

# Dung beetle (Coleoptera: Scarabaeinae) community structure across a forest-agriculture habitat ecotone in South Western Ghats

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**Abstract**— Ecotones are zones of transition between biomes or ecosystems. Ecotones, natural or anthropogenic, can greatly affect insect community structure across habitats. Scarabaeinae dung beetles are ideal biological indicators that are used to study effects of habitat modification, fragmentation and edge effects on biodiversity. Dung beetle community structure across a forest-agriculture habitat ecotone in South Western Ghats, a biodiversity hotspot in India was studied. Dung baited pitfall traps were used to collect dung beetles from forest, ecotone and agriculture habitat. Community attributes such as species richness, abundance, diversity, indicator and detector species were recorded in the study sites. Species composition varied between the three habitats. Greater similarity in species composition was observed between forest and ecotone. This is attributed to the presence of heliophilic species in the region, adapted to survive in forest and the open edge. Though forest recorded higher abundance, ecotone and agriculture habitat recorded higher species richness and diversity. Low diversity in forest resulted from decreased equitability in the overall forest assemblage resulting from increased dominance of few species such as *Onthophagus fuscicollis* and *O. pacificus*. Higher species richness in ecotone and agriculture habitat was associated with heliophilic species that responded positively to disturbance, whereas stenotopic species adapted to closed canopy such as *Ochicanthon mussardi* was negatively affected in the region. *Onthophagus fuscicollis*, the indicator species in the forest and ecotone was also the detector species in agriculture habitat. Presence of such species in the region that are adapted to survive in widely different habitat types is a result of decades of forest degradation and fragmentation in the Western Ghats which led to the establishment of heliophiles and synanthropic species in the region. Such increase in species richness in disturbed habitat is not considered a

positive attribute, as original species composition is altered to favor disturbance adapted species in the region.

**Keywords**— Agriculture habitat, community structure, dung beetles, ecotone, forest, heliophiles, synanthropic species, South Western Ghats.

## I. INTRODUCTION

Deforestation over the past half century, has resulted in the loss of more than a third of all forest cover worldwide (Hansen *et al.*, 2013). Nearly 70% of the world's remaining forests, lies within 1km of an edge and is in close proximity to human modified landscapes. These forest ecosystems are influenced by human activities, altered microclimate, and non-forest species invasion (Haddad *et al.*, 2015). Reduced fragment area, increased isolation, and increased edge, initiate changes in the forest ecosystems which can have unpredictable outcomes (Haddad *et al.*, 2015).

Anthropogenic edges created by habitat fragmentation affects biodiversity across ecotones (Laurance, 2000; Murcia, 1995; Risser, 1995). Ecotones are zones of transition between biomes or ecosystems (Hansen and di Castri, 1992). Ecotones can be sharp or gradual and is characterized by unique sets of environmental conditions dissimilar from the adjacent habitats, collectively called edge effects (Murcia, 1995). The intensity and direction of edge effects on population level of organisms can be extremely variable across species. Different species respond positively, negatively or neutrally to edges (Murcia, 1995; Baker *et al.*, 2002).

Invertebrates such as insects has important functional role to play in an ecosystem. Ecotones natural or anthropogenic, can greatly affect insect abundance and diversity (Didham *et al.*, 1996); faunal movement (Yahner, 1988; Wiens *et al.*, 1995, 1997; Desrochers and Fortin, 2000); population dynamics (Leopold, 1933); species interactions and

community structure (Didham *et al.*, 1998). Scarabaeinae dung beetles are a group of predominantly dung feeding detritivorous beetles, abundant and widely distributed in the terrestrial ecosystems (Halffter and Mathews, 1966). Through their dung feeding and dung burial activities, they increase soil fertility (Bertone, 2004; Bang *et al.*, 2005; Losey and Vaughan, 2006), soil permeability (Bang *et al.*, 2005); plant growth (Galbiati *et al.*, 1995, Bang *et al.*, 2005); seed dispersal (Andresen and Levy, 2004) and control populations of disease causing parasites (Hingston, 1923; Miller *et al.*, 1961). They are ideal biological indicators that are effectively used to study the effects of habitat modification, fragmentation and edge effects on biodiversity (Duraes *et al.*, 2005; Feer, 2008; Filgueiras *et al.*, 2015; Klein, 1989; Nichols *et al.*, 2008; Spector and Ayzama, 2003).

The Western Ghats in the Indian subcontinent is one of the 34 biodiversity 'hotspots' of the world (Myers, 2003; Mittermeier *et al.*, 2004). Nearly three-fourths of the natural vegetation in the ecoregion are cleared or converted. Due to their fragility, biological richness, high rates of endemism and multiple anthropogenic threats, the remaining severely fragmented forests of the Western Ghats are of major conservation priority on a global scale (Pascal, 1991). There is very limited information on effects of habitat fragmentation and creation of anthropogenic edges on ecologically important insect communities in the region. In the present study, dung beetle community structure attributes such as species richness, abundance, species composition and diversity was investigated across a forest-agriculture habitat ecotone in South Western Ghats. We hypothesize that dung beetle community structure attributes will vary across the habitats.

## II. MATERIALS AND METHODS

### 2.1 Study site

The study site Nelliampathi is located on the "edge" of Palghat gap in South Western Ghats (Pearson and Ghorpade, 1989). The collection site Kaikatty in Nelliampathi is located at 10° 31'N longitude and 76° 40'E latitude, at an elevation of 960 msI (Fig. 1). Though extensive in area, Nelliampathi forests presents a fragmented landscape interspersed by large number of plantations, dams, and roads. It is an ecologically high sensitive area forming a corridor for the movement of long ranging species such as *Panthera tigris* Linnaeus, 1758 (tiger), *Panthera pardus* Linnaeus, 1758 (leopard), *Bos gaurus* Smith, 1827 (wild gaur), and is also a crucial migratory route for *Elephas maximus* Linnaeus, 1758 (elephant) (Sukumar and Easa, 2006).

The vegetation in the forest habitat is characterized by west coast semi-evergreen forest consisting of a mixture of evergreen and deciduous trees (Kerala Forests and Wildlife Department, 2004). Mammalian fauna in the region consists of *Elephas maximus* Linnaeus, 1758 (elephant), *Bos gaurus* Smith, 1827 (gaur), *Cervus unicolor* Kerr, 1792 (sambar deer), *Sus scrofa scrofa* Linnaeus, 1758 (wild boar), *Semnopithecus sp.*(langur), *Macaca silenus silenus* Linnaeus, 1758 (lion tailed macaque), *Martes gwatkinsii* Corbet and Hill, 1992 (Nilgiri marten), *Petinomys fuscicapillus* Jerdon, 1847 (small Travancore flying squirrel), *Herpestes fuscus* Thomas, 1924 (brown mongoose), *Viverra megaspila* Blyth, 1862 (Malabar civet) (Kerala Forests and Wildlife Department, 2004). The study sites consisted of a 971 hectare reserve forest, 372 hectare agriculture habitat of banana and orange plantations and a well-defined ecotone separating the two habitats, characterized by scattered trees and less undergrowth. Traps were placed in the reserve forest, ecotone and in the portion of the agriculture habitat with the banana plantation (Fig. 2).

### 2.2 Sampling

Dung beetles were collected using dung baited pit fall traps in the year 2007-08. Three collections were made during the study period (monsoon, presummer, summer). Each collection effort involved placing ten traps each in the three habitats (forest, ecotone and agriculture habitat). Traps were placed along ten transverse transects. Each transect was composed of three traps, one trap was placed in forest, one in ecotone and one in agriculture habitat. The traps were separated by a distance of 50 m. Each transect was separated by a distance of 50 m. Traps were baited with 200g fresh cow dung. A 25 x 25 cm plastic sheet was set over each trap to protect it from rain and sun. The trap contents were collected at 12 h interval (6:00-18:00h and 18:00-6:00h). The collected beetles were identified to species levels using taxonomic keys available in Arrow (1931) and Balthasar (1963 a, b) and also by verifying with type specimens available in the Coleoptera collections of St. Joseph's College, Devagiri, Kozhikode.

### 2.3 Data analysis

For the purpose of data analysis, the diurnal and nocturnal collections and the three seasonal collections for each habitat were pooled. Sample based species accumulation curves were plotted for each habitat to assess sampling adequacy (Gotelli and Colwell, 2001). Nonparametric species richness estimator Chao 2 was used to compare observed species richness (Sobs) to estimated species richness (Gotteli and Colwell, 2001). Estimate Sv9 was used for both analyses. Indicator and detector species for each habitat was selected

by Indicator Value Method (IndVal) (Dufrene and Legendre, 1997). Shannon-Weaver diversity index ( $H'$ ) (Shannon and Weaver, 1949) was computed for each habitat. Bray-Curtis similarity coefficient (Bray and Curtis 1957) was used to quantify and compare the similarity of dung beetle species composition among habitats. SIMPER analysis was performed to assess the average percent contribution of individual species to dissimilarity between habitats (Clarke, 1993). Analysis of similarities (ANOSIM) was used to test differences in species composition between habitats. PAST 3 was used to compute all diversity analysis. Patterns in species composition of dung beetle assemblages were analysed by constructing species-abundance plot for each habitat (Whittaker, 1965). These graphs are also useful to explore attributes of the assemblage, such as species richness (number of points), evenness (slope) and number of rare species (tail of the curve).

All data used for statistical analysis were tested for normality using Anderson-Darling test. Since the data was not normally distributed, non-parametric statistics, Kruskal-Wallis H test was used to test the significant levels of variation in abundance and diversity between habitats (Sachs, 1992). Differences with a p-value  $<0.05$  was compared using Mann-Whitney Test. Statistical analysis was performed using Megastat version 10.0 (Orris, 2005).

### III. RESULTS

A total of 1425 dung beetles were collected from the three habitats during the study period; 622 beetles from forest, 460 from ecotone and 343 from agriculture habitat. Twenty one species and seven genera were collected from forest; 25 species and eight genera were collected from agriculture habitat; and 25 species and eight genera were collected from ecotone (Table 1). Species accumulation curve for forest did not reach an asymptote (Fig. 3). Chao 2 values for ecotone and agriculture habitat showed 86% inventory completeness but for forest only 44.6% inventory completeness indicating that more species could be collected in forest with additional sampling effort. Overall abundance varied significantly between habitats ( $H= 11.31$ ,  $df=2$ ,  $p<0.05$ ). Abundance between forest and ecotone; ecotone and agriculture habitat showed no significant difference ( $p>0.05$ ) but between forest and agriculture habitat showed significant difference ( $p<0.05$ ). *Onthophagus furcillifer* and *O. pacificus* were the indicator species in forest; *O. furcillifer* in edge and *O. fasciatus* in agriculture habitat. *Copris repertus* and *Paracopris cribratus* were the detector species in forest, *Onthophagus bronzeus*, *O. pacificus* and *Copris repertus* in

edge and *Caccobius meridionalis* and *Onthophagus furcillifer* in agriculture habitat (Fig 4).

Shannon-Weaver diversity ( $H'$ ) values did not vary significantly between habitats but were highest in ecotone and lowest in forest ( $H= 3.24$ ,  $df= 2$ ,  $p>0.05$ ) (Table 1; Fig.5). Bray Curtis similarity coefficient showed highest similarity between the dung beetle assemblages of forest and ecotone (77.30%) followed by ecotone and agriculture habitat (56.59%) and least similarity between agriculture habitat and forest (45.80%) (Fig.6). Percentage contribution of each species towards dissimilarity between habitats is provided in Table 2. Highest average dissimilarity was observed between forest and agriculture habitat (54.20%) contributed mainly by the species *Onthophagus pacificus* (13.79 %), *Caccobius meridionalis* (11.03%) and *Onthophagus fasciatus* (10.12%). Ecotone and agriculture habitat showed a dissimilarity of 43.38%, largely contributed by *Caccobius meridionalis* (13.32%) and *Onthophagus fasciatus* (10.80%). Forest and edge showed a dissimilarity of 22.69% principally contributed by *Onthophagus pacificus* (14.32%). Composition of assemblage varied significantly between habitats (ANOSIM;  $R= 0.34$ ,  $p = 0.0001$ ). Rank abundance plot in all the three habitats showed a steep slope as a result of dominance of few species and a long tail of several rare species (Fig.7).

### IV. DISCUSSION

In the present study, species composition varied between habitats. Ecotone shared species with forest and agriculture habitat, and least similarity existed between forest and agriculture habitat. Similarity in species composition and abundance between forest and ecotone is in contrast to results of earlier studies done across a forest-savanna ecotone in Bolivia (Spector and Ayzama, 2003), forest-cerrado ecotone in Brazil (Duraes *et al.*, 2005), bushland and agriculture habitat in Tanzania (Nielsen, 2007), forest-savanna edge and forest-roadside edge in French Guiana (Feer, 2008) and forest-pasture edges in Los Tuxtlas Biosphere Reserve (Diaz *et al.*, 2010), where species composition and abundance varied between forest and edge with significant decrease in abundance observed in edge.

Forest edges have a relatively higher temperature, lower humidity and is exposed to higher solar radiation when compared to forest interior and this impacts organisms (Kapos, 1989; Brown, 1993). Though ecotone in Nelliampathi had less shade and higher sun exposure, such microclimatic conditions did not deter forest dung beetles in the region from colonizing the edge habitat. Decades of anthropogenic pressures such as fragmentation, logging and

habitat conversion exerted on the forests in the Western Ghats (Sukumar and Easa, 2006; Latha and Unnikrishnan, 2007; Prabhakaran, 2011) had led to the establishment of heliophilic species in the forest of the region which are adapted to tolerate the warmer microclimatic conditions of the edge. Earlier studies done in forest and modified habitats had revealed the presence of heliophilic species in the region (Vinod, 2009; Sabu *et al.*, 2011, Venugopal, 2012). In addition, intrusions of wild animals from forest into the edge provides adequate food resource for dung beetles of ecotone. This is because the forests in the region is fragmented, this results in frequent incursions of long ranging herbivorous mammals such as elephant, gaur into forest edges and even agriculture habitats in the region.

High species richness and Shannon-Weaver diversity in ecotone and agriculture habitat when compared to forest is in contrast to records from Borneo (Davis *et al.*, 2001), Neotropics (Avenidaño-Mendoza *et al.*, 2005), Southeast Asia (Shahabuddin *et al.* 2005), Africa (Nielsen, 2007), and Wayanad (Vinod, 2009). Studies have shown that increase in species richness in disturbed habitats is associated with species that respond positively to disturbance whereas stenotopic species adapted to closed canopy are negatively affected (Davis *et al.*, 2001, Janzen, 1987). Such increase in species richness in disturbed habitat is not considered a positive attribute, as original species composition is altered to favor disturbance adapted species in the region (Davis *et al.*, 2001).

Nelliampathi is a mosaic of forest fragments and agriculture habitats. Decades of habitat degradation in the region has negatively affected the community attributes of dung beetles in the forest habitats of Nelliampathi. High species richness and diversity in ecotone and agriculture habitat is attributed to arrival of tourist species, adapted to disturbance, from remnant forest habitats into ecotone and agriculture habitat. Such species are *Catharsius molossus*, *Copris repertus*, *Onthophagus amphicomma*, *O. andrewesi*, *O. bronzeus*, *O. ensifer*, *O. favrei*, *O. furcillifer*, *O. insignicollis*, *O. laevis*, *O. manipurensis*, *O. pacificus*, *O. turbatus*, *Paracopris cribratus*, *Tibiodrepanus setosus*. In addition, synanthropic species with preference towards cow dung, such as *Caccobius meridionalis*, *C. gallinus*, *C. ulitor*, *Onthophagus fasciatus* and *Paracopris davisoni* were absent in forest but recorded from agriculture habitat and/or ecotone. Such movement of tourist species (Avenidaño-Mendoza *et al.*, 2005, Estrada *et al.*, 1998, Filguieras *et al.*, 2015, Quintero and Rosalin, 2005; Quintero and Halfter, 2009) and establishment of synanthropic species in a region were observed in forests of Colombia (Escobar, 2004), in guamil

patches of Guatemala (Avenidaño-Mendoza *et al.*, 2005), in pastures of Central America (Horgan, 2007), isolated fragmented forest and disturbed forests of Belize (Latha *et al.*, 2016 a, b). Low diversity values in the forest is due to decreased equitability in the overall assemblage resulting from increased dominance of certain species (Davis *et al.*, 2001) such as *O. furcillifer* and *O. pacificus* in the forest of Nelliampathi whereas stenotopic species adapted to closed canopy such as *Ochicanthon mussardi* was negatively affected in the region.

The indicator species selected for each habitat are highly specific to that particular environment (McGeoch *et al.*, 2002), and are therefore more susceptible to changes in a habitat while detector species possess moderate specificity, with different degrees of preference among various ecological states (McGeoch *et al.*, 2002). The presence of *O. furcillifer*, as the indicator species for both forest and ecotone and detector species in agriculture habitat indicates the establishment of heliophilic beetles tolerant to open habitat in the forests of Nelliampathi.

## V. CONCLUSION

This is the first reported study on the effects of habitat fragmentation and creation of anthropogenic edges on dung beetle community structure across habitats in South Western Ghats. Decades of anthropogenic disturbance in the region has resulted in the establishment of heliophiles and synanthropic species. Further deterioration of the forests can lead to species loss in the region (Sabu *et al.*, 2011). Hence, it is recommended to conduct similar studies to fully understand the effects of anthropogenic disturbance on biodiversity of the South Western Ghats, as such studies assists to plan adequate conservation strategies for the region in the future.

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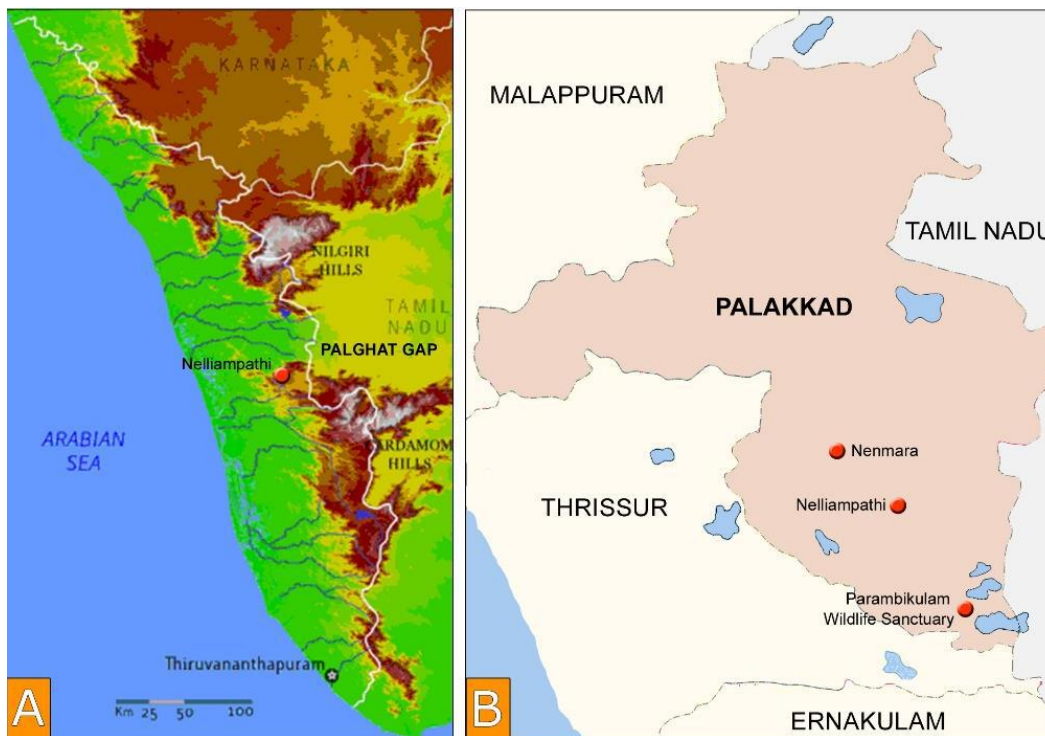


Fig. 1: A. Map showing Western Ghats; B. Map of study region Nelliampathi.





Fig. 2: Habitat types under study in Nelliampathi in South Western Ghats, A. Semi-evergreen forest; B. Ecotone; C. Agriculture habitat.

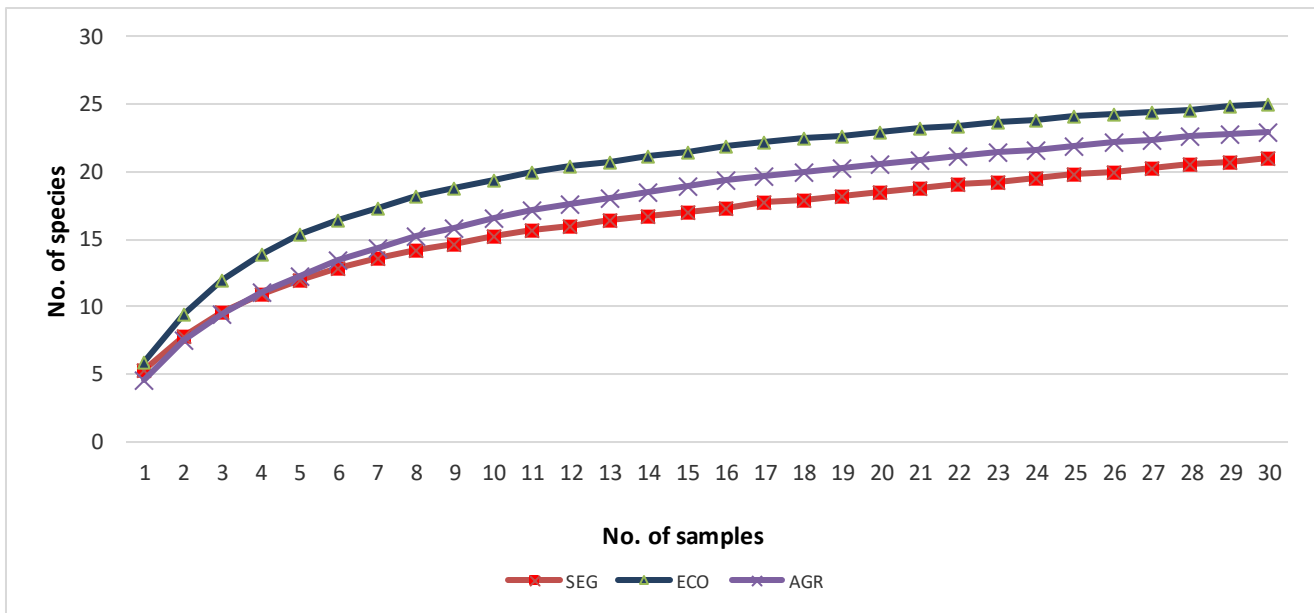


Fig. 3: Sample based species accumulation curve (Mao Tau) for dung beetles collected from a semi-evergreen forest (SEG), ecotone (ECO) and agriculture habitat (AGR) of Nelliampathi in South Western Ghats for the 2007-08 study period.

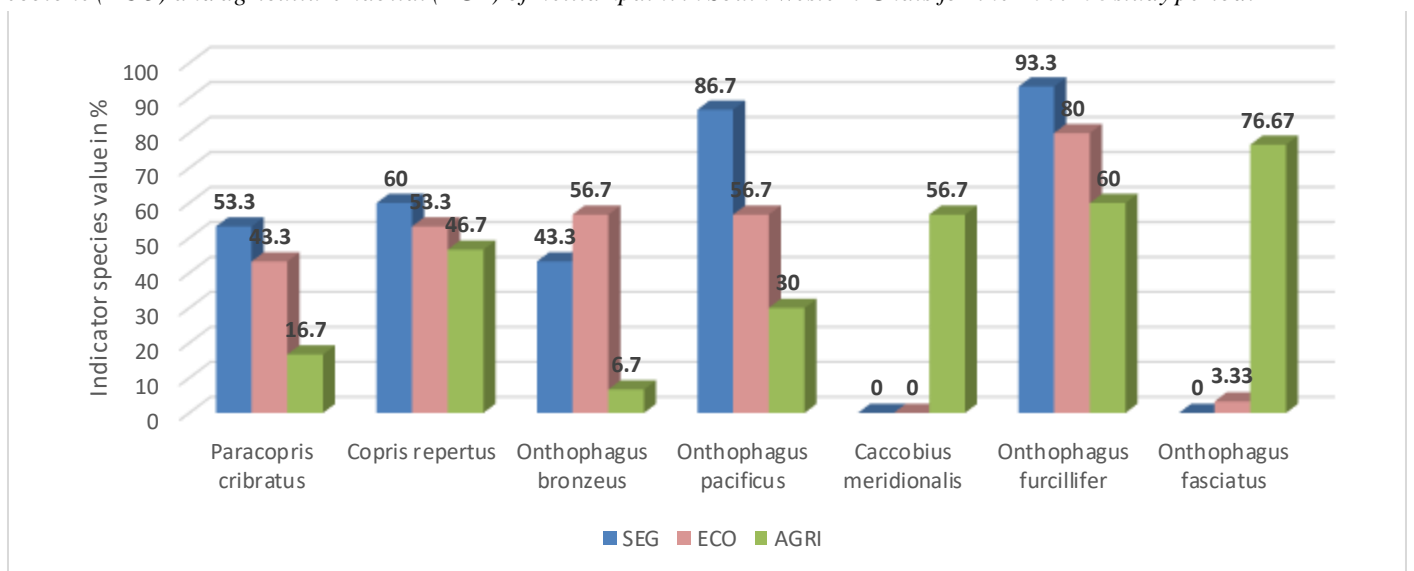


Fig. 4: Indicator and detector species of dung beetles in a semi-evergreen forest (SEG), ecotone (ECO) and agriculture habitat (AGR) of Nelliampathi in South Western Ghats for the 2007-08 study period.



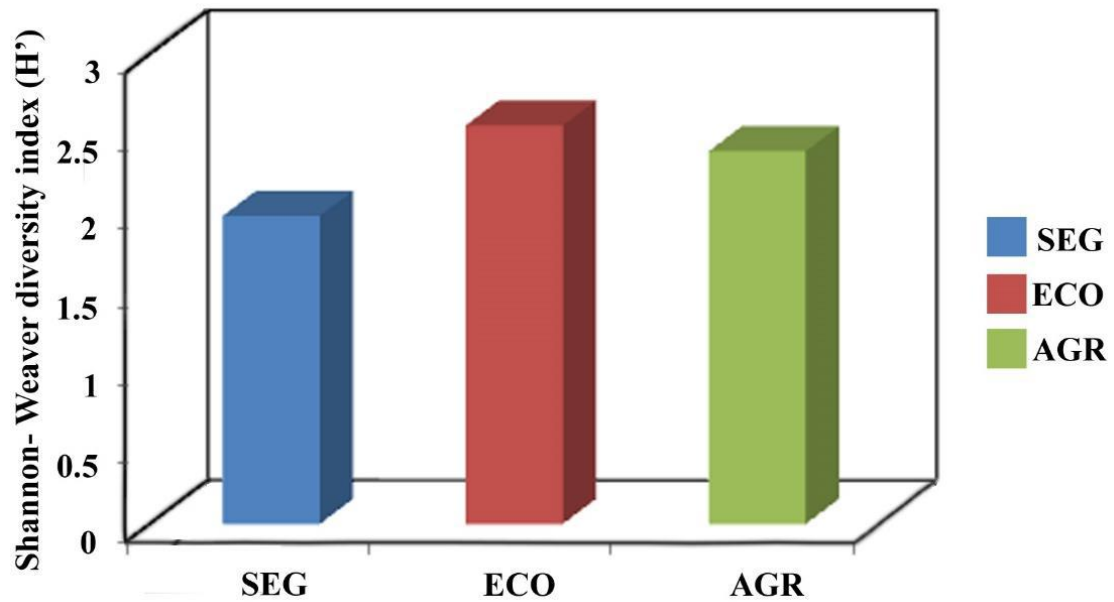


Fig. 5: Shannon-Weaver diversity Index ( $H'$ ) values in a semi-evergreen forest (SEG), ecotone (ECO) and agriculture habitat (AGR) of Nelliampathi in South Western Ghats for the 2007-08 study period.

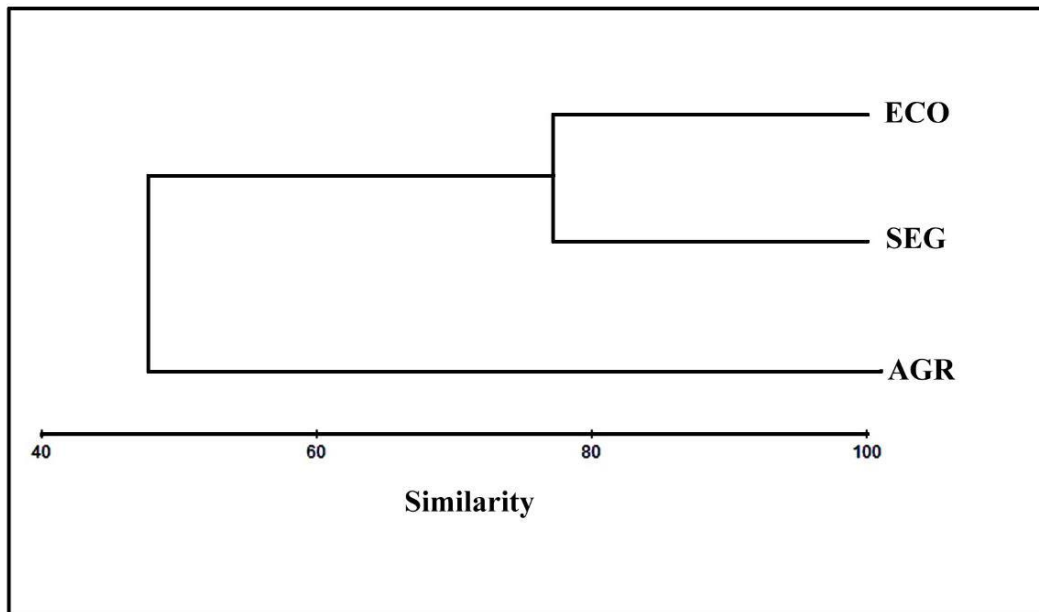


Fig.6: Cluster diagram of Bray Curtis Similarity Index between semi-evergreen forest (SEG), ecotone (ECO) and agriculture habitat (AGR) of Nelliampathi in South Western Ghats for the 2007-08 study period.

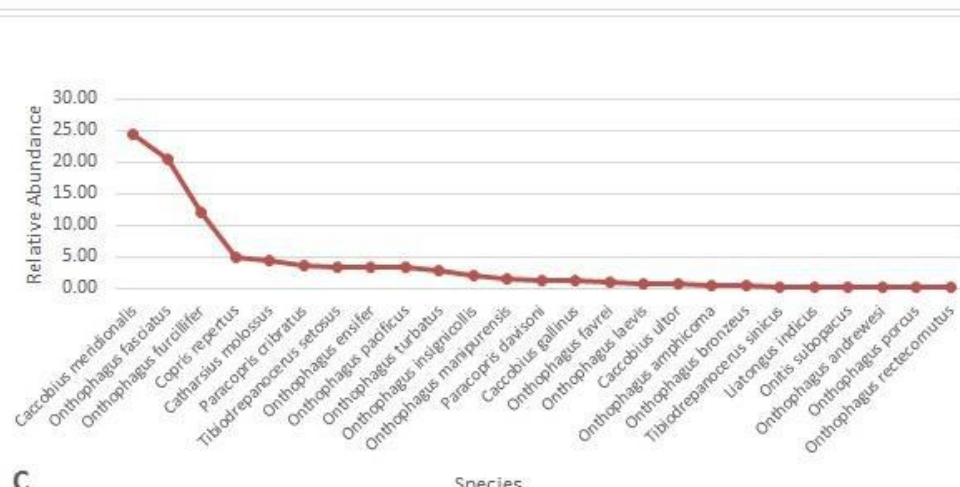
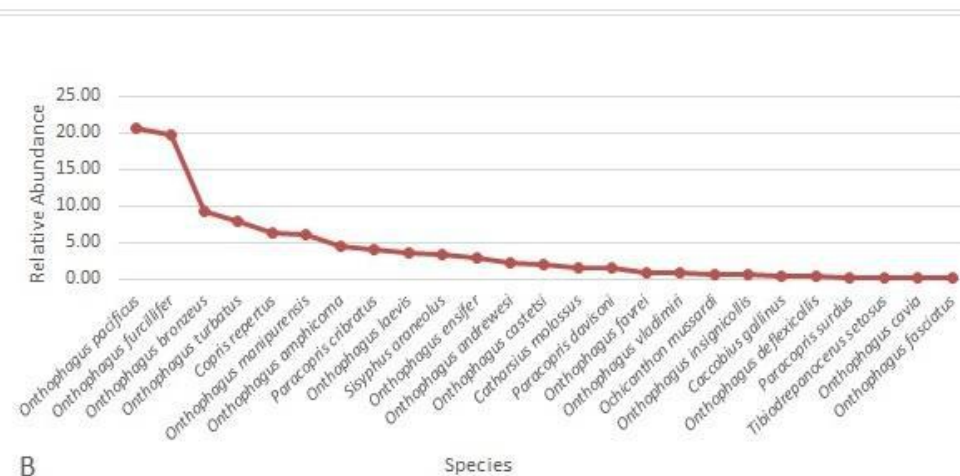
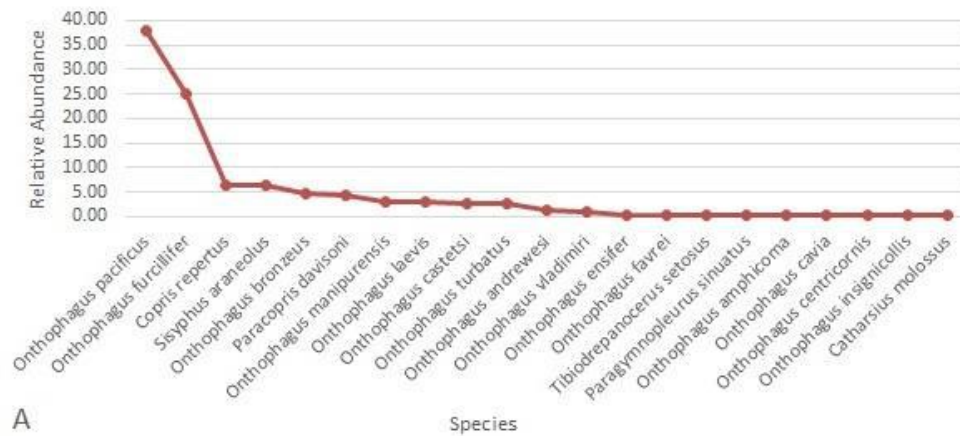


Fig. 7: Species abundance curve for dung beetle species in a semi-evergreen forest (SEG), ecotone (ECO) and agriculture habitat (AGR) of Nelliampathi in South Western Ghats for the 2007-08 study period.

Table 1: Dung beetle species abundance, overall abundance, species richness, Chao 2, Shannon-Weaver diversity index ( $H'$ ) values in a semi-evergreen forest (SEG), ecotone (ECO) and agriculture habitat (AGR) of Nelliampathi in South Western Ghats for the 2007-08 study period.

| Species                           | SEG            | ECO           | AGR             |
|-----------------------------------|----------------|---------------|-----------------|
| <i>Caccobius gallinus</i>         | 0              | 2             | 5               |
| <i>Caccobius meridionalis</i>     | 0              | 0             | 88              |
| <i>Caccobius ultor</i>            | 0              | 0             | 3               |
| <i>Catharsius molossus</i>        | 1              | 7             | 12              |
| <i>Copris repertus</i>            | 28             | 29            | 27              |
| <i>Liatongus indicus</i>          | 0              | 0             | 1               |
| <i>Ochicanthon mussardi</i>       | 0              | 3             | 0               |
| <i>Onitis subopacus</i>           | 0              | 0             | 1               |
| <i>Onthophagus amphicoma</i>      | 1              | 21            | 3               |
| <i>Onthophagus andrewesi</i>      | 8              | 7             | 1               |
| <i>Onthophagus bronzeus</i>       | 29             | 39            | 2               |
| <i>Onthophagus castetsi</i>       | 16             | 9             | 0               |
| <i>Onthophagus cavia</i>          | 1              | 1             | 0               |
| <i>Onthophagus centricornis</i>   | 1              | 0             | 0               |
| <i>Onthophagus deflexicollis</i>  | 0              | 2             | 0               |
| <i>Onthophagus ensifer</i>        | 3              | 13            | 12              |
| <i>Onthophagus fasciatus</i>      | 0              | 1             | 74              |
| <i>Onthophagus favrei</i>         | 2              | 6             | 5               |
| <i>Onthophagus furcillifer</i>    | 155            | 91            | 44              |
| <i>Onthophagus insignicollis</i>  | 1              | 2             | 2               |
| <i>Onthophagus laevis</i>         | 18             | 17            | 4               |
| <i>Onthophagus manipurensis</i>   | 19             | 28            | 8               |
| <i>Onthophagus pacificus</i>      | 235            | 96            | 13              |
| <i>Onthophagus porcus</i>         | 0              | 0             | 1               |
| <i>Onthophagus rectecornutus</i>  | 0              | 0             | 1               |
| <i>Onthophagus turbatus</i>       | 16             | 36            | 12              |
| <i>Onthophagus vladimiri</i>      | 7              | 4             | 0               |
| <i>Paracopris cribratus</i>       | 40             | 18            | 7               |
| <i>Paracopris davisoni</i>        | 0              | 7             | 6               |
| <i>Paracopris surdus</i>          | 0              | 1             | 0               |
| <i>Paragymnopleurus sinuatus</i>  | 1              | 0             | 0               |
| <i>Sisyphus araneolus</i>         | 39             | 15            | 0               |
| <i>Tibiodrepanus setosus</i>      | 1              | 1             | 10              |
| <i>Tibiodrepanus sinicus</i>      | 0              | 0             | 1               |
| Abundance                         | 622            | 460           | 343             |
| Species Richness                  | 21             | 25            | 25              |
| Chao 2                            | 44.68<br>(47%) | 2903<br>(86%) | 28.8<br>(86.8%) |
| Shannon-Weaver diversity ( $H'$ ) | 1.97           | 2.55          | 2.3             |

Table 2: Percentage contribution of species towards dissimilarity between a semi- evergreen forest, ecotone and agriculture habitat of Nelliampathi in South Western Ghats for the 2007-08 study period.

| Species                          | Semi-evergreen forest v/s Ecotone | Ecotone v/s Agriculture habitat | Semi-evergreen forest v/s Agriculture habitat |
|----------------------------------|-----------------------------------|---------------------------------|---|
| <i>Caccobius gallinus</i>        | 3.63                              | 1.17                            | 2.63  |
| <i>Caccobius meridionalis</i>    | 0                                 | 13.32                           | 11.03   |
| <i>Caccobiu sultor</i>           | 0                                 | 2.46                            | 2.04  |
| <i>Catharsius molossus</i>       | 4.22                              | 1.16                            | 2.9   |
| <i>Copris repertus</i>           | 0.24                              | 0.27                            | 0.11  |
| <i>Liatongus indicus</i>         | 0                                 | 1.42                            | 1.18  |
| <i>Ochicanthon mussardi</i>      | 4.44                              | 2.46                            | 0   |
| <i>Onitis subopacus</i>          | 0                                 | 1.42                            | 1.18  |
| <i>Onthophagus amphicoma</i>     | 9.19                              | 4.05                            | 0.86  |
| <i>Onthophagus andrewesi</i>     | 0.86                              | 3.07                            | 2.15  |
| <i>Onthophagus bronzeus</i>      | 3.01                              | 7.3                             | 4.67  |
| <i>Onthophagus castetsi</i>      | 2.56                              | 4.26                            | 4.7   |
| <i>Onthophagu scavia</i>         | 0                                 | 1.42                            | 1.18  |
| <i>Onthophagus centricornis</i>  | 2.56                              | 0                               | 1.18  |
| <i>Onthophagus deflexicollis</i> | 3.63                              | 2.01                            | 0   |
| <i>Onthophagus ensifer</i>       | 4.8                               | 0.2                             | 2.04  |
| <i>Onthophagus fasciatus</i>     | 2.56                              | 10.8                            | 10.12   |
| <i>Onthophagus favrei</i>        | 1.5                               | 0.34                            | 0.97  |
| <i>Onthophagus furcillifer</i>   | 7.46                              | 4.13                            | 6.84  |
| <i>Onthophagus insignicollis</i> | 1.88                              | 0.45                            | 0.49  |
| <i>Onthophagus laevis</i>        | 0.62                              | 2.84                            | 2.64  |
| <i>Onthophagus manipurensis</i>  | 2.39                              | 3.5                             | 1.8   |
| <i>Onthophagus pacificus</i>     | 14.32                             | 8.72                            | 13.79   |
| <i>Onthophagus porcus</i>        | 0                                 | 1.42                            | 1.18  |
| <i>Onthophagus rectecornutus</i> | 0                                 | 1.42                            | 1.18  |
| <i>Onthophagus turbatus</i>      | 5.13                              | 3.6                             | 0.63  |
| <i>Onthophagus vladimiri</i>     | 1.66                              | 2.84                            | 3.11  |
| <i>Paracopris cribratus</i>      | 5.34                              | 2.27                            | 4.33  |
| <i>Paracopris davisoni</i>       | 6.79                              | 0.28                            | 2.88  |
| <i>Paracopris surdus</i>         | 2.56                              | 1.42                            | 0   |
| <i>Paragymnopleurus sinuatus</i> | 2.56                              | 0                               | 1.18  |
| <i>Sisyphus araneolus</i>        | 6.08                              | 5.5                             | 7.34  |
| <i>Tibiodrepanus setosus</i>     | 0                                 | 3.07                            | 2.54  |
| <i>Tibiodrepanus sinicus</i>     | 0                                 | 1.42                            | 1.18  |