lowlands and uniform homogeneity in continuous forested landscapes in highlands. The study has shown greater species diversity in certain habitats with more deciduous tree species that are indigenous to this habitat and could thereby predict the richness and diversity of meliponine bee species.

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