DIVERSITY AND COMPOSITION OF DUNG BEETLES (SCARABAEIDAE: SCARABAEINAE AND APHODIINAE) ASSEMBLAGES IN SINGHORI WILDLIFE SANCTUARY, RAISEN, MADHYA PRADESH (INDIA)

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ABSTRACT: Diversity and composition of dung beetles (Scarabaeidae: Scarabaeinae and Aphodiinae) assemblages were sampled, analyzed and studied in Singhori Wildlife Sanctuary (SWLS), Madhya Pradesh. Collection of specimens yielded a total of 669 beetles representing 26 species belonging to 12 genera and two subfamilies. The subfamily Scarabaeinae with 24 species is dominating (71.59% of total individuals) over Aphodiinae (27.40%) with two species. Twenty species were collected in mixed forests (n=398) and nineteen species in agricultural lands (n=271), wherein thirteen species were present in both the habitats. Though the species richness is almost similar in SWLS, but there is significant difference in guild structure and composition. Tunnellers were the most speciose (22 species) and abundant (55.3%) followed by dwellers which constitute three species with 42.8% abundance in the assemblage.

KEY WORDS: Species diversity, Scarabaeinae, Aphodiinae, Singhori Wildlife Sanctuary, Madhya Pradesh, India.

Dung beetles are a globally distributed insect group, with their high diversity in tropical forests and savannas (Hanski & Cambefort, 1991) and are member of family Scarabaeidae of insect's largest order Coleoptera representing about 7000 species throughout the world. The beetles mostly feed on the microorganism rich liquid component of mammalian dung and use the more fibrous material to brood their larvae (Halffter & Edmonds, 1982; Halffter & Matthews, 1966). Based on their nesting strategies dung beetles are broadly classified into three functional groups viz. rollers (telocoprid), tunnelers (paracoprid) and dwellers (endocoprid). Rollers form balls from a dung pat, which are rolled away and buried in the ground for feeding and breeding while tunnelers make underground vertical chambers in close proximity to the dung pat and construct their nest using the dung from pat whereas dwellers breed in dung pats itself (Halffter & Edmonds, 1982). Geotrupidae and most of the tribes of subfamily Scarabaeinae (Dichotomiini, Coprini, Onitini, Phanaeini, Onthophagini and Oniticellini) are tunnelers and the tribes Canthonini, Scarabaeini, Eucraniini, Sisyphini, Gymnopleurini and Eurysternini are considered to be rollers. Some Oniticellini along with members of subfamily Aphodiinae are dwellers and various Onthophagini and Dichotomiini are kleptoparasites. Through their dung consumption and relocation activities, dung beetles are involved in the ecological functions of parasite suppression, secondary seed dispersal, nutrient cycling and bioturbation (Andresen 2002, 2003; Nichols et al., 2008; Stokstad, 2004; Waterhouse, 1974).

There are several studies from tropical and temperate systems that indicate a severe impact of local and regional-scale anthropogenic habitat changes on patterns of dung beetle abundance and species diversity (Nichols et al., 2008). Because of well documented, feeding, nesting behaviors and natural histories of dung beetles (Hanski & Cambefort, 1991; Halffter & Edmonds, 1982; Halffter & Matthews, 1966), they fulfill all the criteria of an ideal bio-indicator for investigating impacts of anthropogenic disturbances to ecosystems.

Monographic and faunal works on the diversity and distribution of dung beetles in the Oriental region was mostly carried out by Arrow (1931) and Balthasar, (1963a,b and 1964) wherein a complete taxonomic checklist along with identification keys to the species is discussed thoroughly. A well documented taxonomic record of the scarab beetles of Madhya Pradesh and Chhattisgarh (Chandra, 1999, 2000, 2008, 2009; Chandra & Ahirwar, 2005, 2007) exits which illustrates diversity and distribution of these beetles in different protected areas of the state. Numerous ecological and biodiversity conservation studies have already used them in many regions of the world while India accounts for only few publications (Kakkar & Gupta, 2009; Mittal & Kakkar, 2005; Sabu et al., 2006, 2011; Vinod & Sabu, 2007). Thus the main goal of our study was to gain knowledge about diversity and composition of the dung beetle communities in Singhori Wildlife Sanctuary.

The main objectives of the studies are:

1) Analyze and compare species diversity and community structure of dung beetles in SWLS.

2) Determine the variations in species richness and abundance of dung beetle assemblages in different localities of the sanctuary.

3) Analyze taxonomic and functional composition of subfamily Scarabaeinae and Aphodiinae in mixed forests and agricultural lands of the sanctuary.

MATERIAL AND METHODS

STUDY SITE:

The study was conducted in SWLS located in Bari Tehsil of Raisen district of Madhya Pradesh. Geographically the sanctuary spreads between 22045' and 22055' N latitudes and 77015' and 7800' E longitudes and covers over an area of 287.910 km2. The forests in the SWLS are of two types (i) Teak forests and (ii) mixed dry deciduous forests. Other species found in teak forests and mixed deciduous forests include *Anogeissus latifolia*, *Pterocarpus marsupium*, *Boswellia serrata*, *Acacia catechu* and *Butea monosperma*.

SAMPLING DESIGN:

Random sampling of dung beetles was done from nine different sampling sites comprising mixed forests (MF) and agriculture lands (AL) of SWLS, during September, 2009-2011. Five sites from MF (MF1, MF2, MF3, MF4 and MF5) and four sites from AL (AL1, AL2, AL3 and AL4) were selected for collection of beetles using light trap and handpicking methods. At each sampling sites few dung pats of almost equal size were selected thereafter the beetles were extracted and sorted out using floating methods. Collected beetles were then pinned and preserved in the lab. In order to obtain the most complete species list of the sanctuary, the individuals were identified with the comparison of reference collections present in Zoological Survey of India, Jabalpur and classified using available literature and monographic works (Arrow, 1931; Balthasar, 1963a,b and 1964).

COLLECTION LOCALITIES IN SINGHORI WILDLIFE SANCTUARY

S. No.	Latitude	Longitude	Altitude
Agricultural lands			
AL1	N 23°12.174'	E 078°17.527'	1186 ft
AL2	N 23°12.586'	E 078°15.144'	1191ft
AL3	N 23°10.307'	E 078°14.501'	1160ft
AL4	N 23°02.826'	E 078°03.899'	1090 ft
Mixed forests			
MF1	N 23°14.296'	E 078°11.486'	1320 ft
MF2	N 23°06.596'	E 078°15.229'	1191 ft
MF3	N 23°09.642'	E 078°14.229'	1149 ft
MF4	N 23°11.200'	E 078°12.085'	1375 ft
MF5	N 23°13.260'	E 078°13.674'	1333 ft

According to the mode of feeding, beetles were classified as rollers, tunnelers and dwellers. Finally species were divided by their size (total length) into small bodied (≤ 10 mm) and large-bodied (≥ 10 mm). Specimens studied are deposited at national zoological collections of Zoological Survey of India, Jabalpur. Habitat photographs of eight dung beetle species are also included, taken with the help of Nikon, DSLR-D7000 (Plate-1).

DATA ANALYSIS:

ALPHA DIVERSITY:

Number of observed species per site, were considered as alpha diversity. EstimateS 8.2.0 (Colwell, 2009) was used to generate fitted species accumulation curves for each habitat as well as to obtain the estimated value of species richness for each of the sampling site in SWLS. To assess the true species richness for each habitat two non-parametric estimators ACE (Abundance-based Coverage Estimator) and Jacknife 1 was estimated with Chao1 using EstimateS 8.2.0 software package (Colwell, 2009). These non-parametric estimators are considered to more accurate and less sensitive to problems related to sample coverage and variation in species capture probability (Colwell & Coddington, 1994). Diversity dominance plots were drawn to assess changes in abundance per species in each locality. In order to provide instantly comprehensive expressions of diversity, other indices viz. Shannon index, Simpson index and Fisher alpha index were also calculated. Shannon index takes into account the evenness of the abundance of species and assumes that individuals are randomly sampled from a large population while Simpson index is less sensitive to species richness and more sensitive to the most abundant species. Graphs were designed using SigmaPlot 11.0 software.

BETA DIVERSITY:

Beta diversity was calculated Bray-Curtis index to estimate species similarity between two habitats also among different sampling sites. The index is sometimes called as Sorension quantitative index,

$$CN = \frac{2jN}{(Na+Nb)}$$

Where Na = the total number individuals in site Aj Nb= the total number of individuals in site Bj and 2jN = the sum of the lower of the two abundance for species found in both sites. The index value ranges from one (or 100) when two samples are identical, 0 when there are no shared species between them. The index is selected because it reflects differences in total abundance rather than relative abundance. (Magurann, 2004).

RESULTS

Alpha and Gamma diversity

In total 669 individuals belonging to 26 species distributed in 12 genera, 10 subgenera and two subfamilies were collected (Table 1). The dominant subfamily Scarabaeinae includes 24 species while Aphodiinae is represented by only two species. Thus Gamma diversity for SWLS (mixed forest and agricultural lands) was 26 species (n=669) collected from nine different localities. Twenty species were collected in mixed forests (n=398) and nineteen species in agricultural land (n=271). Out of total 26 species, seven species viz. *Catharsius* (*Catharsius*) *sagax*, *Catharsius* (*Catharsius*) *molossus*, *Onitis brahma*, *Copris* (*Paracopris*) *imitans*, *Heliocopris gigas*, *Onthophagus* (*Onthophagus*) *laborans* and *Chironitis arrowi* were exclusively present in mixed forests while five species viz. *Caccobius* sp. *Catharsius* (*Catharsius*) *pithecius*, *Copris* (*Copris*) *repertus*, *Onthophagus* (*Onthophagus*) *duporti*, and *Onthophagus* (*Onthophagus*) *sternalis* in agriculture land.

With the sampling effort performed at each habitat, all species accumulation curves almost reached an asymptotic phase (Fig. 2). Non-parametric methods for estimating the true species richness indicated that the inventory for each habitat was more than 90% complete. With these results, comparisons among the sampled habitats are valid (Table, 3). The general diversity for each site is shown in Table 3. All of the diversity indices estimate that the agricultural lands harbor highest diversity over all. All indices are in agreement that mixed forests to have lower diversity compared to the agricultural lands.

Dominance diversity plots show differences between habitats in abundance, distribution and dominance (Fig. 1). The shapes of the curves for MF and AL show greater evenness among species, with several species of moderate abundance and no pronounced numerical dominance. Species abundance showed little variation between the two habitats. There is an importance difference in the abundance of some species; while *Tiniocellus spinipes* (n=179) and *Aphodius* (*Calaphodius*) *moestus* (n=107) are most abundant in mixed forests, *Drepanocerus setosus* (n=90) were the most abundant in agricultural lands of the sanctuary.

Beetles belonging to all nesting strategies were present. *Tiniocellus spinipes*, a tunneler (26.75%) and *Aphodius* (*Calaphodius*) *moestus* (24.8%) and *Drepanocerus setosus* (14.49%) dwellers dominated the assemblage (Table 1). Tunnelers were the most speciose (22 species) and abundant (55.15%) while dwellers constituting three species were the second abundant (42.89%) functional group. Rollers were represented by only single *Sisyphus* sp. with least abundance (1.79 %). Smaller beetles with 11 species dominated the assemblage (75.78 % of total population), while larger beetles with 15 species representing 24.21 % of the total abundance. Within the habitat, the abundance of functional group also varied as in mixed forests, small tunnelers (44.72 %) dominated followed by dwellers (33.91 %) and large tunnelers (21.35 %) (Fig. 3). In agricultural lands the abundance of dwellers (56.08%) was found to be moderately high as compared to large tunnelers (28.41 %) and small tunnelers (11.07 %) (Fig. 3). Rollers were exclusively captured in agricultural lands.

Beta diversity:

The shared species statistics between different collection localities are given in Table 4. For comparison of diversity between different sites Bray Curtis index is calculated. The Bray Curtis index resulted in a similarity of 37.1 % between mixed forests and agricultural lands with 13 shared species between the two habitats. Within habitats the same index varied 58.3% between MF1 and MF5, 55.2% in MF1 and AL2, and 54.2% in MF3 and AL3. It was interesting to find these wide ranges of similarity values as well as significant beta diversity among sites within same habitat.

DISCUSSION

SPECIES DIVERSITY:

The first report on the diversity and composition of dung beetle community structure, in one of the protected areas viz. Singhori Wildlife Sanctuary of Central India is provided. In the present study, an attempt has been made to assess species diversity and abundance of Scarab dung beetles in mixed forests and agricultural lands of SWLS. As a result, the inventory of beetles incorporates 26 species belonging to 12 genera, 10 sub genera and two subfamilies. Eighty six species of dung beetles have been reported so far from Madhya Pradesh and Chhattisgarh (Chandra & Ahirwar, 2007; Chandra & Gupta, 2011a,b,c). Thus Species diversity of this sanctuary is comparatively low as compared to the overall diversity of dung beetles in Madhya Pradesh and Chhattisgarh.

The subfamily Scarabaeinae (n=479) is reported to be dominating (71.59%) the total population of the beetles and includes 24 species which are distributed in 11 genera and 8 subgenera under five major tribes viz. Coprini, Onitini, Oniticellini, Onthophagini and Sisyphini. Within the subfamily Scarabaeinae the dominant genus comes out *Onthophagus* (17.39% of total abundance), representing nine species under four subgenera. Aphodiinae (n=190) with 28.40% abundance includes only two species under single *Aphodius* genus within two subgenera, of which the dominant species *Aphodius* (*Calaphodius*) *moestus* was collected from all the sampling sites and uniformly distributed in SWLS (Table 2). *Onthophagus* (*Onthophagus*) *laborans* is recorded second time from Central India as Arrow (1931) recorded this species from Bombay (Maharashtra).

Abundance and distribution of coprophagous beetles in a given locality is mainly influenced by a variety of biotic and abiotic factors including, fauna, flora, solar radiation, temperature, soil type, soil pH, rainfall, and most significantly the supply of dung for food (Fincher et. al., 1970). Several studies indicated that dung beetles respond negatively to the fragmentation and transformation of natural habitats (Davis et. al., 2001; Howden & Nealis, 1975; Klein, 1987; Medina et al., 2002). In accordance diversity and composition of dung beetle assemblages in two different habitats (mixed forests and agricultural lands) of the sanctuary were compared. In addition to species richness and abundance, differences in the community species composition between both types of habitats were found. Out of 26 species, twenty species were collected in mixed forests (n=398) and nineteen species in agricultural land (n=271). Though observed richness of dung beetles is relatively high in mixed forests, all the computed diversity indices estimate that the agricultural lands harbor highest diversity over all (Table 3). AL3 showed highest species diversity with fourteen species represented from the locality. Thus the results presented here show a little variation in forests and agricultural lands.

Species richness and composition of dung beetles are directly correlated with the altitudinal variation in a particular area. Hanski (1986) stated that while one proceeds from subtropical to tropical areas to grassland habitats in temperate areas, there is a large decrease in species of family Scarabaeidae. Six species of large tunnelers viz. *Catharsius* (*Catharsius*) *sagax*, *Catharsius* (*Catharsius*) *molossus*, *Onitis brahma*, *Copris* (*Paracopris*) *imitans*, *Heliocopris gigas*, *Chironitis arrowi* and one small tunneler *Onthophagus* (*Onthophagus*) *laborans* was found to be exclusively present at high altitude (mixed forests). While five species viz. *Caccobius* sp. *Catharsius* (*Catharsius*) *pithecius*, *Copris* (*Copris*) *repertus*, *Onthophagus* (*Onthophagus*) *duporti* and *Onthophagus* (*Onthophagus*) *sternalis* are reported to occur in relatively lower altitudes (agriculture lands).

Most conspicuous differences were observed in the relative abundance, of the guild structure of the dung beetle community in the sanctuary. Tunnelers were most speciose (22 species) and abundant (55.3%) in guild after dwellers with three species representing 42.8% total population. Rollers are represented by only single *Sisyphus* sp. representing lowest richness and abundance and constrained in agricultural lands only. The abundance of rollers was significantly low as compared to the overall abundance of the beetles in the assemblage and in contrast with their high abundance and richness in South East Asian forests of Borneo (Davis et al., 2000).

Relatively high abundance of *Aphodius* (*Calaphodius*) *moestus* (24.8%) and *Drepanocerus setosus* (14.49%) leads to the dominance of dwellers after tunnelers. (Fig. 1 and Table 1) The abundance of tunnelers, dwellers and rollers in SWLS favors the composition and distribution of these guilds in moist forests of the Ivory Coast where tunnelers and dweller guilds (29.1% to 25.3%) dominate over rollers (Cambefort & Walter, 1991).

CONSERVATION PROSPECTS

Biodiversity surveys provide fundamental information needed for conservation planning, protected area justification and design, and development of management plans (Spector & Forsyth, 1998). Thus here an attempt is made to explore dung beetle diversity in the sanctuary so that this may be utilized in biodiversity conservation and management plans of the sanctuary. The occurrence and abundance of coprophagous beetles in a given locality is mainly affected by a variety of biotic and abiotic factors including fauna, flora, solar radiation, temperature, soil type, soil pH, rainfall, and most significantly the supply of dung for food (Fincher et al., 1970). There are several studies from tropical and temperate systems that indicate a severe impact of local and regional-scale anthropogenic habitat changes on patterns of dung beetle abundance and species diversity (Nichols et al., 2008). The global modification, fragmentation and loss of tropical forest habitat are reported to lead to high local extinction rates across forest restricted dung beetle communities (Nichols et al., 2007). In an investigation in the tropical rain forest in central Panama, Andresen & Laurant (2007) observed a decline in dung beetle abundances and diversities as well as altered community composition across a gradient of decreasing mammal abundance due to heavy hunting pressure and are vulnerable to habitat changes such as deforestation or shifts in the mammal faunal elements and are thought to be useful indicators of ecosystem health because of this sensitivity (Halffter et al., 1992; Klein, 1989). Moreover, the natural histories and nesting behaviors of dung beetles are well documented and understood (Hanski & Cambefort, 1991; Halffter & Edmonds, 1982; Halffter & Matthews, 1966). Thus they satisfy all of the criteria of an ideal bio-indicator for investigating impacts of anthropogenic disturbances to ecosystems.

Studies on ecology and conservation of dung beetles from India is completely lacking despite few publication. Recently Mittal (2005) studied the diversity and conservation status of dung beetles in North India wherein he reported decline in the richness and diversity of these beetles due to loss of habitat, altered food quality because of pollutants and increased cattle antibiotics and other environmental changes. Though the inventory of dung beetles from Madhya Pradesh includes eighty six species (Chandra & Ahirwar, 2007; Chandra & Gupta, 2011a,b,c), there is no publication concentrating the conservation status of these beetles from the state. The results of the study show that the abundance of tunnelers such as members of genus *Catharsius*, *Heliocopris* and *Onthophagus* is comparatively low. Larsen (Stokstad, 2004) in his study in also Venezuela noticed that it was the large beetles that disappeared first on ant disturbances effecting ecological service to the maximum as they are best at burying dung.

To conclude, species collected in this study represents patterns of diversity, richness, abundance, distribution of functional groups, altitudinal and habitat variations in dung beetle assemblage in SWLS. Using diversity measures agricultural lands found to be more diverse than mixed forests in the sanctuary. The present study tries to give a brief account on the diversity of one of protected areas from the state so that these results may be utilized in future to assess diversity and conservation problems from the region. Further studies will include more standardize additional methods of collections.

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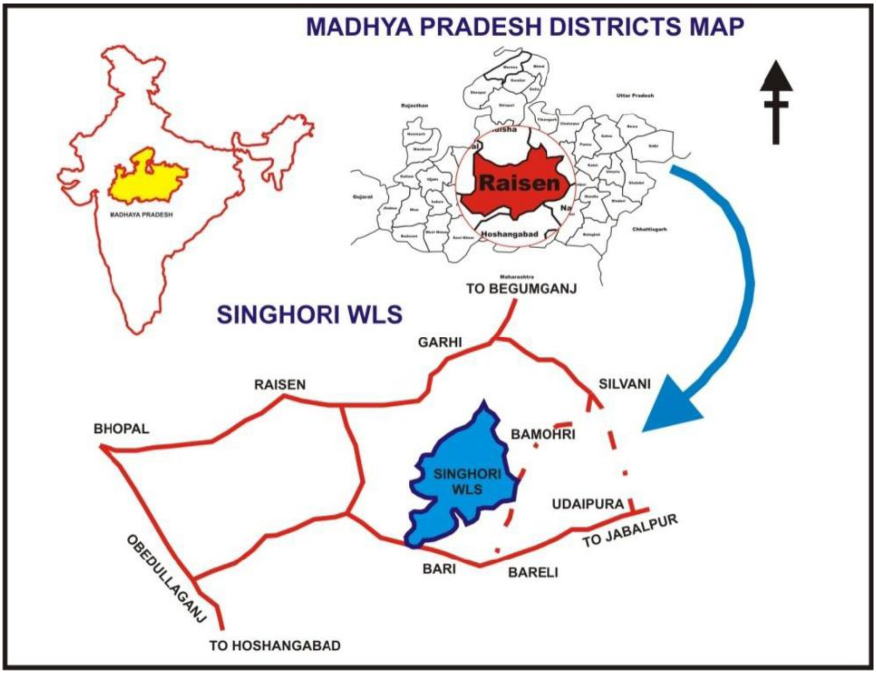

Map of SWLS

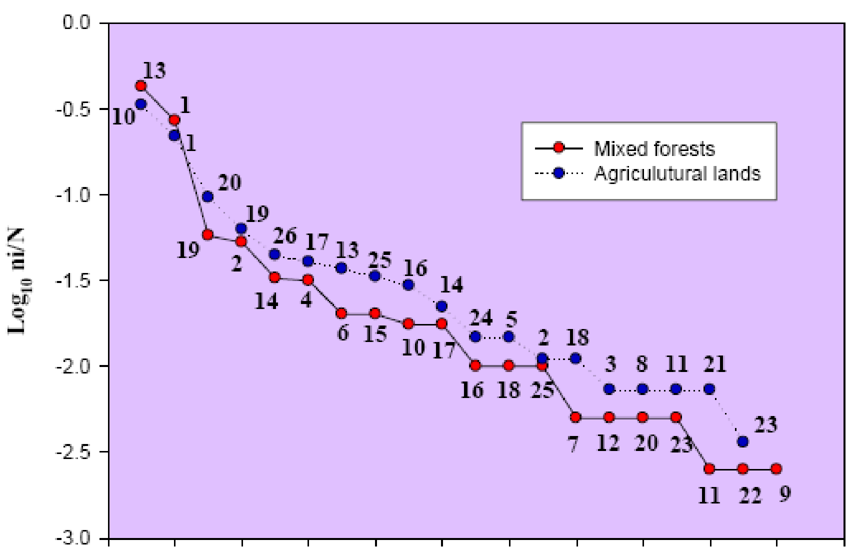

Figure 1. Dominance diversity plot. Numeric codes for each species correspond to those in Table 1.

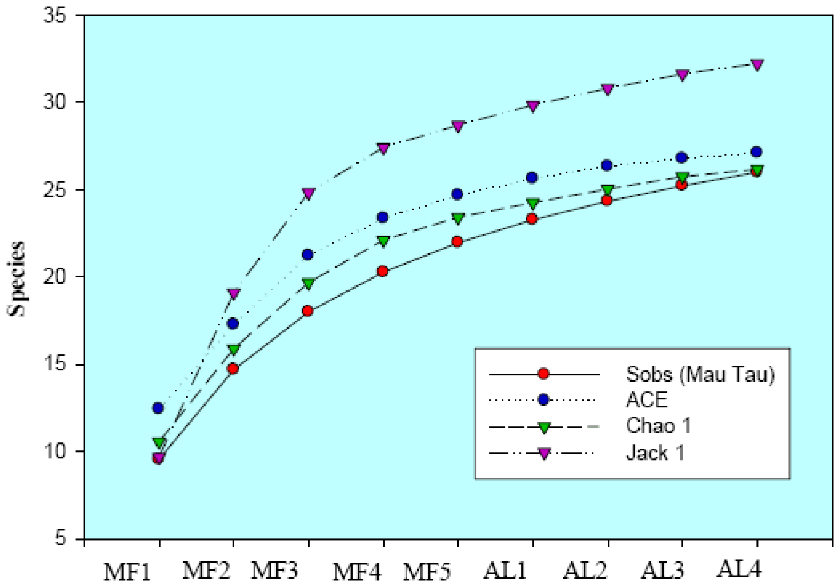

Figure 2. Randomized species accumulation curves of dung beetles for diffrent localities in SWLS.

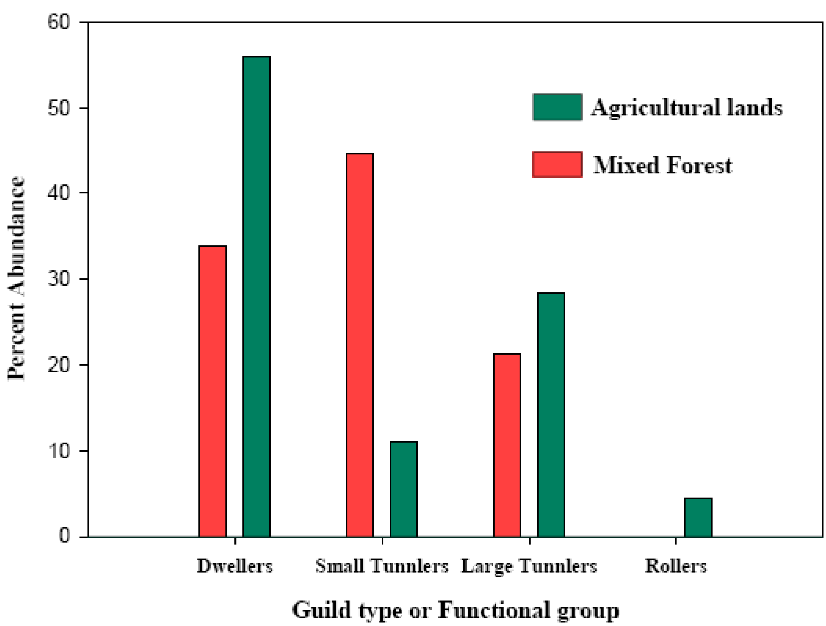

Figure 3. Comparative abundance of functional groups in agricultural landsand mixed forests.

Table 1. Number of individuals collected for each species of dung beetles per site in each habitat in Singhori Wildlife Sanctuary, Madhya Pradesh (India).

	Mixed forests					Agriculture lands					
Species	**MF$_1$**	**MF$_2$**	**MF$_3$**	**MF$_4$**	**MF$_5$**	**AL$_1$**	**AL$_2$**	**AL$_3$**	**AL$_4$**	**Total individuals**	**% of individuals**
SUBFAMILY: APHODIINAE											
1) *Aphodius* (*Calaphodius*) *moestus* Fabricius	7	44	15	19	22	9	7	10	33	166	24.8%
2) *Aphodius* (*Pharaphodius*) *crenatus* Harold	0	16	0	5	0	1	0	1	1	24	3.58%
SUBFAMILY: SCARABAEINAE											
3) *Caccobius* sp.	0	0	0	0	0	2	0	0	0	2	0.29%
4) *Catharsius* (*Catharsius*) *molossus* (Linnaeus)	3	5	0	4	0	0	0	0	0	12	1.79%
5) *Catharsius* (*Catharsius*) *pithecius* (Fabricius)	0	0	0	0	0	0	0	2	2	4	0.59%
6) *Catharsius* (*Catharsius*) *sagax* (Quenstedt)	2	1	3	2	0	0	0	0	0	8	1.19%
7) *Copris* (*Paracopris*) *imitans* Felsche	0	1	0	0	1	0	0	0	0	2	0.29%
8) *Copris* (*Copris*) *repertus* Walker	0	0	0	0	0	0	0	2	0	2	0.29%
9) *Chironitis arrowi* Janssens	0	0	1	0	0	0	0	0	0	1	0.14%
10) *Drepanocerus setosus* (Wiedmann)	0	5	0	2	0	14	0	13	63	97	14.49%
11) *Heliocopris bucephalus* (Fabricius)	0	0	1	0	0	1	0	1	0	3	0.44%
12) *Heliocopris gigas* (Linnaeus)	0	1	1	0	0	0	0	0	0	2	0.29%
13) *Tiniocellus spinipes* (Roth)	13	127	4	0	25	0	1	5	4	179	26.75%
14) *Oniticellus* (*Oniticellus*) *cinctus* (Fabricius)	5	0	8	0	0	0	0	6	0	19	2.84%
15) *Onitis brahma* Lansberge	0	0	0	8	0	0	0	0	0	8	1.19%
16) *Onitis philemon* Fabricius	0	0	2	0	2	0	0	7	1	12	1.79%
17) *Onthophagus* (*Digitonthophagus*) *gazelle* (Fabricius)	2	0	4	0	1	0	3	2	6	18	2.69%
18) *Onthophagus* (*Onthophagus*) *cervus* (Fabricius)	0	0	0	4	0	0	0	2	1	7	1.04%
19) *Onthophagus* (*Onthophagus*) *dama* (Fabricius)	8	3	4	0	8	0	0	8	9	40	5.97%
20) *Onthophagus* (*Colobonthophagus*) *hindu* Arrow	0	0	2	0	0	10	10	0	6	28	4.18%
21) *Onthophagus* (*Onthophagus*) *duporti* Boucomont	0	0	0	0	0	0	0	0	2	2	0.29%
22) *Onthophagus* (*Onthophagus*) *laborans* Arrow	0	0	0	1	0	0	0	0	0	1	0.14%
23) *Onthophagus* (*Proagoderus*) *pactolus* (Fabricius)	1	0	0	0	1	0	1	0	0	3	0.44%
24) *Onthophagus* (*Onthophagus*) *sternalis* Arrow	0	0	0	0	0	3	0	1	0	4	0.59%
25) *Onthophagus* (*Onthophagus*) *quadridentatus* (Fabricius)	2	2	0	0	0	4	1	2	2	13	1.94%
26) *Sisyphus* sp.	0	0	0	0	0	12	0	0	0	12	1.79%
Total species=26						**Total individuals:**				**669**	**100%**
Species richness/site	9	10	11	8	7	9	6	14	12		
Total individuals/site	43	205	45	45	60	56	23	62	130		
Species richness/habitat	**20**					**19**					
Total individuals/habitat	**398**					**271**					

Table 2. Data matrix for dung beetles and their natural history per habitat.

Name of the Species	Size	Guild	MF	AL
SUBFAMILY: APHODIINAE				
1) *Aphodius* (*Calaphodius*) *moestus* Fabricius	S	D	107	59
2) *Aphodius* (*Pharaphodius*) *crenatus* Harold	S	D	21	3
SUBFAMILY: SCARABAEINAE				
3) *Caccobius* sp.	S	TN	0	2
4) *Catharsius* (*Catharsius*) *molossus* (Linnaeus)	L	TN	12	0
5) *Catharsius* (*Catharsius*) *pithecius* (Fabricius)	L	TN	0	4
6) *Catharsius* (*Catharsius*) *sagax* (Quenstedt)	L	TN	8	0
7) *Copris* (*Paracopris*) *imitans* Felsche	L	TN	2	0
8) *Copris* (*Copris*) *repertus* Walker	L	TN	0	2
9) *Chironitis arrowi* Janssens	L	TN	1	0
10) *Drepanocerus setosus* (Wiedmann)	S	D	7	90
11) *Heliocopris bucephalus* (Fabricius)	L	TN	1	2
12) *Heliocopris gigas* (Linnaeus)	L	TN	2	0
13) *Tiniocellus spinipes* (Roth)	S	TN	169	10
14) *Oniticellus* (*Oniticellus*) *cinctus* (Fabricius)	L	TN	13	6
15) *Onitis brahma* Lansberge	L	TN	8	0
16) *Onitis philemon* Fabricius	L	TN	4	8
17) *Onthophagus* (*Digitonthophagus*) *gazella* (Fabricius)	L	TN	7	11
18) *Onthophagus* (*Onthophagus*) *cervus* (Fabricius)	S	TN	4	3
19) *Onthophagus* (*Onthophagus*) *dama* (Fabricius),	L	TN	23	17
20) *Onthophagus* (*Colobonthophagus*) *hindu* Arrow	L	TN	2	26
21) *Onthophagus* (*Onthophagus*) *duporti* Boucomont	S	TN	0	2
22) *Onthophagus* (*Onthophagus*) *laborans* Arrow	S	TN	1	0
23) *Onthophagus* (*Proagoderus*) *pactolus* (Fabricius)	L	TN	2	1
24) *Onthophagus* (*Onthophagus*) *sternalis* Arrow	S	TN	0	4
25) *Onthophagus* (*Onthophagus*) *quadridentatus* (Fabricius)	S	TN	4	9
26) *Sisyphus* sp.	S	R	0	12

S-small, L-large; TN- Tunneler, R- Roller, D- dweller

Table 3. Species Richness estimators per site for SWLS.

Sampling sites	Sobs (Mau Tau)	ACE	Chao 1	Jack 1	Alpha	Shannon	Simpson
Mixed forests	**19.5**	**21.13**	**19.8**	**19.5**	**4.55**	**2.01**	**4.76**
MF_1	9.56	12.43	10.56	9.68	3.28	1.69	4.96
MF_2	14.69	17.26	15.89	19.09	4.24	1.94	5.57
MF_3	17.99	21.22	19.67	24.83	4.83	2.06	5.58
MF_4	20.27	23.35	22.1	27.42	5.11	2.14	5.8
MF_5	21.96	24.68	23.41	28.68	5.17	2.17	5.79
Agricultural lands	**26**	**27.4**	**26.17**	**32.5**	**5.38**	**2.26**	**6.14**
AL_1	23.27	25.63	24.25	29.84	5.28	2.2	5.87
AL_2	24.33	26.34	25.03	30.8	5.36	2.23	6
AL_3	25.22	26.78	25.74	31.62	5.4	2.26	6.14
AL_4	26	27.1	26.17	32.22	5.38	2.26	6.14

Table 4. Data matrix with beta diversity values obtained through Bray-Curtis index with number of species per site and number of shared species.

FS	SS	OSF	OSS	SSO	Bray-Curtis
MF_1	MF_2	9	10	6	0.234
MF_1	MF_3	9	11	6	0.545
MF_1	MF_4	9	8	3	0.273
MF_1	MF_5	9	7	5	**0.583**
MF_1	AL_1	9	9	2	0.182
MF_1	AL_2	9	6	5	0.364
MF_1	AL_3	9	14	6	**0.552**
MF_1	AL_4	9	12	5	0.266
MF_2	MF_3	10	11	5	0.192
MF_2	MF_4	10	8	5	0.248
MF_2	MF_5	10	7	4	0.385
MF_2	AL_1	10	9	4	0.13
MF_2	AL_2	10	6	3	0.079
MF_2	AL_3	10	14	6	0.195
MF_2	AL_4	10	12	6	0.287
MF_3	MF_4	11	8	2	0.378
MF_3	MF_5	11	7	5	0.495
MF_3	AL_1	11	9	3	0.238
MF_3	AL_2	11	6	4	0.382
MF_3	AL_3	11	14	7	**0.542**
MF_3	AL_4	11	12	6	0.343
MF_4	MF_5	8	7	1	0.362
MF_4	AL_1	8	9	3	0.238
MF_4	AL_2	8	6	1	0.206
MF_4	AL_3	8	14	4	0.28
MF_4	AL_4	8	12	4	0.263
MF_5	AL_1	7	9	1	0.155
MF_5	AL_2	7	6	4	0.241
MF_5	AL_3	7	14	5	0.426
MF_5	AL_4	7	12	5	0.379
AL_1	AL_2	9	6	3	0.456
AL_1	AL_3	9	14	6	0.458
AL_1	AL_4	9	12	5	0.344
AL_2	AL_3	6	14	4	0.259
AL_2	AL_4	6	12	5	0.235
AL_3	AL_4	14	12	10	0.458
MF	**AL**	**20**	**19**	**13**	**0.371**

(FS= First sample; SS=Second sample; SSO = Shared species observed; OSF= Observed species in first sample; OSS=Observed species in second sample)

Plate I. A. *Onthophagus* (*Proagoderus*) *pactolus* (Fabricius), B. *Heliocopris bucephalus* (Fabricius), C. *Onthophagus* (*Onthophagus*) *dama* (Fabricius), D. *Onitis philemon* Fabricius, E. *Chironitis arrowi* Janssens, F. *Onthophagus* (*Digitonthophagus*) *gazella* (Fabricius), G. *Catharsius* (*Catharsius*) *sagax* (Quenstedt), H. *Catharsius* (*Catharsius*) *molossus* (Linnaeus).