SYSTEMATICS AND ECOLOGY OF DUNG BEETLES (COLEOPTERA: SCARABAEIDAE: SCARABAEINAE) IN THE NELLIAMPATHI REGION OF SOUTH WESTERN GHATS

Thesis submitted to the
UNIVERSITY OF CALICUT
in partial fulfilment of the requirements for the award of the degree of
DOCTOR OF PHILOSOPHY IN ZOOLOGY

By

Latha Mathews

Under the guidance

Dr. Sabu K. Thomas

P.G. & RESEARCH DEPARTMENT OF ZOOLOGY
ST. JOSEPH'S COLLEGE, DEVAGIRI
CALICUT - 673008, KERALA

2013

P.G. & RESEARCH DEPARTMENT OF ZOOLOGY
ST. JOSEPH'S COLLEGE, DEVAGIRI
CALICUT - 673 008, KERALA
INDIA

Dr. Sabu K. Thomas
Associate Professor

☎ 91- 495-2352145 (O), 91-9447349744 (M)

CERTIFICATE

Certified that the thesis entitled "**Systematics and Ecology of Dung Beetles (Coleoptera: Scarabaeidae: Scarabaeinae) in the Nelliampathi region of South Western Ghats**" submitted by **Mrs. Latha Mathews** to the University of Calicut for the award of the degree of Doctor of Philosophy in Zoology, is a bonafide record of research work done by her in this department under my guidance and supervision. This has not previously formed the basis for any award of degree or diploma.

Mrs. Latha Mathews has succesfully completed the preliminary qualifying examination prescribed by the University of Calicut.

Place : Devagiri
Date : 02-01-2013

Sabu K. Thomas

DECLARATION

I do hereby declare that the thesis entitled "**Systematics and Ecology of Dung Beetles (Coleoptera: Scarabaeidae: Scarabaeinae) in the Nelliampathi region of South Western Ghats**" submitted to the University of Calicut for the award of the Degree of Doctor of Philosophy in Zoology has not been submitted for the award of any other degree or diploma and represents the original work done by me.

Place : Devagiri

Date : 02-01-2013

Latha Mathews

Latha Mathews

ACKNOWLEDGEMENTS

With immense pleasure I record my profound sense of gratitude to **Dr. Sabu K. Thomas**, my guide and supervisor, Associate Professor, P.G. and Research Dept. of Zoology, St. Joseph's College, Devagiri, Calicut, for introducing me to the fascinating world of beetles. I am extremely thankful for his tireless mentoring, guidance, inspiration and constant encouragement throughout the course of this study.

I am grateful to the **Principal**, St. Joseph's College, Devagiri, Calicut for providing all the necessary facilities during the course of my work.

I express my sincere thanks to **Dr. A.T. Thomas**, Head, P.G. and Research Dept. of Zoology, St. Joseph's College, Devagiri for providing me the required facilities throughout my research work and for his support, understanding and encouragement.

I wish to express my sincere thanks to all the staff members of the P.G. and Research Dept. of Zoology, St. Joseph's College, Devagiri for all the help rendered during the course of my research.

I am grateful to the **Chief Wild life Warden**, Kerala, for providing all the necessary facilities during the course of my work.

I am extremely thankful to my friends **Arunraj C.**, **Nirdev P.M.**, **Shobana K.A.**, **Aswati P.** and **Seena C.M.** who were of tremendous help to me throughout the course of my research, especially towards the end this thesis would not have been possible without their assistance.

I am deeply indebted to my family for their wholehearted support, cooperation, encouragement and prayers which formed the basis of my research work. Above all I thank God for blessing me with health and confidence to carry out the work successfully.

CONTENTS

	Page No.
Chapter 1: **INTRODUCTION**	
1.1. Taxonomy of dung beetles	2
1.2. Ecology of dung beetles	4
1.2.1. Diversity	4
1.2.2. Functional guild composition	5
1.2.3. Temporal guild composition	7
1.2.4. Seasonality	7
1.2.5. Biological indicator	8
1.2.6. Habitat specificity	9
1.2.7. Habitat modifications	11
1.2.8. Edge effect	13
1.3. Significance of the study	15
1.4. Objectives	18
Chapter 2: **REVIEW OF LITERATURE**	
2.1 Taxonomy of dung beetles	19
2.1.1 Taxonomy of dung beetles of the World	19
2.1.2. Taxonomy of dung beetles of the Indian region	22
2.2. Ecology of dung beetles	25
2.2.1. Diversity	25
2.2.2. Functional guild composition	27
2.2.3. Temporal guild composition	29
2.2.4. Seasonality	31
2.2.5. Biological indicator	32
2.2.6. Habitat specificity	34
2.2.7. Habitat modifications	34
2.2.8. Edge effect	39
2.2.9. Ecology and biology of dung beetles in India	40
Chapter 3: **MATERIALS AND METHODS**	
3.1. Study region	43
3.1.1. Study site	45

3.2. Sampling methodology 47
3.3. Preservation and identification 48
3.4. Checklist and pictorial key 50
3.5. Diversity analysis 50
3.6. Statistical analysis 55
Chapter 4: **RESULTS**
4.1. Taxonomy 59
4.1.1. Check list of dung beetles of Nelliampathi region 60
4.1.2. Pictorial key to the dung beetles of Nelliampathi region 75
4.2. Ecology 89
4.2.1. Forest habitat 89
4.2.1.1. Abundance, species richness and diversity 89
4.2.1.2. Functional guild composition 90
4.2.1.3. Temporal guild composition 90
4.2.1.4. Seasonality 91
4.2.2. Agriculture habitat 92
4.2.2.1. Abundance, species richness and diversity 92
4.2.2.2. Functional guild composition 94
4.2.2.3. Temporal guild composition 94
4.2.2.4. Seasonality 94
4.2.3. Edge 96
4.2.3.1. Abundance, species richness and diversity 96
4.2.3.2. Functional guild composition 97
4.2.3.3. Temporal guild composition 97
4.2.3.4. Seasonality 98
4.2.4. Comparative analysis of dung beetle assemblages of semi-evergreen forest, agriculture habitat and ecotone of Nelliampathi region 99
Chapter 5: **DISCUSSION**
5.1. Taxonomy 154
5.2. Ecology 155
5.2.1. Forest 155
5.2.1.1. Abundance, species richness and diversity 155

5.2.1.2. Functional guild composition 159
5.2.1.3. Temporal guild composition 161
5.2.1.4. Seasonality 162
5.2.2. Agriculture habitat 165
5.2.2.1. Abundance, species richness and diversity 165
5.2.2.2. Functional guild composition 166
5.2.2.3. Temporal guild composition 167
5.2.2.4. Seasonality 168
5.2.3. Edge 170
5.2.3.1. Abundance, species richness and diversity 170
5.2.3.2. Functional guild composition 171
5.2.3.3. Temporal guild composition 172
5.2.3.4. Seasonality 172
5.2.4. Comparative study on dung beetle assemblages across a forest-agriculture habitat ecotone with reference to edge effects 173
Chapter 6: **CONCLUSION** 188
Chapter 7: **REFERENCES** 191

LIST OF PLATES I
LIST OF FIGURES II
LIST OF TABLES V
LIST OF SYMBOLS AND ABBREVIATIONS VIII

INTRODUCTION

Latha Mathews “Systematics and ecology of dung beetles (coleoptra: scarabaeidae: scarabaeinae) in the Nelliampathi region of South Western Ghats” Thesis. Department of Zoology, St. Joseph's College Devagiri , University of Calicut, 2013

Chapter 1

INTRODUCTION

Dung beetles belong to three sub families of Scarabaeidae (Insecta: Coleoptera), the Aphodiinae, Geotrupinae and Scarabaeinae and are characterized by their use of dung and other organic debris at the larval and adult stages (Scheffler 2002). World wide there are approximately 6000 species of Scarabaeinae the true dung beetles, which are predominantly coprophagous (faeces eating) included in approximately 200 genera (Halffter 1991; Krajcik 2006). The majority of Aphodiinae and Geotrupinae are saprophagous (eaters of decaying organic matter) (Halffter & Matthews 1966; Scheffler 2002). The Scarabaeinae subfamily is cosmopolitan in distribution, found in tropical and warm-temperate areas where the average temperature exceeds 15^{o}C and average precipitation exceeds 250 mm per year (Halffter 1991).

Coprophagy is the fundamental feature of the biology of Scarabaeinae and the one which determines the characteristics of their behaviour, distribution, morphology and development. Scarabaeinae exhibits a number of morphological adaptations, both in larval and adult stages related to coprophagy (Halffter & Matthews 1966). The head in adult beetles have a rather well developed broad clypeus overhanging the mouth, capable of shoveling earth and dung (Arrow 1931). The mouth parts in adult is adapted to feed on liquid and colloidal content of more or less fresh dung (microorganisms and undigested food molecules) where as in larvae, it is of typical chewing type adapted to feed on solid contents of partially dried dung, several weeks or months old (Halffter & Mathews 1966). The extraordinarily long and coiled intestine of the adult when compared to the larvae is an adaptation to this special type of microphagous coprophagy (Halffter & Mathews 1966). The legs, especially the fore legs are useful digging implements with well developed muscles. In ball rolling genera the four posterior legs are slender for rolling dung balls and for making shallow burrows in loose soil (Arrow 1931). In Scarabaeinae, the middle coxae are widely separated and the hind pair of leg attached far back on the greatly developed metasternum. A considerable mass of dung can thus be held between the legs and compressed into globular shape (Arrow 1931). Dung beetles have low fecundity which is directly related to the high degree of brood care involved and their larval development is shorter owing to the perishable nature of the food on which the larva subsists (Halffter & Mathews 1966).

Dung beetles play an important role in the ecosystem through their dung feeding behaviour. They aerate the soil, improve its structure and water circulation, increase the content of organic carbon, nitrogen and other nutrients (Rougon & Rougon 1991); remove dung from the soil surface (Tyndale-Biscoe 1994); protect seeds from predation (Estrada & Coates-Estrada 1991; Feer 1999; Andresen 2001); and reduce populations of disease-causing organisms such as flies and hookworms by competing for food (faecal) resources and destroying their eggs and larvae (Halffter & Mathews 1966; Smith 2004).

1.1. Taxonomy of dung beetles

Dung beetle taxonomy is well studied, the major contributors being Arrow 1931, Janssens 1949, Balthasar 1963a, b and Lawrence & Newton 1995. Arrow (1931) placed dung beetles in four divisions (=tribes): Scarabaeini, Sisyphini, Coprini and Panelini which he placed under the subfamily Coprinae with which he considered the Scarabaeinae synonymous. Janssens (1949) subdivided Scarabaeinae into six tribes: Coprini, Eurysternini, Oniticellini, Onitini, Onthophagini and Scarabaeini. Balthasar (1963a, b) ranked the dung beetles into two distinct subfamilies: Coprinae and Scarabaeinae. The former subfamily included the tribes Coprini, Dichotomini, Phanaeini, Oniticellini, Onitini, and Onthophagini whereas the latter subfamily included the tribes Eucraniini, Eurysternini, Canthonini, Gymnopleurini, Scarabaeini and Sisyphini. Lawrence & Newton (1995) classified dung beetles into 12 tribes which included Coprini, Dichotomini, Phanaeini, Oniticellini, Onitini, Onthophagini, Eucraniini, Eurysternini, Canthonini, Gymnopleurini, Scarabaeini and Sisyphini and included them in the subfamily Scarabaeinae with which he considered the Coprinae synonymous. New phylogenic studies based on 200 internal and external morphological characters support this classification (Philips *et al*. 2004) and indicate that the subdivision of dung beetles into two subfamilies-Scarabaeinae and Coprinae (Balthasar 1963a, b), is not supportable as ball-rolling taxa are polyphyletic. The classification system of Lawrence & Newton (1995) is being widely followed in recent taxonomic and ecological works (Davis *et al*. 2002; Scheffler 2002, 2005; Arellano & Halffter 2003; Vinod 2009; Sabu *et al*. 2011a). In the present study also the classification system of Lawrence & Newton (1995) is followed.

1.2. Ecology of dung beetles

1.2.1. Diversity

Species diversity of a landscape includes, the richness of species in the individual communities that make up the landscape (alpha diversity) and the degree of difference between those communities (beta diversity) (Arellano & Halffter 2003). Taxonomic diversity, another measure of biodiversity is the number of taxon represented in a habitat (Magurran 2004). Measure of taxonomic diversity has potential in environmental monitoring (Clarke & Warwick 1998, 1999) and conservation priorities (Vane-Wright *et al.* 1991; Vane-Wright 1996; Williams 1996).

Dung beetles are recognized as a useful taxon for describing and monitoring spatial and temporal patterns of biodiversity (Favila & Halffter 1997; Spector & Forsyth 1998; Davis *et al.* 2001). Studies on species richness and diversity of dung beetle assemblages conducted across different habitats (Hanski & Krikken 1991; Hill 1993, 1996; Estrada *et al.* 1998; Lobo 2000; Shahabuddin *et al.* 2005; Nielsen 2007; Arellano *et al.* 2008; Navarrete & Halffter 2008; Vinod 2009) typically reveal more unique species than species in common, signifying that communities are variable in time and/or space within a broad geographical area.

The species diversity of dung beetles is not as high compared with many other groups of insects. Competition probably limits the number of extant dung beetle species world wide (Hanski 1991). Pattern in species richness of dung beetles shows an increase in species number with decreasing latitudes and decrease in species richness with increasing altitude (Hanski & Cambefort 1991d). Three aspects of mammalian species richness have direct consequences for dung beetles, the general abundance of mammals determines the level of availability of resources for dung beetles; range of different kinds of mammals determines the range of dung types available; and the size of mammals is important to large species of dung beetles which are dependant on large droppings for breeding (Hanski & Cambefort 1991d).

Habitat heterogeneity is another parameter that determines species diversity at a regional scale (Schoener 1974; Huston 1994; Rosenzweig 1995; Begon *et al*. 1996). Habitat heterogeneity generally increases species diversity by enabling species that are competitively inferior in one habitat to be competitively superior in another (Krell-Westerwalbesloh *et al.* 2004).

Studies on diversity of dung beetle assemblages across different habitats in a given geographic region helps us to understand the factors that influence the dung beetle richness and diversity and influence of habitat modifications on the same (Avendaño-Mendoza *et al.* 2005; Quintero & Rosalin 2005; Shahabuddin *et al*. 2005; Halffter *et al.* 2007; Vinod 2009).

1.2.2. Functional guild composition

Food used by most Scarabaeinae in both larval and adult stages is the excrement of large mammals, especially Bovidae and man (Halffter & Mathews 1966). They use this substrate in different ways for feeding and breeding by which they are classified into guilds. Cambefort & Hanski (1991) classified dung beetles into three functional groups namely, dwellers, tunnelers and rollers. Dwellers eat their way through the dung and most species deposit their eggs in dung pats without constructing any kind of nest or chamber. Tunnelers dig a more or less vertical tunnel below the dung pat and transport dung into the bottom of the burrow; this resource may be used either for adult feeding or breeding. Rollers make balls of dung, a transportable resource unit, rolls it for a shorter or longer distance before burying it at a suitable spot. Some adult tunnelers and rollers feed directly in dung pats, but many others feed on their relocated dung reserves (Cambefort & Hanski 1991). In Scarabaeinae, dung rolling is associated with tribes Scarabaeini, Gymnopleurini, Sisyphini and Canthonini, dwelling with tribe Oniticellini and tunneling with tribes Coprini, Onitini and Onthophagini (Hanski & Cambefort 1991b).

Studies on the functional guild composition of dung beetles in diverse habitats like undisturbed forest, secondary forest, cropland, cattle pastures, edge between habitats across the world revealed significant differences, as the different ecological parameters influencing functional guild composition vary with habitats (Klein 1989; Cambefort & Walter 1991; Estrada *et al.* 1999; Vulinec 2000; Spector & Ayzama 2003; Escobar 2004; Navarrete & Halffter 2008; Vinod 2009). A general trend of decline in size of dung beetle population composing each guild was observed in fragmented forests across the world (Howden & Nealis 1975; Peck & Forsyth 1982; Klein 1989; Gill 1991; Estrada & Coates-Estrada 2002).

1.2.3. Temporal guild composition

The exact time and place of appearance of feces is unpredictable in natural habitats and they are patchily distributed. Furthermore, they are mostly used up by dung beetles within less than 24 h (Krell-Westerwalbesloh *et al.* 2004). Hence success of any species is determined by its early arrival at the resource (Doube 1987; Hanski 1989). Thus temporal differentiation appears particularly relevant in tropical forests where high rates of exploitation of carrion and dung occur (Feer & Pincebourde 2005) and is an important parameter determining their success (Hanski 1990). It is a widespread mechanism to avoid competition between closely related species or phylogenetically distant groups (Krell-Westerwalbesloh *et al.* 2004).

Diel periodicity studies commonly distinguishes two major groups of dung beetle species namely, nocturnal and diurnal. Temporal guild composition of different habitats varies and is influenced by vegetation cover, physical parameters and trophic resource availability (Fincher *et al*. 1971; Walter 1985; Gill 1991; Davis 1999; Krell-Westerwalbesloh *et al*. 2004; Feer & Pincebourde 2005). Temporal guild composition was also found to be influenced by habitat modification. Large-bodied, nocturnal species with specific requirements of soil temperature and compaction are found to be more sensitive to anthropogenic changes (Navarrete & Halffter 2008; Barragan *et al*. 2011).

1.2.4. Seasonality

Seasonality in dung beetles is determined by factors like temperature, rainfall, resource availability and life history strategies (Doube 1991; Hanski &

Cambefort 1991c; Lumaret & Kirk 1991). Dung beetle activity is found to be related to precipitation (Deloya *et al*. 2007). Rainfall provides humidity to the soil and triggers the emergence and/or the onset of activity in the beetle species (Doube 1991; Halffter 1991; Hanski & Cambefort 1991c). Dung beetle activity is greatest during moist and minimal during dry periods (Doube *et al.* 1991) and abundance of scarab beetles increases strongly after heavy rainfall (Walter 1985). Seasonal variation in the dung characteristics of herbivores is another factor that affects the reproductive performance of dung beetles (Edwards 1991). Seasonal activity is less pronounced in areas without a severe dry season (Peck & Forsyth 1982; Waage & Best 1985; Berytenbach & Berytenbach 1986; Hanski & Krikken 1991).

Majority of dung beetle species that exhibit environmentally induced seasonality are active during favourable periods. However there are species which avoid competition by increasing their activity during periods of harsh environmental conditions (Montes de Oca & Halffter 1995) because fewer species are active during environmentally unfavourable periods and those that are active, experience much less competition for resources. Studies on seasonality help in determining how the various environmental factors that vary with seasons affect the dung beetle assemblages.

1.2.5. Biological indicator

A biological indicator is a species or group of species that readily reflects the abiotic or biotic state of an environment and represents the impact of environmental change on a habitat, community or ecosystem (McGeoch

1998). The effect of human activity on biodiversity has been analyzed using indicator groups (Noss 1990; Pearson & Cassola 1992; McGeoch & Chown 1998). Special emphasis has been placed on dung and carrion beetles to analyze the effects of tropical rain forest fragmentation on insect communities (Halffter & Favila 1993; Favila & Halffter 1997). Dung and carrion beetles are good biological indicators of disturbance by human activity in tropical terrestrial environments because they are very sensitive to changes in microclimatic variables, vegetation structure, soil characteristics, and abundance of food resources in the habitats they live (Nealis 1977; Halffter *et al.* 1992; Lumaret *et al.* 1992; Osberg *et al.* 1994; Davis 1996; Lumaret & Iborra 1996; Estrada *et al.* 1999; Escobar 2000). Selection of indicator species for habitats helps in monitoring the habitats for changes in the future.

1.2.6. Habitat specificity

From African savannahs to Neotropical forests, dung beetles are highly habitat specific and there are distinct guilds of beetles associated with forests, edges, agriculture and pasture habitats. Although some species can utilize more than a single habitat type, certain species may never be found outside their preferred habitat (Scheffler 2002). This is because during the long evolutionary history dominated by their specialization to dung (Halffter & Mathews 1966; Davis *et al.* 2002), dung beetles have developed close associations with particular regional and local environmental conditions. Tropical forest species are stenotopic, when their habitats are destroyed or modified; they are reduced to small populations (Halffter & Mathews 1966). Factors that control the distribution of stenotopic species are the temperature and humidity conditions of the microclimate (Halffter & Mathews 1966). Dung beetle species assemblages as part of the ground fauna are associated with the influence of plant physiognomy on microclimatic factors such as insolation, temperature, and light intensity (Davis 1996, Davis *et al.* 2002).

Distinct associations of dung beetles with climatic regions, soil, vegetation and dung types are available (Nealis 1977; Jankielsohn *et al.* 2001, Spector & Ayzama 2003, Duraes *et al.* 2005). Nature of soil is found to determine dung beetle abundance and species richness (Nealis 1977). Habitats with clayey soils lack the high species richness and high beetle numbers of sandy soils as it is difficult to tunnel in, which thus reduces the amount of brood a female can produce leading to smaller population sizes. Moreover clayey soil gets saturated with rain leading to suffocation of brood (Nealis 1977). Also soil temperature differences because of differences in shade were found to affect biomass and abundance of dung beetles (Jankielsohn *et al.* 2001).

Many species do not traverse ecological gradients, such as forest-pasture boundaries, even when food resources are readily available on the other side and may never be found outside their preferred habitat (Klein 1989; Scheffler 2002). Studies indicate that species adapted to grassland, even if introduced from other continents, would not alter or compete with the forest adapted species (Howden & Nealis 1975). Studies conducted across a Bolivian Neotropical forest-savannah ecotone observed high habitat specificity with complete species turn over between forest and savannah habitats (Spector & Ayzama 2003). Studies on dung beetle assemblages across a natural forest-grassland ecotone in Brazil also recorded that the effect of the forest vs. grassland habitat had a much stronger effect on the assemblage rather than proximity to edges (Durães *et al.* 2005).

Contrary to the above observations Doube (1983) found several grassland species in Bushland in South Africa owing to the openness of the bushland, presence of sandy loam soil and availability of bovine dung in both the habitats. Also, Horgan (2007) found similar dung beetle species composition in pastures from a dry-forest region in El Salvador and a rainforest region in Nicaragua. This strong convergence, not only in community structure, but also in community composition in pastures throughout the Central American Isthmus, suggests a general loss in dung beetle diversity at a regional scale as synanthropogenic species invade new areas (Horgan 2007). Hence studies on dung beetle communities across habitats are important as communities vary across habitats and comparison helps in determining the various factors that decide dung beetle community structure.

1.2.7. Habitat modifications

The fragmentation of habitats features among the top disrupters of ecosystem functioning and underlies most of the current biodiversity losses at a global scale (Saunders *et al.* 1991; Vitousek 1994). Landscape transformation all over the world has resulted in a heterogeneous mosaic made up of forest patches that vary in density and connectivity, all of which are immersed in a matrix of pastures and crop fields (Arellano *et al.* 2008).

Various aspects of spatial configuration of remnant forests and agro pastoral systems affect dung beetle assemblages, such as patch size where small patches recorded fewer species and sparser population (Klein 1989; Estrada & Coates-Estrada 2002; Andresen 2003), distance from other patches, where smaller isolating distance between patches favored dispersal and richer assemblage of species (Estrada *et al.* 1998); presence of corridors like live fences, human made islands of vegetation which facilitated dispersal between patches (Hill 1995; Estrada *et al.* 1998) and maintain connectivity between remnant patches is important for biodiversity conservation (Bustamante-Sánchez *et al.* 2004; Quintero & Roslin 2005).

Larger dung beetles were found to be more affected from a change in habitat from natural habitat to disturbed habitat (farms) (Jankielsohn *et al.* 2001). Trampling and overgrazing by cattle on the farms change the ecological status of the vegetation, the basal cover, and the relative veld condition. This might influence the larger dung beetle species more severely than the smaller species (Jankielsohn *et al.* 2001). Botes *et al.* (2006) found that dung beetle diversity was lower in human- disturbed Sand Forest when compared to undisturbed Sand Forest in Africa. Navarrete & Halffter (2008) reported loss of species richness in disturbed habitats along a disturbance gradient namely, undisturbed forests to clear-cuts. The reduction in species richness and diversity in most habitats was mainly influenced by the arboreal nature of the matrix (Avendaño-Mendoza *et al.* 2005; Quintero & Rosalin 2005; Halffter *et al.* 2007). Studies in Wayanad revealed decreased species richness and diversity in modified habitat when compared to natural forests (Vinod 2009). Ecosystem function of dung beetles, especially dung burial activity was also remarkably disrupted by land use changes in Sulawesi, Indonesia (Shahabuddin 2011).

On the contrary, it was observed in Colombia that creation of new environments such as cropland and pasture favours the presence of few forest species that can tolerate modification of their habitat, and also allows for colonization by non-forest species that arrive from other regions (Escobar 2004). Similarly, though expansion of cattle pastures has caused a regional decline in dung beetle diversity in Peru, forest fragments and small isolated patches of native trees and shrubs maintained some of the diversity of the original landscape (Horgan 2007). Also the development of secondary vegetation favored connection between fragments and continuous forest which led to the recovery of dung beetle population in Manaus, Brazil (Quintero & Halffter 2009). Similar result of recovery was observed by Quintero & Roselin (2005) in Central Amazonia while sampling the same sites as Klein (1989). Moreover some man-made habitats like cacao agroforestry in Sulawesi had similar dung beetle assemblages as forest due to similar vegetation structure and microclimate (Shahabuddin 2010).

1.2.8. Edge effect

The fragmentation of habitats results in edges, which exposes the organisms to a wide range of both biotic and abiotic factors associated with boundaries between adjacent habitats, whether natural or anthropogenic (Wilcove *et al.* 1986; Foggo *et al.* 2001). These effects usually penetrate deep into forest fragments, leading to changes in the distribution, abundance, interaction, and diversity of species (Laurance & Yensen 1991; Schelhas & Greensberg 1996; Laurance & Bierregaard 1997; Gascon & Lovejoy 1998). The transition between adjacent environments can be sharp or gradual and be characterized by abiotic and biotic conditions dissimilar from the adjacent habitats, collectively called edge effects (Murcia 1995). The intensity and direction of edge effects on the population levels of organisms can be extremely variable across species (Heliöla *et al*. 2001; Kotze & Samways 2001; Baker *et al*. 2002), and even among populations of a single species (Baker *et al*. 2002). Thus, although the term edge effect was first introduced to describe the tendency for increased population abundance at the transition between two habitats (Odum 1971), it is clear that different species can respond positively, negatively or neutrally to edges (Murcia 1995; Baker *et al.* 2002).

Dung beetle species richness and abundance declined from forest toward edges in several studies conducted on forest dung beetles in Australia (Hill 1996), Bolivia (Spector & Ayzama 2003), Mexico (Kohlman 1991; Favila & Halffter 1997; Estrada *et al*. 1998) and French Guiana (Feer 2008) but other studies showed different trends. Escobar (1997) found that species richness at edges is similar or higher than that in two forest habitats in Colombia. In

Brazil, dung beetles respond strongly to change in habitats, forest and cerrado, but weakly to the proximity of the edge between these habitats (Durães *et al.* 2005).

Edge effect may be remnant size-related (Laurance *et al*. 2002). While in forest fragments no edge effect was evident, in the continuous forest the abundance and dung decomposition differed between the interior and border of the habitat (Bustamante- Sánchez *et al.* 2004).

1.3. Significance of the study

Tropical forests are recognized as the most complex ecosystem in the world and richest in biodiversity. They are the 'cradle of evolution' and are constantly parenting newer and newer species (Manilal 1997). Due to urbanization and increased agricultural practices, natural forests are disappearing or being transformed into plantation forests at alarming rates worldwide (Laurance 1999). This appears to be the single greatest threat to the world's biodiversity (Whitmore 1990; Huston 1994).

With a wide array of bioclimatic and topographic conditions, the Western Ghats, is extraordinarily rich in biodiversity and endemism and is at the same time threatened with destruction due to various human pressures. It is one of the 34 biodiversity 'hotspots' of the world and one of the two on the Indian subcontinent (Myers 2003; Bossuyt *et al.* 2004; Mittermeier *et al.* 2004; Bawa *et al.* 2007). Nearly three-fourths of the natural vegetation in the ecoregion has been cleared or converted, and the remaining severely fragmented forests are one of the major conservation priorities on a global scale due to their fragility, biological richness, high rates of endemism and multiple anthropogenic threats (Pascal 1991). Some of the major conservation issues facing the South Western Ghats landscape region are 1) Human Wildlife conflict; 2) timber smuggling and poaching of wild life (Commercial); 3) unregulated tourism; 4) improperly planned infrastructure development; 5) forest encroachment (illegal); 6) forest conversion (legal); 7) unsustainable extraction/use of forest products for subsistence and for commercial use; 8) invasive alien species and 9) forest fires (WWF 2008).

Nelliampathi located in the south-western edge of Palghat Gap was known for its large population of flora and fauna including rare and endangered species. The land forms a corridor for the movement of long ranging mammals like elephant and is the core zone of the Parambikulam Tiger Reserve (Joy 1991). In the later part of 19th century thousands of acres of forest lands were leased to private owners to plant coffee and cardamom. But the land is now used for other purpose like cultivating rubber and is promoted for tourism. Indiscriminate destruction of forests in the region has led to increased incidence of natural disasters like landslides in the region (Prabhakaran 2011). There is serious concern now that these estates are violating the lease agreement and their continuous occupation will lead to large scale destruction of habitat of the region. Amidst this scenario the taxonomic and ecological studies of dung beetles of this region gains significance; since a proper appreciation of the biodiversity and a meticulous cataloguing of it are the essential first step in any effort for its conservation (Manilal 1997).

Although the taxonomy of dung beetles of India and the Western Ghats were well studied by Arrow (1931) and Balthasar (1963a, b) the inaccessible dense forests of the Western Ghats region in the early 20th century must have hindered their collection efforts. Other important contributors of the taxonomy of dung beetles in the Western Ghats region are Paulian (1980), Biswas & Chatterjee (1986), Biswas & Mulay (2001), Anu (2006), Vinod (2009), Latha *et al.* (2011) and Sabu *et al.*(2011a). But most recent studies were done north of the Palghat Gap which differs in climate and vegetation from regions south of the Palghat Gap. Except for the work of Paulian (1980) no collections of dung beetles was done in the Nelliampathi region in recent years. Moreover the collection efforts done in the1980's were not as comprehensive or rigorous as the present study.

Studies on ecology of dung beetles of Western Ghats have been very minimal and include the works of Sabu and Vinod (2005), Sabu *et al.* (2006, 2007), Vinod & Sabu (2007) and Vinod (2009) all in regions north of the Palghat Gap. No studies exist on the effect of habitat disturbance and edge effect on the community structure of dung beetles from the Western Ghats where fragmentation of forests for the creation of plantations, agriculture habitats and human settlements and there by the creation of habitat edges is a recurring phenomenon. Hence with the current rate of habitat fragmentation and degradation in the region it is important to document the biodiversity of the region before local extirpation due to habitat modifications can take place (Sabu *et al.* 2011a).

This study seeks to understand the differences in diversity, functional and temporal guild structure, seasonality and identification of indicator species of dung beetles, in a forest, agriculture habitat and ecotone between the two habitats at Nelliampathi and effects of habitat modification and edges resulting from habitat fragmentation, on the dung beetle assemblages. Dung beetles were selected for the study because 1) they have a relatively well-known taxonomy; 2) they are known to be highly habitat specific and different species specialize in different habitat types such as forest, edge, clearing, tree and crop plantations (Nealis 1977; Klein 1989; Halffter *et al*. 1992; Halffter & Favila 1993); 3) their communities are known to be particularly speciose (Hanski & Cambefort 1991d) which allows the comparison of biodiversity within a single taxa; 4) majority of dung beetle species rely on mid to large sized mammals for food and are directly affected by changes in mammalian populations (Estrada *et al*. 1999) and 5) in addition, they are highly disturbance sensitive (Halffter *et al*. 1992; Halffter & Favila 1993).

1.4. Objectives

1. Taxonomy of dung beetles associated with a semi- evergreen forest, agriculture habitat and an ecotone of Nelliampathi in the South Western Ghats.
2. Taxonomic studies, preparation of a checklist and pictorial key.
3. Community diversity across the habitats.
4. Selection of indicator species for each habitat.
5. Guild structure, diel periodicity and seasonality of dung beetles.

REVIEW OF LITERATURE

Latha Mathews “Systematics and ecology of dung beetles (coleoptra: scarabaeidae: scarabaeinae) in the Nelliampathi region of South Western Ghats” Thesis. Department of Zoology, St. Joseph's College Devagiri , University of Calicut, 2013

Chapter 2

REVIEW OF LITERATURE

2.1. Taxonomy of dung beetles

2.1.1. Taxonomy of dung beetles of the World

Listed below are significant contributions done to taxonomy of dung beetles worldwide. Dung beetles now classified under subfamily Scarabaeinae and members of the suborder Lamellicornia were included by Linnaeus (1758) under a single genus, the *Scarabaeus.* Fourcroy (1785) separated the dung beetles from the Linnean *Scarabaeus* and constituted a new genus *Copris*. Fabricius (1798) separated genus *Onitis* from genus *Copris.* Creutzer (1799) proposed the name *Actinophorus* for the ball rolling beetles now included in the genera *Scarabaeus* and *Gymnopleurus*.

Weber (1801) introduced the name *Ateuchus* for *Scarabaeus sacer* and its congeners. Latreille (1802) introduced the largest dung beetle genus, *Onthophagus.* The genus *Gymnopleurus* was established by Illiger (1803). Latreille (1807) introduced the genus *Sisyphus.* Serville in 1825 introduced the genus *Oniticellus*. *Drepanocerus* was introduced by Kirby (1828). Hope (1837) introduced two new genera, *Catharsius* and *Heliocopris* comprising large dung beetles. Thomson (1863) established the genus *Caccobius*. The genus *Liatongus* was introduced by Reitter (1892) and *Tiniocellus* by Péringuey (1900). Boucomont (1914) established the genus *Phacosoma.* Due to homonymy, Vaz-de-Mello (2003) renamed the genus *Phacosoma* as *Ochicanthon.*

Arrow (1931) placed dung beetles in four divisions (=tribes) namely, Scarabaeini, Sisyphini, Coprini and Panelini under the subfamily Coprinae with which he considered the Scarabaeinae synonymous. Janssens (1949) subdivided Scarabaeinae into six tribes: Coprini, Eurysternini, Oniticellini, Onitini, Onthophagini and Scarabaeini. Balthasar (1959) described *Digitonthophagus* as a subgenus of *Onthophagus* Latreille.

Later, Balthasar (1963a, b) ranked the dung beetles as a family comprising two behaviourally distinct subfamilies: Coprinae and Scarabaeinae. Subfamily Coprinae included the tribes Coprini, Dichotomini, Phanaeini, Oniticellini, Onitini, and Onthophagini and the subfamily Scarabaeinae included the tribes Eucraniini, Eurysternini, Canthonini, Gymnopleurini, Scarabaeini and Sisyphini.

Zunino (1981) raised *Digitonthophagus* to genus level. Phylogeny of Zunino (1983) based on relatively few aedeagal characters, showed a basal split with one lineage comprising tribes primarily with tunneling habits and the other dominated by ball-rolling tribes, supporting Balthasar's system of classification. A new genus *Cleptocaccobius* introduced by Cambefort (1984) was added to the tribe Onthophagini. The comparative analysis of the male and female genitalia of subfamily Scarabaeinae, disputed the monophyly of the tribes Onitini, Coprini and Dichotomini (Zunino 1984). Cambefort (1985) provided the revision of the oriental species of *Cleptocaccobius* and four new species *C. arrowi*, *C. khatimae*, *C. durantoni* and *C. boucomonti* together with a new subspecies *C. simplex meridionalis* were added. Larval and adult characters were used to study the phylogenetic relationships within the most speciose tribe Onthophagini (Zunino 1979; Martin-Piera & Zunino 1983, 1986;

Palestrini 1985; Martin-Piera 1986, 2000; Lumaret & Kim 1989). Lawrence and Newton (1995) placed all 12 tribes in the subfamily Scarabaeinae with which they considered the Coprinae synonymous. Browne & Scholtz (1995, 1998) studied the phylogeny of Scarabaeidae based on the characters and evolution of hind wing articulation and wing base. Montreuil (1998) confirmed the monophyly of Coprini and Dichotomini. Recent and complete phylogeny of the Onthophagini was based on 12 external and internal morphological traits (Martin-Piera 2000).

New phylogenic studies of Philips *et al.* (2004) based on 200 internal and external morphological characters support this classification. Krikken (2009) revised and discussed the taxonomic and biogeographic status of genus *Drepanocerus* Kirby and the related genera and split the genus into five new subgenera namely, *Afrodrepanus, Clypeodrepanus, Latodrepanus, Sulcodrepanus* and *Tibiodrepanus*.

Regional lists of dung beetles are available from South Africa (Peringuey 1900), African Tropical region (Gillet 1908, 1911), Sumatra (Gillet 1924), China (Gillet 1935; Nakane & Shirahata 1957), Southwest Arabia (Paulian 1938), Mexico, Central America, the West Indies and South America (Blackwelder 1944), Afganistan (Balthasar 1955), Japan (Nakane & Tsukamoto 1956), Florida (Woodruff 1973), Panama and Costa Rica (Howden & Young 1981; Howden & Gill 1987; González-Maya & Mata-Lorenzen 2008), Nebraska (Ratcliffe 1991), Europe (Baraud 1992), Colombia (Lopera 1996), Nearctic Realm (Smith 2003) and Palaearctic region (Löbl & Smetana

2006). Check list of dung beetles of the world were prepared by Krajcik (2006) and Schoolmeesters (2011).

2.1.2. Taxonomy of dung beetles of the Indian region

The first comprehensive account of Scarabaeid beetles of the Indian subcontinent was published by Arrow (1931), in which he reported four divisions, 26 genera and 354 species. An addition to the knowledge on Indian dung beetles was given only after three decades by Balthasar (1963a, b) in his monograph on Scarabaeidae and Aphodiidae in the Palearctic and Oriental region. Subsequent to the efforts of Arrow (1931) and Balthasar (1963a, b) taxonomic studies on dung beetles were limited to the occasional catalogues and regional check lists published by Zoological Survey of India from different regions.

Biswas (1978a, b) described four new species namely, *Onthophagus* (*Strandius*) *subansiriensis, Copris siangensis*, *Onitis assamensis* and *Drepanocerus kazirangensis* from Arunachal Pradesh and Assam. Biswas and Chatterjee (1985) reported seven new species from Namdapha Wildlife Sanctuary namely, *Oniticellus namdaphensis*, *O. subhendui*, *O. gayeni*, *Onthophagus tirapensis*, *O. arunachalensis*, *O. songsokensis* and *O. royi.* Newton and Malcolm (1985) recorded 22 species from the Kanha Tiger Reserve. Sewak (1985) reported eight species from Gujarat. Male genitalia of three Indian genera namely, *Catharsius* (Sewak 1985), *Onthophagus* (Sewak 1986) and *Oniticellus* (Sewak 1988) and taxonomic importance were studied.

Sewak & Yadva (1991) collected 36 species from Western Uttar Pradesh. Veenakumari & Veeresh (1996a) recorded 61 species of Scarabaeinae belonging to three tribes from Bangalore in the Deccan region with 33 first reports from the locality; Biswas *et al.* (1997) recorded three species from Delhi; Chatterjee & Biswas (2000) recorded 27 species from Tripura State; Chandra (2000) made an inventory of Scarabaeid beetles of Madhya Pradesh and Chattisgarh; Chandra & Rajan (2004) reported *Onthophagus cervus* (Fabricius) from Mount Harriett National Park, South Andaman. Chandra and Singh (2004) recorded 10 dung beetles from Pachmarhi Biosphere Reserve, Madhya Pradesh. Forty nine species were reported from Gujarat (Sewak 2004).

Chandra (2005) collected 69 species of Scarabaeinae dung beetles from Western Himalaya of which 34 species belong to the genus *Onthophagus*. Chandra & Ahirwar (2005) recorded 34 species from Kanha Tiger Reserve, Madhya Pradesh. Rajan (2006) prepared a checklist of 88 dung beetles based on collections from 1997-2001 and provided species level keys to the dung beetles from Biligiri Rangaswamy Temple Wildlife Sanctuary, Karnataka. Sewak (2006) reported 73 species from Arunachal Pradesh of which 22 species were first records from the region. 67 species of dung beetles along with their district-wise distribution was provided from Madhya Pradesh (Chandra & Ahirwar 2007).

Since the systematic studies on the dung beetles from the region by Arrow (1931), very few studies have assessed the taxonomy of dung beetles in Western Ghats. Though Arrow (1931) reported 48 species of dung beetles from the western slopes of the South Western Ghats, it is unable to decipher the habitats from which the beetles were collected as locality details were not provided along with site descriptions. Paulian (1980) reported five new species of Canthonines from South India namely, *Phacosoma nitidus*, *P. loebli*, *Panelus mussardi*, *P. besucheti*, and *P. keralai*. Biswas and Chatterjee (1986) reported 3 new species namely, *Onthophagus keralicus*, *O. sahai* and *O. taruni* and recorded 16 species from the Silent Valley National Park.

Biswas & Mulay (2001) recorded 71 species from Nilgiri Biosphere Reserve. As a part of the biodiversity documentation programme by Kerala Forest Research Institute, Mathew (2004) recorded 37 species from Kerala. A new species, *Onthophagus devagiriensis* from a moist deciduous forest in the Wayanad region of Kerala State was recorded (Schoolmeesters & Thomas 2006). Anu (2006) prepared a checklist of 29 species from a wet evergreen forest in the Wayanad region of Nilgiri Biosphere Reserve. Vinod (2009) prepared a checklist of 58 species, comprising 13 genera and 7 tribes of the Wayanad region. Seven new synonyms within the genus *Onthophagus* (Coleoptera: Scarabaeidae) from the oriental region including the synonymisation of *Onthophagus anamalaiensis* with *O. vladimiri* was reported (Tarasov 2010). Taxonomy of dung beetle genus *Ochicanthon* Vaz-de- Mello (Coleoptera: Scarabaeidae) of the Indian subcontinent was revised and eight new species of *Ochicanthon* was added to the list (Latha *et al.* 2011). Sabu *et al*. (2011a) prepared a checklist of dung beetles from the moist South Western Ghats.

2.2. Ecology of dung beetles

The two most inclusive works on the ecology of dung beetles are 'The natural history of dung beetles of the sub family Scarabaeinae (Coleoptera, Scarabaeidae)' (Halffter & Mathews 1966) and 'Dung beetle ecology' (Hanski & Cambefort 1991a). 'Natural history of dung beetle' is an extensive work on food relationships, relations to the biome, feeding behaviour, sexual relationships and evolutionary trends of dung beetles. 'Ecology of dung beetles' includes population biology, biogeography and evolution, and comprehensive account on regional dung beetle assemblages of north (Hanski 1991) and south (Lumaret & Kirk 1991) temperate region, subtropical North America (Kohlmann 1991), South Africa (Doube 1991), tropical savannahs (Cambefort 1991), tropical forests in southeast Asia (Hanski & Krikken 1991), tropical forests in Africa (Cambefort & Walter, 1991), tropical American forests (Gill 1991), Sahel region of Africa (Rougon & Rougon 1991), montane dung beetles (Lumaret & Stiernet 1991) and native introduced dung beetles in Australia (Doube *et al.* 1991).

2.2.1. Diversity

Species richness and diversity of dung beetle assemblages were studied in tropical rain forests of southeast Asia (Hanski 1983; Hanski & Krikken 1991; Davis *et al.* 1997; Davis 2000b), forests of Australia (Howden *et al.* 1991; Vernes *et al.* 2005), rain forests of Africa (Cambefort & Walter 1991), forest-pasture ecotones of Mexico (Estrada *et al.* 1998), agriculture fields of north India (Mittal & Vadhera 1998), forests of Malaysia (Davis 2000b), forests of Colombia (Escobar 2000), French Guyana (Feer 2000), temperate North America (Lobo 2000), Peru (Valencia *et al.* 2001), rain forests of Mexico (Estrada & Coates-Estrada 2002), Columbia (Escobar 2004), agroecosystems of Guatemala (Avendano-Mendoza *et al.* 2005), Sulawesi, Indonesia (Shahabuddin *et al.* 2005), Africa (Nielsen 2007), in natural and modified habitats in southern Mexico (Arellano *et al.* 2008) in forest of Chiapas, Mexico (Navarrete & Halffter 2008), monoculture plantation and agriculture field of Wayanad (Vinod 2009).

Jameson (1989) compared dung beetle communities in grazed and ungrazed habitats of western Nebraska and observed slightly higher diversity on the grazed site. Klein (1989) found that forest fragments in Central Amazonia had reduced richness and abundance of dung beetles when compared to the continuous forest. Galante *et al.* (1991) found that smaller species inhabited open pasture lands when compared to the adjacent woodlands. Abundance declined with increasing disturbance but partially modified habitats showed few differences in Scarabaeinae biomass between undisturbed and secondary grown forest (Vulinec 2000; Scheffler 2005; Vulinec *et al.* 2006). Horgan (2002) studied dung beetle communities in shaded and open habitats and reported the importance of soil moisture in determining dung beetle diversity.

Studies by Andresen (2005) in tropical dry forests pointed out that change in community organization of dung beetles can include changes in species richness, species composition, abundance and guild structure. In a comparative study on the dung beetle communities in cloud forest and coffee agroecosystems, Pineda *et al.* (2005) recorded significantly higher species richness and abundance in coffee plantations. Harvey *et al.* (2006) compared the abundance, species richness and diversity of dung beetles across a gradient of different land use types, from agriculture monocultures (plantains) to agroforestry ecosystems (cocoa and banana) and forests in two indigenous reserves in Costa Rica. Dung beetle species richness and diversity were greatest in the forests, intermediate in the agroforestry systems and lowest in the plantain monocultures; while dung beetle abundance was greatest in the plantain monocultures. Lobo *et al.* (2006) analysed regional and local influence of grazing activity on the diversity of a semi-arid dung beetle community and found that grazing intensity and the associated increase in the amount of trophic resources (dung) is a key factor in determining local variation in the diversity and composition of dung beetle assemblages. Andresen and Laurance (2007) reported lower species richness and abundance in Panamanian rainforest due to increased hunting of mammals. Shahabuddin (2010) recorded significant decrease in species richness of dung beetles from natural forests to open area.

2.2.2. Functional guild composition

Cambefort & Hanski (1991) classified dung beetles into three functional guilds based on their feeding and nesting strategies namely, rollers (telecoprid nesters), tunnelers (paracoprid nesters) and dwellers (endocoprid nesters). The studies in functional guild composition of dung beetle assemblages of different habitats across the world include studies done in forests of Colombia (Howden

& Nealis 1975; Escobar 2000), forest-pasture ecotones of Amazonia (Klein 1989; Vulinec 2000), moist forest of Ivory Coast in Africa (Cambefort & Walter 1991), Australia (Howden *et al*. 1991), Panama (Gill 1991), forest pasture ecotones of Mexico (Estrada *et al.* 1998, 1999), rain forests in Malaysia (Davis *et al*. 2000), Guyana (Feer 2000), Brazil (Andresen 2002), forest-savanna ecotone in Bolivia (Spector & Ayzama 2003), in natural and anthropogenic habitats of montane region of Colombia (Escobar 2004), in mountain grasslands of southern Alps (Errouissi *et al*. 2004), agriculture field in Guatemala (Avendano-Mendoza *et al.* 2005), agriculture field in Indonesia (Shahabuddin *et al.* 2005), agriculture field of Wayanad (Sabu & Vinod 2005), in elephant and bison dung of moist forests in south Western Ghats (Sabu *et al.* 2006; Vinod & Sabu 2007), in continuous forests, forest fragments and cattle pastures of Chiapas, Mexico (Navarrete & Halffter 2008), in forest, monoculture plantation and agriculture field of Wayanad (Vinod 2009).

Tunnelers were the dominant guild in most assemblages (Cambefort & Walter 1991; Hanski & Cambefort 1991c; Halffter *et al*. 1992; Escobar 2004; Sabu *et al.* 2006; Navarrete & Halffter 2008, Vinod 2009). Rollers were the second dominant guild in the assemblages of Mexico (Estrada *et al.* 1998) and Tanzania (Nielsen 2007). Rollers were not recorded in the agroecosystems of North India (Mittal & Vadhera 1998). Moist forests of Ivory Coast (Cambefort & Walter 1991) and Wayanad (Vinod 2009) are the only exceptions where the dominant species are distributed between tunneler and dweller guilds.

Dwellers were found to be associated with large undisturbed herbivore dung pats (Hanski & Cambefort 1991c; Krell *et al.* 2003; Krell-Westerwalbesloh *et al.* 2004) the availability of which determines their presence. Surface crust formation in dung pats was found to reduce dweller abundance in summer (Doube 1991; Hanski 1991; Sowig & Wassmer 1994; Horgan 2001; Vinod 2009).

Krell *et al.* (2003) found that the abundance of rollers and their kleptoparasites is positively correlated with the temperature of faeces and soil, whereas the number of dwellers increases with decreasing temperature during the exposure period.

2.2.3. Temporal guild composition

Temporal differentiation appears particularly relevant in tropical forests where high rates of exploitation of carrion and dung occur especially because the resource is presumably limited (Peck & Forsyth 1982; Klein 1989; Feer 1999). Hanski (1990) reported that success of any dung beetle species is determined by their early arrival at the resource; hence diel activity of species is an important parameter determining their success. Diel resource partitioning within dung beetle assemblages have been studied several times (Fincher *et al.* 1971; Peck & Forsyth 1982; Janzen 1983; Walter 1985; Hanski 1986; Cambefort 1991; Cambefort & Walter 1991; Doube 1991; Gill 1991; Caveney *et al.* 1995; Davis 1999; Krell *et al.* 2003; Krell-Westerwalbesloh *et al.* 2004; Feer & Pincebourde 2005).

In tropical ecosystems, species compositions of diurnal and nocturnal dung beetle assemblages were clearly different (Hanski & Cambefort 1991c), particularly in open habitats (Cambefort & Walter 1991).

Dung beetles were generally found to show an abundance peak at dusk and around midday (Peck & Forsyth 1982; Walter 1985; Fincher *et al.* 1986; Davis 1996; Davis 1999; Feer 2000). Light intensity was found several times to be responsible for the onset of flight of crepuscular dung beetles (Carne 1956; Houston & McIntyre 1985). In Africa, Walter (1985) distinguished various temporal patterns among diurnal and nocturnal species. In Panama, diurnal species display several distinctive patterns of flight activity and some species are possibly auroral/crepuscular (Howden & Young 1981; Gill 1991) or active both by night and day. A similar grouping of species by temporal activity seems to prevail also in French Guiana (Feer 2000). Krell-Westerwalbesloh *et al.* (2004) reported different patterns of guild structure during the day, with time of day and temperature influencing the presence of guilds.

Diurnal species tend to be smaller than nocturnal and crepuscular species and nocturnal species are black or dark in body colour whereas diurnal species show colour patterns (Feer & Pincebourde 2005). Diurnal species were more numerous than nocturnal species in several studies (Hanski 1989; Gill 1991; Davis 1999; Andresen 2000; Feer & Pincebourde 2005) but equal or higher numbers of nocturnal species exist in other forests (Cambefort 1984; Walter 1985; Howden *et al.* 1991; Halffter *et al.* 1992; Escobar & Chacon de Ulloa 2000). Navarrete & Halffter (2008) reported that large bodied, nocturnal species with specific requirements of soil temperature and compaction are more sensitive to anthropogenic changes.

2.2.4. Seasonality

Several studies have been done on seasonality in dung beetles in southern Europe (Lumaret 1983), forests of Barro Colorado Island, Panama (Howden & Young 1981), Neotropics (Janzen 1983; Andresen 2005), south western Australia (Ridsdill-Smith & Hall 1984a, b) south western Cape (Davis 1987), southeast Asia (Paarmann & Stork 1987), Africa (Doube 1991; Rougon & Rougon 1991) and southeast Asia (Hanski & Krikken 1991).

Kingston (1977) reported extreme seasonality of dung beetles in African savanna. In a more seasonal forest on Barro Colorado Island, Panama different pattern of seasonality was observed. Most species of Scarabaeinae occur throughout the year or are more abundant in the wet season and one or two species appear to be restricted to dry season (Howden & Young 1981). Howden & Young (1981) also noticed that many species are most abundant in particular phases of the wet season. Peck & Forsyth (1982) observed no marked seasonality in an Ecuadorian rain forest with no severe dry season. In a deciduous Costa Rican forest with six month of dry season, dung beetle activity was markedly seasonal and peak in richness was recorded during the rainy period (Janzen 1983).

In forests of Ivory Coast, scarab numbers followed bimonthly rainfall patterns rather closely (Cambefort 1984). Dung beetle seasonality suggests that activity is greatest during moist and minimal during dry periods and the abundance of scarab beetles increases strongly after heavy rainfall (Walter 1985; Doube *et al.* 1991; Hanski & Krikken 1991; Andresen 2005). Edwards (1991) studied the influence of seasonal variations in the dung of grazing mammals on dung beetles in a summer-rainfall forest in South Africa. Both Hill (1993) and Wright (1997) demonstrated that most species in tropical Australia were found only in the wetter months. Seasonal activity of dung beetles associated with cattle dung was studied (Floate & Gill 1998; Bertone *et al*. 2005). A comparison of seasonality of coprophagous beetles in bovine dung was conducted by Morelli *et al*. (2002). Deloya *et al*. (2007) found that beetle activity increased with precipitation in Veracruz, Mexico. Vinod (2009) reported peak in species richness during the post rainy or presummer period in contrast to the seasonality pattern of other forest dung beetle assemblages, where peak in richness was recorded during the wet rainy period (Janzen 1983; Andresen 2005; Vernes *et al*. 2005).

2.2.5. Biological indicator

The rationale for using dung beetles as indicators of disturbance has been reviewed by Halffter & Favila (1993). They are useful indicators of biodiversity in the tropics because they respond rapidly to environmental changes, their biology is relatively well known and they are relatively easy to sample (Favila & Halffter 1997; McGeoh *et al.* 2002; Nichols *et al.* 2007; Arellano *et al.* 2008). Dung beetles are recognized as a focal taxon for describing and monitoring spatial and temporal patterns of biodiversity (Spector & Forsyth 1998; Davis *et al.* 2001). Several researchers devised the

IndVal method (Dufrêne & Legendre 1997) to assess the indicator responses of dung beetles to study the direction of ecological change (van Rensburg *et al.* 1999; McGeoch *et al.* 2002; Botes *et al.* 2006).

Davis *et al.* (2001) reviewed the use of dung beetles as indicators of environmental change, highlighting the influence of natural forest dynamics on species distributions in primary forest. McGeoch *et al.* (2002) suggested that, although dependence on particular environmental factors may not be synonymous with usefulness as bioindicators, dung beetles are good ecological indicators of environmental differences or of habitat change. Furthermore, their alpha taxonomy is fairly advanced and convenient methods exist for quantitative collection of field data using dung-baited pitfall traps (Davis 2002).

Usefulness of dung beetles as indicators of effects related to local transformation from natural habitat to farm land was studied by Davis *et al.* (2004). In his review of Scarabaeinae dung beetles as indicators of biodiversity, habitat transformation and pest control chemicals in agro-ecosystems; use of dung beetles as biodiversity, ecological and environmental indicators at regional, local and pasture scales were out lined and recommendations were made on the conservation of dung beetles in agro-ecosystems (Davis *et al.* 2004). Dung beetles were used in Costa Rica as bioindicators to priorities forest areas for conservation (Aguilar-Amuchastegui & Henebry 2007).

2.2.6. Habitat specificity

Howden & Nealis (1975) recorded that dung beetle species did not move between forest and manmade clearings which is mainly attributed to temperature difference between the two habitats in Colombia. Hill (1996) demonstrated high degrees of biotope specificity related to vegetation type in dung beetle species in rain forest and more open areas in north-eastern Australia. Jankielsohn *et al*. (2001) observed habitat specificity related to soil temperature due to shaded and unshaded condition in South Africa. Scheffler (2002) reported that though some species can utilize more than a single habitat type, certain species may never be found outside their preferred habitat. Durães *et al.* (2005) found effect of habitat on the distribution of forest and grassland species of dung beetles in Brazil. Andresen (2005) recorded how forest structure determined dung beetle community organization in Mexican tropical dry forest. Diaz *et al*. (2010) noted high habitat specificity in beetles in dissimilar habitats in Mexico.

2.2.7. Habitat modifications

Reports on dung beetle species response to destruction, fragmentation and isolation of tropical rain forests are available from Central and South America (Howden & Nealis 1975; Peck & Forsyth 1982; Klein 1989; Halffter *et al*. 1992; Horgan 2002; Andresen 2003, 2005, 2007; Durães *et al*. 2005; Scheffler 2005), Africa (Cambefort 1984), Malaysian rainforests (Davis 2000a; Davis *et al*. 2001). Studies reported important negative effects such as, fewer species and sparser populations as a result of clear-cutting (Howden & Nealis

1975; Klein 1989; Estrada *et al*. 1998; Horgan 2002; Krell *et al*. 2003). Habitat modifications was found to affect functional guild composition in Columbian rainforest which was earlier described with high dweller abundance (Howden & Nealis 1975), but showed an entirely different guild structure in more recent reports with low presence of dwellers (Escobar 2000), which is probably related to the extensive deforestation of Amazonian forests (Anderson 1990; Skole & Tucker 1993).

Klein (1989) documented the effects of forest fragmentation on insects in the tropics, and recorded that dung beetle communities in 1-ha and 10-ha forest fragments differed from those in contiguous forest, even though the fragments had been isolated by less than 350 m for an ecologically short time (2-6 yr). Nummalin & Hanski (1989) compared dung beetle species assemblages of virgin and managed forests in Africa. Deforested places were found to be less species rich, their evenness and biomass decline and there is an abundance of few small bodied species (Klein 1989; Halffter *et al.* 1992, 2007; Halffter & Arellano 2002; Avendaño-Mendoza *et al.* 2005; Pineda *et al.* 2005; Quintero & Rosalin 2005).

Range contraction and survival of dung beetles due to habitat degradation and overexploitation have been studied (Chown *et al*. 1995). Davis & Sutton (1998) examined the effect of selective timber extraction on dung beetles in the tropical rain forests. Dung beetle communities in tropical rain forest fragments and agricultural habitats were compared (Estrada *et al*. 1998). They found that presence of arboreal agricultural habitats and live fences in the landscape may compensate in part not only to the loss of area of rain forest vegetation, but also to the lost heterogeneity of the landscape when the forest was converted. Amézquita *et al.* (1999) compared the composition and species richness of dung beetles in two types of forest remnants, a forest corridor versus three isolated patches in Columbia and reported similar richness and diversity in all the habitats. Estrada *et al.* (1999) studied tropical rain forest fragmentation in Mexico. Davis (2000a) discussed the role of logging on the diversity of dung beetles.

Davis *et al*. (2001) conducted detailed studies on the effect of habitat disturbance and species abundance distributions of dung beetles in the south-east Asian region. During a historical compilation of data on roller dung beetle occurrence in the Iberian Peninsula between the first and second half of the 20th century, Lobo (2001) reported the decline of roller dung beetles as a result of urban development. Roslin & Koivunen (2001) found that different species show very dissimilar responses to changes in landscape structure.

With the aim of determining what kind of landscape mosaics might sustain maximum diversity and minimum species loss, Estrada & Coates-Estrada (2002) sampled dung beetles in a tract of continuous forest, forest fragments and a habitat island consisting of mosaic of forest and arboreal crops in Mexico. Continuous forest showed increased abundance. Studies proved that these consequences are primarily related to modification of natural vegetation (Estrada & Coates-Estrada 2002; Halffter & Arellano 2002) and the loss of indigenous mammals, primarily large monogastric taxa that void large, fibrous droppings (Owen-Smith 1988; Davis 2002).

Hutton & Giller (2003) analysed the effect of intensification of agriculture on dung beetles in temperate region. Anduaga (2004) assessed the impact of the activity of dung beetles in the pasture land in Mexico. In a study which analyzed the diversity and composition of the dung beetle assemblages in natural and anthropogenic habitats such as primary forest, secondary forest, pasture and crop land, Escobar (2004) found that the creation of new environments such as cropland and pasture favours the presence of the few forest species that can tolerate the modification of their habitat, and also allows for colonization by non-forest species that arrive from other regions.

Studies in Mexican and Central American cloud forests and adjacent shaded coffee plantations demonstrated that some types of land use and agricultural practices, such as shaded cropland provide a buffer for various taxonomic groups against the damage caused by the transformation of native forest (Pineda & Halffter 2004). Diversity of dung beetles in a disturbed Mexican tropical montane cloud forest and in shade coffee plantations were studied, all habitats had similar richness, species composition and assemblage structure of dung beetles (Arellano *et al*. 2005). Pineda *et al*. (2005) demonstrated that a matrix habitat with a structure partly similar to the original vegetation may help to sustain diverse dung beetle assemblages in the fragments and even within the matrix itself.

Quintero & Roslin (2005) assessed how rapidly dung beetle communities recover following rain forest loss and fragmentation through the preservation of forest fragments and secondary vegetation. The reduction in species richness and diversity in disturbed habitats was mainly influenced by the arboreal nature of the matrix (Quintero & Rosalin 2005; Avendaño-Mendoza *et al.* 2005; Halffter *et al.* 2007).

Severe disturbances such as clear-cutting and conversion to pasture results in abundance of small-bodied beetles, a notable decline in beetle species richness and diversity, and a change in species composition in Amazonian forests (Scheffler 2005). Shahabuddin *et al*. (2005) found that dung beetle fauna of the natural forest appeared to be relatively robust to manmade habitat changes and majority of species did not exhibit strong habitat preferences. Studies done by Botes *et al*. (2006) recorded that dung beetle diversity was lower in human- disturbed Sand forest compared to undisturbed Sand Forest in Africa.

In Peru, forest fragments and small isolated patches of native trees and shrubs maintained some of the diversity of the original landscape in cattle pastures (Horgan 2007). Gardner *et al.* (2008) reported low value for secondary forest for offsetting dung beetle species loss. From an overview of published materials on dung beetle ecology, Navarrete & Halffter (2008) reported loss of species richness in disturbed habitats along a disturbance gradient namely, undisturbed forests to clear-cuts.

Nyeko (2009) found dung beetle abundance higher in larger fragments (100–150 ha) than in the smaller ones (10–50 ha) in sub-Saharan Africa. Quintero & Halffter (2009) in Manaus, Brazil found recovery of dung beetle population in forest fragments due to development of secondary vegetation which formed connectivity between fragments and the continuous forest. Studies done in Wayanad also revealed decreased species richness and diversity in modified habitat when compared to natural forests (Vinod 2009). Ecosystem function especially dung burial activity were remarkably disrupted by land use changes from natural forest to open agricultural area in Sulawesi, Indonesia (Shahabuddin 2011).

2.2.8. Edge effect

Habitat fragmentation and the widespread creation of habitat edges have recently stimulated interest in assessing the effects of ecotones on biodiversity (Murcia 1995; Risser 1995; Laurance 2000). Ecotones have also been the focus of wildlife management and ecological research for some time (Clements 1916; Leopold 1933; Grange 1949) as the creation of habitat mosaics favourable to species that exploit the edges of multiple habitats has been a game management strategy for much of the 20th century (Leopold 1933; Grange 1949). Murcia (1995) observed three types of edge effects: abiotic effects, direct biological effects and indirect biological effects. Edge effects caused by forest fragmentation are known to affect insect abundance and diversity (Webb *et al*. 1984; Klein 1989; Webb 1989; Margules *et al*. 2002; Didham 1997; Didham *et al*. 1998; Harris & Burns 2000; Spector & Ayzama 2003). Dung beetle assemblages have been studied across forest-pasture ecotones (Howden & Nealis 1975; Klein 1989; Estrada *et al.* 1998; Vulinec 2000), forest- savanna ecotones (Spector & Ayzama 2003), forest-savanna edge and forest-roadside edge (Feer 2008). Didham *et al.* (1998) found that beetle density and richness near Manaus, Brazil, increased toward forest fragment edges. Laurance *et al*. (2002) noted that edge effect is related to fragment size. Spector & Ayzama (2003) observed that the edge habitat assemblage of dung beetles was essentially a diminished sample of the forest habitat assemblage.

Bustamante-Sanchez *et al*. (2004) observed that in forest fragments no edge effect was evident but in continuous forest the abundance and dung decomposition differed between the interior and border of the habitat. Durães *et al*. (2005) detected no edge effect on richness or species composition, and only weak effects were observed on abundance in a forest- cerrado ecotone in Brazil. Feer (2008) did not observe any edge effect in a forest-savannah and roadside edge in French Guiana. Diaz *et al*. (2010) in Mexico found that forest-pasture edges function as hard edges and prevent movement between forest fragments, but living fences seem to act as continuous habitat corridors when connected to forest fragments, allowing forest beetles to move between the fragments.

2.2.9. Ecology and biology of dung beetles in India

Few studies address the ecology of dung beetles in the Indian subcontinent. Hingston (1923) made observations on Indian dung beetles and reported the role of these nature's scavengers in the removal of excrement of men and cattle, in his ‘A naturalist in Hindustan’. Oppenheimer (1977) reported low abundance of rollers in Bengal. Ecology and community structure of dung beetles in the urban and agricultural landscapes of northwest India was analyzed by Mittal during 1981-2005 periods (Mittal 1981, 1986, 1993, 2005; Mittal & Bhati 1998; Mittal & Vadhera 1998; Mittal & Kakkar 2005). He analyzed various aspects of dung beetles namely, distributional trends (Mittal 1981), attraction towards human faeces (Mittal 1986), natural manuring and soil conditioning (Mittal 1993), food preferences (Mittal & Bhati 1998), succession and community structure of dung beetles attracted to cow dung (Mittal & Vadhera 1998) and community dynamics, diversity and conservation status (Mittal 2005; Mittal & Kakkar 2005) in agricultural landscapes of northwest India. According to Mittal (2005) loss of habitat in urban and rural areas, and the altered food quality because of pollutants and the increased use of cattle antibiotics are the major causes for the decline in dung beetle diversity.

Few studies on the biology of dung beetle from south Indian region exists and details are as follows; studies on the feeding and breeding behavior of *Gymnopleurus gemmatus* Harold and *Gymnopleurus miliaris* Fabricius with details of feeding, ball making and rolling, mating, competition and predation (Veenakumari & Veeresh 1996b); subsociality in *Copris repertus* Walker and *Copris indicus* Gill (Veenakumari & Veeresh 1997); reproductive biology of the two commonly occurring South Indian species- *Onthophagus gazella* Fabricius and *Onthophagus rectecornutus* Lansberge (Veenakumari & Veeresh

1996c); SEM study of the stridulatory organs with observations on the significance of the sound production in the giant dung beetle *Heliocopris dominus* Bates (Joseph 1991), sexual dimorphism and intra sex variations (Joseph 1994), biology and breeding behavior (Joseph 1998) and the life cycle, ecological role and biology of immature stages of *Heliocopris dominus* (Joseph 2003).

Studies on the ecology and community structure of dung beetles in South Western Ghats are minimal. Sabu & Vinod (2005) analysed the guild structure and taxonomic diversity of two dung beetle assemblages in intact forest and nearby pasture in North Wayanad. Sabu *et al*. (2006) analysed the guild structure, diversity and succession of dung beetles associated with Indian elephant dung in the forests of Thirunelly in South Western Ghats. In another similar study, Vinod & Sabu (2007) compared the species composition and community structure of dung beetles associated with the dung of gaur and elephant from the same locality. Succession of dung beetles in the dung pats of gaur, from the moist deciduous forests of South Western Ghats was also studied (Sabu *et al.* 2007). Vinod (2009) provided data on the systematics and ecology of dung beetles in the forest and agricultural habitat of the Wayanad region of South Western Ghats. Comprehensive data on the community structure, species composition and regional endemism of dung beetle assemblage in a tropical montane cloud forest (TMCF) from South Asia was provided by Sabu *et al.* (2011b).

MATERIALS AND METHODS

Latha Mathews “Systematics and ecology of dung beetles (coleoptra: scarabaeidae: scarabaeinae) in the Nelliampathi region of South Western Ghats” Thesis. Department of Zoology, St. Joseph's College Devagiri , University of Calicut, 2013

Chapter 3

MATERIALS & METHODS

3.1. Study region

The study region Nelliampathi is situated in the Western Ghats just south of the Palghat Gap. The Palghat Gap is a transverse valley about 32 km wide and is the only major break in the continuous mountain range, that sharply divides Wayanad and the Nilgiris in the north, from the Nelliampathi Hills of the Thrissur district to the south (Ali 1999). The Palghat Gap is important to the climate of southern India. It allows the moisture-laden Southwest monsoon winds into the Coimbatore region, which moderates Coimbatore's summer temperatures and generates greater rainfall in the region relative to the rest of lowland Tamil Nadu. Also, in the summer, the district of Palghat is warmer than the rest of the state because hot winds from Tamil Nadu blows in. The amount of rainfall differs to the north and south of the Palghat Gap. Rainfall along Western Ghats decreases from south to north, especially north of the Palghat Gap (Nair 2006). Palghat Gap is also considered as a major barrier for faunal movement between the north and south regions of the Western Ghats (Pearson & Ghorpade 1989).

The remarkable biological richness and endemism of the Western Ghats region is inherent in its inclusion among the 34 global hotspots and inclusion as UNESCO world natural heritage site. Superimposed on this biological diversity is the human diversity in the form of richness of cultures, ethnicity, and traditional knowledge systems. However, its forests face tremendous population pressure and have been dramatically impacted by demands for timber and agricultural land. Of the approximately 1,80,000 square-kilometer area in the Western Ghats region, only one-third is under natural vegetation. Moreover, the existing forests are highly fragmented and facing the prospect of increasing degradation (Bawa *et al.* 2007).

Until recently, the forests of the Western Ghats extended uninterrupted from north to the south and extended down, in particular on the western side, almost up to the sea shore. The Palghat plains had many scattered hillocks with dense vegetation even in 1971, when they were nationalized along with other private forests and cleared for distribution among the landless. By the middle of the 19^{th} century, the Palghat Gap became the first major forest discontinuity in the South Western Ghats with the laying of arterial communication between the east and the west by the British. With the advent of the Second World War, construction of extensive network of roads fragmented the hill slopes very severely. This was followed by the river valley projects of the fifties, sixties and seventies. The dams, reservoirs, network of roads, power houses, telephone lines, pockets of settlement, monoculture plantations and cash crop plantations further degraded the forests of the region (Nair 1991).

Nelliampathi is located at a height of 467 to 1572 m above sea level and is spread over a total area of 82 sq. km at a distance of about 52 km from Palghat town (Plate 1). Apart from the scenic beauty, Nelliampathi also boasts large population of fauna. The place is the abode of rare and endangered species of animals and a diversity of medicinal plants. It is an ecologically high sensitive area enclosing the Nelliampathi Reserve forest and is bordered by the Parambikulam wildlife Sanctuary (Nair 1991) (proposed project tiger reserve) towards the south and southeast. The land forms a corridor for the movement of long ranging species such as tiger, leopard, wild gaur and is also a crucial elephant migratory route (Elephant Range No. 9) (Sukumar & Easa 2006). The forests in eastern region of Nelliampathi considered as ‘wind belts’ stops the dry winds coming from Coimbatore and maintains the temperature of Kerala moderate (Joy 1991).

Nelliampathi is highly degraded at present characterized by forest fragments interspersed predominantly by coffee, tea, cardamom and orange plantations (Joy 1991; Latha & Unnikrishnan 2007). The large number of leased estates operating in the region has degraded the forests of the region. This has resulted in regular incidents of environmental catastrophes such as landslides and landslips in the entire Nelliampathi tract in the recent past. Some of the tributaries of Pothundi, Meenkara, Chulliyar, Mangalam and Peechi dam originate from the Nelliampathi hills. The storage of these reservoirs is badly affected due to deforestation and indiscriminate felling in this area (Prabhakaran 2011). Amidst this scenario, the biodiversity study on dung beetles which are considered as important indicators of habitat change gains significance as such large scale destruction of habitats can lead to species extinction and documenting their diversity is of priority concern in planning conservation strategy (Bawa *et al.* 2007).

3.1.1. Study site

The study was carried out in Kaikatty located at 10^0 31’N and 76^0 40’E, at an elevation of 960 msl. The temperature of the region varies between 15^0C-

30^0C and annual rainfall exceeds 3000 mm (Nair 1991). Three seasons characterizes the region namely, presummer (December to February), summer (March to May) and monsoon period (June to November).

The vegetation in the study site is characterized by West Coast Semi-Evergreen forest (Champion & Seth 1968). Evergreen undergrowth is rather copious and climbers tend to be very heavy. Epiphytes are abundant, including many ferns and orchids. About 40% to 80% trees are evergreen. Top canopy trees are characterized by *Terminalia tomentosa, Dalbergia latifolia, Haldina cordifolia, Xylia xylocarpa, Artocarpus hirsutus, Hopea parviflora, Mesua lerrea;* second storey trees by *Hydnocarpus pentandra, Bischofia javanica, Mallotus philippensis, Kydia calycina* (Kerala Forests and Wildlife Department 2004).

Nelliampathi forests present a rich mammal fauna represented by elephant (*Elephas maximus*), gaur (*Bos gaurus*), sambar deer (*Cervus unicolor*), wild boar (*Sus scrofa*), langur (*Semnopithecus sp*), lion tailed macaque (*Macaca silenus*), Nilgiri marten (*Martes gwatkinsii*), small Travancore flying squirrel (*Petinomys fuscocapillus*), brown mongoose (*Herpestes fuscus)*, Malabar civet (*Viverra megaspila*) (Kerala Forests and Wildlife Department 2004).

The collection sites included the government reserve forest which is 2,400 acres, the government owned agriculture land which is 920 acres of predominantly orange trees along with other fruit trees like sapodilla, banana etc. lying adjacent to the forest with a well defined ecotone separating the two different habitats. Traps were placed in the reserve forest, ecotone and in the portion of the agriculture land with banana plantation (Plate 2).

3.2. Sampling methodology

Dung beetles were collected using dung baited pitfall traps of the bait-surface-grid type (Lobo *et al*. 1988; Veiga *et al*. 1989). Since, dung beetles are excellent fliers and actively forage for food, they can be efficiently sampled using baited pit fall traps (Larsen & Forsyth 2005), pitfall traps also provide fast, inexpensive, and relatively unbiased method for obtaining data on species diversity and abundance distributions (Spector & Forsyth 1998).

Dung beetles were collected on a seasonal basis in May (summer), September (monsoon) and December (presummer) during the year 2007-2008. Sites that represent a semi-evergreen forest and agriculture field separated by a sharp ecotone were selected. The transition between the closed forest habitat and the agriculture field occurred over the space of five to eight metres with the ecotone characterized by narrow band of scattered shrubs.

A series of ten 100 m transects, each separated by 50 m, was established at the study site. Each transect ran perpendicular across the forest-agriculture field ecotone and consisted of three pitfall traps. A trap at the forest-agriculture field ecotone established the midpoint of each transect. Traps were then placed 50 m away from the centre trap, in the forest and agriculture field (Spector & Ayzama 2003). The pit fall traps containing solution of mild detergent (to reduce surface tension and facilitate rapid drowning of the beetles) and salt (to reduce deterioration of the specimens) (Spector & Ayzama 2003) were buried with their rim in level with the soil and topped with a 25 x 25 cm plastic sheet for protection from rain and sun. 200 g of fresh cow dung was placed on a strip of wire grid at the top of the basin as bait.

The trap contents were collected at 12 h interval (6:00-18:00h and 18:00-6:00h) to separate diurnal and nocturnal species because flight activity of dung beetles differs strongly between night and day (Krell *et al*. 2003). The traps were emptied into fine nylon gauze (0.5 mm mesh size) to concentrate the catches from the traps. An ethanol filled wash bottle was used to wash the catch into labelled bottles.

3.3. Preservation and identification

Collected beetles were preserved in 70% alcohol overnight and later identified to species levels using taxonomic keys available in Arrow (1931) and Balthasar (1963a, b) and also by verifying with type specimens available in the Coleoptera collections of St. Joseph's College, Devagiri, Calicut. Once identified to the species level, the specimens were separated and kept in small vials containing 70% alcohol, appropriately labelled with information on site location, trapping date, taxon name, trap type and number. Specimens were subsequently curated in the insect collections of St. Joseph's College, Devagiri, Calicut, and allotypes of rare specimens were deposited in the museums of Zoological Survey of India, Western Ghats regional station, Calicut and Indian Agricultural Research Institute, New Delhi.

Number of species and number of beetles for each season in each habitat were noted. Length of the beetles was measured. Beetles less than 10 mm is designated as small beetles and more than 10 mm is designated as large beetles (Barrágan *et al.* 2011). Species were sorted into three functional guilds namely, dwellers (endocoprids), rollers (telecoprids) and tunnelers (paracoprids) and were identified following Cambefort & Hanski (1991). For identifying temporal guilds namely, diurnal, nocturnal (Krell *et al.* 2003; Krell-Westerwalbesloh *et al.* 2004) and generalists, data was obtained by pooling diurnal and nocturnal collection separately for three seasons in the three habitats (10 pits x 3 seasons) x 3 habitats. Species that were collected only in diurnal traps or nocturnal traps were designated as diurnal or nocturnal. For those that were collected in diurnal and nocturnal collections, significant levels of variation in species abundance between diurnal and nocturnal collections were calculated. Species that showed no significant variation was considered generalist, for species that showed significant variation, their abundance was used to determine if they were diurnal or nocturnal.

For habitat wise study, data was obtained by pooling the three seasonal collections (10 pits x 3 seasons) of each habitat. For seasonal studies of habitat the seasonal data was considered separately. To determine edge effect pooled habitat wise data on abundance and diversity for the three habitats were compared. Singletons were considered as rare and excluded from seasonality and diel periodicity studies (Novotny & Basset 2000). Species whose abundance was less than 5% was considered as minor species and those with more than 5% abundance was considered as major species. All the information was entered into Microsoft Excel work sheet (2003).

3.4. Checklist and pictorial key

Checklist of dung beetles of Nelliampathi region was prepared based on Arrow (1931), Balthasar (1963a, b), Sabu *et al.* (2011a) and Schoolmeesters (2011). Pictorial key was drafted based on Arrow (1931), Balthasar (1963a, b) and Latha *et al.* (2011). Photographs were taken using Nikon D50 digital camera attached to a trinocular stereo zoom microscope (Labomed ASZ-99TR).

3.5. Diversity analysis

To understand the diversity patterns, alpha diversity indices (richness, diversity, dominance and evenness), taxonomic diversity, rank abundance plot, Bray Curtis similarity index (Beta diversity index) and SIMPER analysis were done.

For analyzing species richness, Margalef's index (d) (Clifford & Stephenson 1975; Magurran 2004) was calculated by using the following formula.

$$d = S - 1 / \log(N)$$

S = total number of species

N = total number of individuals

Among the diversity indices, Shannon-Weaver diversity index (Shannon & Weaver 1949) is the most commonly used because it incorporates both species richness and evenness components and can provide heterogeneity of information (Rosenstock 1998; Cheng 1999).

$$H' = - \Sigma_i P_i (\log (P_i)$$

Where P_i is the proportion of the total count arising from the $_i{}^{th}$ species ($\log_e$ was used in its formulation).

Simpson's dominance index (λ) (Simpson 1949) gave the probability of any two individuals drawn at random from an infinitely large community belonging to the same species, its largest value correspond to assemblages whose total abundance is dominated by one or a very few of the species present.

$$\lambda = \Sigma\, p_i^2$$

Where p_i is the proportion of the total count arising from the i th species

Evenness expressed as Simpson's evenness index (1-λ), addresses equitability of the species (Simpson 1949).

$$\lambda = 1 - \Sigma\, p_i^2$$

Although there are many possible indices which can be used to portray diversity, each with strengths and weaknesses, these four are chosen because they are familiar to and readily interpretable for most ecologists.

Bray-Curtis similarity coefficient (Bray & Curtis 1957) was used to quantify and compare the similarity of dung beetle species composition among habitats. This index is calculated as

$$BC_{jk} = 100\left\{1 - \frac{\sum_{i=1}^{p}\left|y_{ij} - y_{ik}\right|}{\sum_{i=1}^{p}\left(y_{ij} + y_{ik}\right)}\right\}$$

Where BC_{jk} is the similarity between the jth and kth habitats and y_{ij} represents the abundance for the ith species in the jth habitat.

A triangular matrix of similarity coefficients was computed between every pair of habitats. To measure the similarity coefficients between various habitats, a data matrix with p rows (dung beetle species) and n columns (habitats), filled with entries of abundance counts of each dung beetle species for each habitat was first constructed. Similarity based on the Bray-Curtis coefficient was calculated between every pair of habitats, and a similarity matrix of abundance was then constructed. Bray-Curtis similarity coefficient, rated often as a satisfactory coefficient for biological data on community structure is selected. Although there are several indices of similarity, Bray Curtis similarity index most accurately reflects changes in the communities (Clarke & Warwick 1994; Magurran 2004). This index ranges from 0 (no shared species) to 100 (no difference in species composition). Furthermore, to reduce the large disparities in counts between species and to validate statistical assumptions for parametric techniques, square root transformation were applied to the original abundance counts of dung beetles before computing the Bray-Curtis coefficient.

Though there are many classes of clustering methods (Johnson & Wichern 1992; Clarke & Warwick 1994), hierarchical clustering with group-average linking was applied as this technique has proven useful in a number of ecological studies conducted during the last two decades (Clarke & Warwick 1994). Habitats were grouped and the groups themselves form clusters at the levels of similarity of dung beetle species present. These take a similarity matrix as their starting point and successively fuse the samples into groups and the groups into large clusters, starting with the highest mutual similarities then gradually lowering the similarity level at which groups are formed. The process ends with a single cluster containing all samples. The result of the hierarchical agglomerative clustering is represented by a dendrogram, with the X axis defining similarity level at which two samples or groups are considered to have fused and the Y axis representing the full set of samples (habitats).

Taxonomic diversity of the forest, agriculture field and edge were analyzed using non-parametric average taxonomic distinctness (Δ+) and variation in taxonomic distinctness (Λ+) indices (Clarke & Warwick 2001; Warwick *et al*. 2002). A regional master list of the dung beetles from Nelliampathi was compiled by combining the data from the three sites. A randomization test was done to detect differences in average taxonomic distinctness and variation in taxonomic distinctness, for any observed set of species, from the 'expected' Δ+ and Λ+ values derived from regional master species list (Clarke & Warwick 1998). Four taxonomic levels namely, species, genus, tribe and subfamily were considered. Branch lengths between taxonomic classes were defined following the standardization proposed by Warwick & Clarke (2001). Equal step lengths were assumed between each successive taxonomic level, setting path length ω to 100 for two species connected at the highest (taxonomically closest) possible level. So the weights used were ω=25 (species in the same genus), ω=50 (same tribe but different genus), ω=75 (same subfamily but different tribe) and ω=100 (same family but different subfamily).

SIMPER analysis was performed to find out the contribution of species to the similarity between habitats. All diversity analysis was done with PRIMER 5 software version 5.2.9 (Clarke & Gorley 2001).

Patterns in species composition of dung beetle assemblages were analyzed by constructing rank-abundance plot for each of the seasons/ habitats. Rank-abundance plot was plotted with relative abundance of each order against rank of species for the seasons/habitats (Whittaker 1965).

Rarefaction plot, a method for intrapolating smaller samples and estimating species richness in the rising part of the species-sampling curve (Colwell & Gotelli 2001) was done using Biodiversity pro software (McAleece *et al.* 1997). Expected numbers of species are plotted against number of individuals on the x-axis. Steeper curves indicate more diverse communities (Hurlbert 1971).

$$ES_n = \Sigma^{S}_{i=1}[1-((N-Ni)!(N-n)!)/((N-Ni-n)!N!)]$$

S = total species

N =number of individuals

ES_n= how many species would have been expected had we observed a smaller number (n) of individuals.

To assess the value of particular species as indicators of habitat change, the indicator species value (ISV) using the Indicator Value Method (IndVal) (Dufrêne & Legendre 1997) was calculated for all the species captured in one habitat. The indicator species value incorporates two components: one that reflects species specificity (species unique to sites in a group of sites), and one that reflects species fidelity (species abundant and widespread within a group of sites). Thus, the ISV of a species expresses the degree (0–100%) to which the species shows specificity and fidelity. Species with high indicator values thus make reliable indicator species not only because they are specific to a locality, but also because they have a high probability of being sampled in that locality during monitoring and assessment (McGeoch & Chown 1998). ISV's were calculated for each species 'i' in each of the three habitats 'j' as

$$ISV_{ij} = A_{ij} \cdot B_{ij} \cdot 100$$

Where Aij is the mean number of species 'i' across the samples 'j' divided by the sum of the mean numbers of individuals of species 'i' over all habitats, and Bij is the number of samples in habitat 'j' where species 'i' is present, divided by the total number of samples in that habitat (Dufrêne & Legendre 1997; McGeoch & Chown 1998). Species with *IndVal*s of greater than 70% were regarded as characteristic indicator species for the habitat in question and species with *IndVal*s of between 50% and < 70% is considered as detector species which will indicate the direction in which ecological change is taking place (McGeoch *et al.* 2002).

3.6. Statistical analysis

All the data used for statistical analysis were tested for normality with Anderson-Darling test. Since all the data were not normally distributed non-parametric statistics, Kruskal-Wallis H tests was used to test the significant levels in variations (Sachs 1992). Differences with a p-value <0.05 was compared using Wilcoxon-Mann/Whitney Test. The data includes the abundance of individual species of dung beetles with seasons and habitats; variations in Shannon diversity value (H') of dung beetle assemblages among habitats; variations in functional guild abundance with seasons and habitats and variations in temporal guild abundance with seasons and habitats. All statistical analyses were performed using Megastat version 10.0 (Orris 2005).

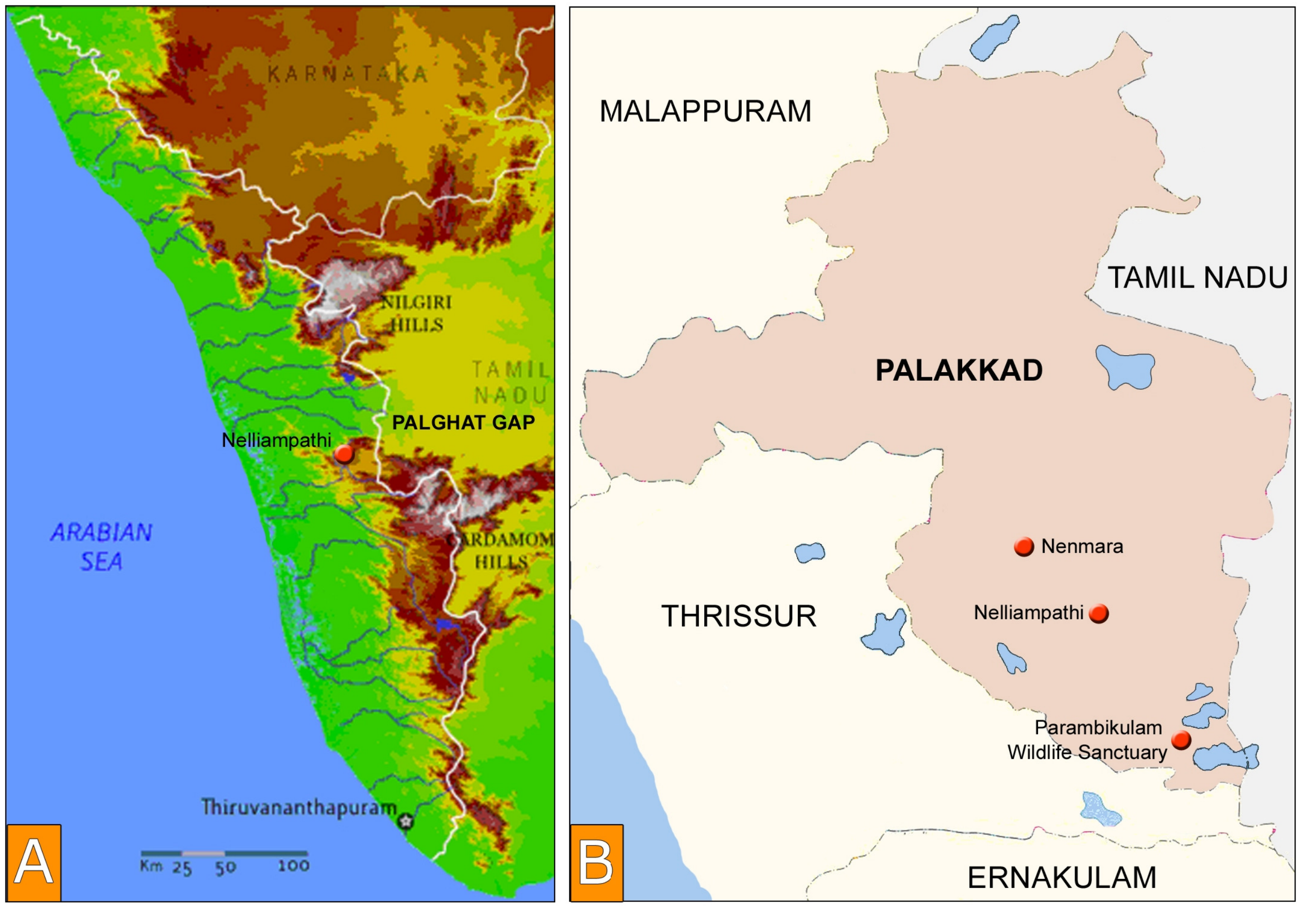


Plate 1: Map showing (A) The Western Ghats and (B) Study region of Nelliampathi.

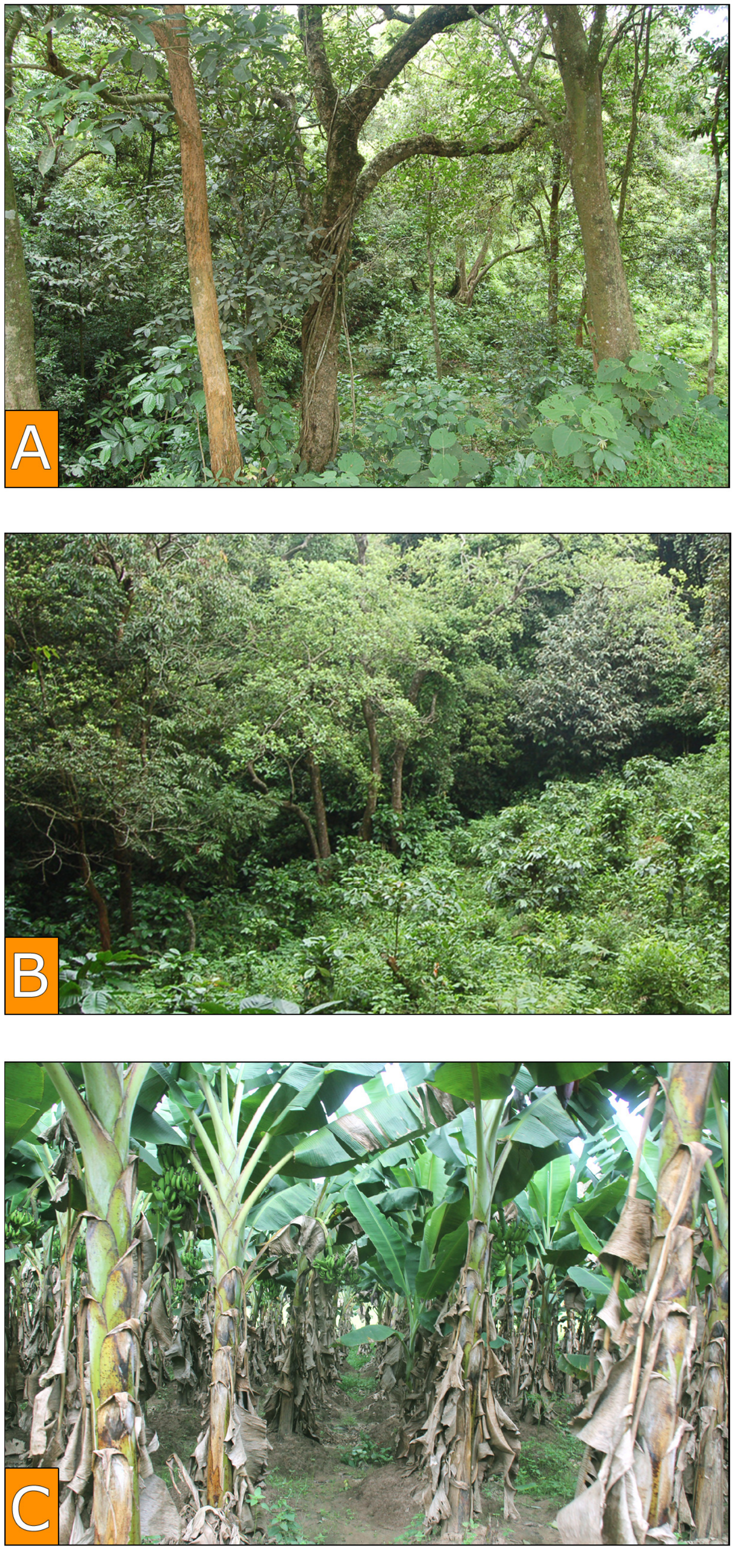


Plate 2: Study sites at Nelliampathi (A) Forest habitat (B) Ecotone and (C) Agriculture habitat.

RESULTS

Latha Mathews “Systematics and ecology of dung beetles (coleoptra: scarabaei-dae: scarabaeinae) in the Nelliampathi region of South Western Ghats” Thesis. Department of Zoology, St. Joseph's College Devagiri , University of Calicut, 2013

Chapter 4

RESULTS

4.1. Taxonomy

Checklist of dung beetle fauna from Nelliampathi region of the Western Ghats revealed the presence of 34 species, comprising 11 genera namely, *Caccobius*, *Catharsius*, *Copris*, *Liatongus*, *Paracopris*, *Paragymnopleurus*, *Ochicanthon*, *Onitis*, *Onthophagus*, *Sisyphus* and *Tibiodrepanus* and seven tribes namely, Canthonini, Coprini, Gymnopleurini, Onitini, Onthophagini, Oniticellini and Sisyphini. *Onthophagus* was the most speciose genus with 22 species. Of the 34 species reported, *Onthophagus deflexicollis* Lansberge, *Onthophagus* (*macronthophagus*) *manipurensis* Arrow and *Tibiodrepanus sinicus* Harold are first record from South India (Plate 3). Nine species endemic to Western Ghats were collected from the region which included *Caccobius gallinus* Arrow, *Liatongus indicus* Arrow, *Ochicanthon mussardi* Cuccodoro, *Onthophagus amphicoma* Boucomont, *O. andrewesi* Arrow, *O. bronzeus* Arrow, *O. vladimiri* Frey 1957, *Paracopris davisoni* Waterhouse 1891 and *Sisyphus araneolus* Arrow 1927 (Plate 3 & 4). Synonymies for genera and species are provided. Superscript provided to species furnishes the following details namely, #first report from South India and @endemic to Western Ghats.

4.1.1. Check list of dung beetles of Nelliampathi region

SCARABAEINAE

GYMNOPLEURINI

***Paragymnopleurus* Shipp, 1897**

Paragymnopleurus Shipp, 1897, Entom., XXX: 166 (pro parte); Janssens, 1941, Mem. R. Hist. Nat. Belg., (2) XVIII: 1-22; Garreta, 1941, Bull. Soc. Ent. France, XIX: 52; Paulian, 1945:51.

***Paragymnopleurus sinuatus* Olivier, 1789**

Paragymnopleurus sinuatus Olivier, 1789, Entom., I: 160; Arrow, 1931: 63; Balthasar, 1935: 47; Janssens, 1940, XVIII: 20; Leei Donovan, 1798; Paulian, 1945: 53.

Distribution: India (Arunachal Pradesh; Karnataka; Kerala: Nelliampathi, Nilambur, Palghat, Ranipuram, Shendurney; Maharashtra: Kanara, S. Bombay; Sikkim; W. Bengal), Myanmar, Nepal.

SISYPHINI

***Sisyphus* Latreille, 1807**

Sisyphus Latreille, 1807, Gen. Crust. et Ins. II: 79; Gory, 1833, Monogr. Du genre Sisyphe:1–15; Lacordaire, 1856, Gen. Col. III: 72; Reitter, 1892 (1893): 158, 164; Péringuey, 1900 (1901): 22, 94–103, 897, 898; Arrow, 1927a: 456–465; Arrow, 1931: 67; Balthasar, 1935: 52; Haaf, 1955: 341 ff.; Balthasar, 1963, I: 233.

***Sisyphus* (s.str.) *araneolus*[@] Arrow, 1927**

Sisyphus (s.str.) araneolus@ Arrow, 1927, Ann. Mag. Nat. Hist. 9(XIX): 464; Arrow, 1931: 71; Haaf, 1955:348, 358; Balthasar, 1963, I: 241.

Distribution: India (Kerala: Nelliampathi; Tamil Nadu: Nilgiri Hills)

CANTHONINI

***Ochicanthon* Vaz-de-Mello, 2003**

Ochicanthon Vaz-de-Mello, 2003, Coleop. Bull. 57(1): 25–26; Boucomont, 1914, Ann. Soc. Ent. Fr. 83: 249 (Phacosoma); Arrow, 1931: 354; Paulian, 1945: 56; Balthasar, 1963, I: 269.

***Ochicanthon mussardi*@ Cuccodoro, 2011**

Ochicanthon mussardi@ Cuccodoro, 2011, Zootaxa, 2745: 18.

Distribution: India (Kerala: Cardamom Hills, Nelliampathi Hills)

COPRINI

***Catharsius* Hope, 1837**

Catharsius Hope, 1837, Col. Man. I: 21; Burmeister, 1846, Gen. Ins. X, No. 27; Péringuey, 1900 (1901): 109, 323; Boucomont and Gillet, 1921:7; Arrow, 1931: 92; Balthasar, 1935: 62; Paulian, 1945: 68; Balthasar, 1963, I: 304.

***Catharsius* (s.str.) *molossus* (Linnaéus, 1758)**

Catharsius (s.str.) *molossus* Linnaéus, 1758, Syst. Nat. Ed. X: 347 (*Scarabaeus*); Harold, 1877, 44; Boucomont and Gillet, 1921: 8; Arrow, 1931: 94; Balthasar, 1935: 65; Paulian, 1945: 69; Balthasar, 1963, I: 307-309.

-*abbreviatus* Herbst, 1789, Käfer II: 53.

-*berbiceus* Herbst, I. c.: 227.

-*janus* Olivier, 1789, Entom. I. Scarab.: 101.

-*ursus* Fabricius, 1801, Syst. Eleuth. I: 43.

-*borneensis* Paulian, 1936, Treubia 15: 396.

-*dubius* Paulian, 1. c.

-*dayacus* Lansberge, 1886, Tijdschr. Entom. XXIX: 6 (syn. n.).

-*timorensis* Lansberge, 1879, Ann. Soc. Ent. Belg. XXII, C. r: 148 (syn. n.).

-*kangeanus* Paulian, 1. c.: 395 (syn. n.).

Distribution: Afghanistan, Cambodia, China, India (Andaman; Arunachal Pradesh; Assam; Bihar; Gujarat; Hariyana; Karnataka; Kerala: Kinavellore, Nelliampathi, Wayanad; Meghalaya; Mumbai; Orissa; Rajasthan; Sikkim; Tamil Nadu; Uttaranchal; W. Bengal), Laos, Malaysia, Nepal, Sri Lanka, Sunda Island, Taiwan, Thailand, Vietnam (Annam).

***Copris* Geoffroy, 1762**

Copris Geoffroy, 1762, Ins. Env. De Paris I:87; Burmeister, 1846, Genera Ins. Heft 10, Col. No. 27; Reitter, 1892 (1893): 39, 93; Péringuey, 1900 (1901): 110, 342; Boucomont and Gillet, 1921: 10; Arrow, 1931: 102; Balthasar, 1933: 263; Balthasar, 1935: 66; Janssens, 1939: 40; Paulian, 1945: 71; Balthasar, 1963, I: 317–319.

***Copris* (s.str.) *repertus* Walker, 1858**

Copris (s.str.) *repertus* Walker, 1858, Ann. Mag. Nat. Hist. (3) II: 208; Gillet, 1911: 290; Arrow, 1931:116; Balthasar, 1933: 272; Balthasar, 1935: 78; 1963, I: 351–352.

-*claudius* Harold, 1877, Ann. Mus. Civ. Genova X: 48.

Distribution: China, India (Arunachal Pradesh, Bihar; Chattisgarh; Gujarath, Karnataka; Kerala: Nelliampathi, Palghat, Ranipuram, Shendurney, Silent valley, Taliparamba, Thekkady, Wayanad); Madhya Pradesh; Maharashtra: Mumbai; Pondicherry, Rajasthan, Tamil Nadu: Anaimalai Hills, Nilgiri Hills; Uttar Pradesh), Sri Lanka, Thailand.

***Paracopris* Balthasar, 1939**

Paracopris Balthasar, 1939a, Redia XXV: 2; Paulian, 1945: 72; Balthasar 1958: 473–474, Balthasar, 1963, I: 329–331.

***Paracopris cribratus* Gillet, 1927**

Paracopris cribratus Gillet, 1927, Ann. Soc. Ent. Belg. LXVII: 253; Arrow, 1931:129

Distribution: India (Gujarat: Karnataka; Kerala: Nelliampathi, Ranipuram, Shendurney, Thekkady; Surat; Tamil Nadu: Anaimalai Hills, Kalyana Pandal).

***Paracopris davisoni*[@] Waterhouse, 1891**

Paracopris davisoni[@] Waterhouse, 1891, Ann. Mag. Nat. Hist. (6), VII: 520; Arrow, 1931: 132; Balthasar, 1963, I: 373.

Distribution: India (Karnataka; Kerala: Nelliampathi, Peerumade, Ranipuram, Thekkady, Travancore, Wayanad; Mumbai; Tamil Nadu: Nilgiri Hills, Palni Hills).

***Paracopris signatus* Walker, 1858**

Paracopris signatus Walker, 1858, Ann. Mag. Nat. Hist. (3), 2: 208; Boucomont and Gillet, 1921: 12; Arrow, 1931: 131; Paulian, 1945: 74; Balthasar, 1963, I: 371.

Distribution: India (Karnataka; Kerala: Mahe, Malabar, Thekkady, Travancore Sendurney, Wayanad; Maharashtra; Tamil Nadu: Coimbatore) Laos, Sri Lanka, Vietnam (Annam).

ONTHOPHAGINI

***Caccobius* Thomson, 1863**

Caccobius Thomson, 1863, Skand. Col. V: 34; Harold, 1867, Col. Hefte I: 5; Harold, 1867, 1.c.II: 1; Mulsant, 1871: 75; Jekel, 1872, Rev. Mag. Zool.: 405; Waterhouse, 1875, Trans. Ent. Soc. London: 73; Reitter, 1892 (1893): 39, 91; d'Orbigny, 1898; 127; Péringuey, 1900 (1901): 275; Péringuey, 1908: 565; d'Orbigny, 1913: 17; Boucomont and Gillet, 1921: 27; Arrow, 1931: 141; Portevin, 1931: 39; Porta, 1932: 412; Matsumura, 1936: 61; Paulian, 1945: 81; Balthasar, 1949: 1; Balthasar, 1963, II: 113.

-subg. *Caccophilus* Jekel, 1872, 1.c.: 410; d'Orbigny, 1898: 130; d'Orbigny, 1913: 21; Balthasar, 1935e: 183; Balthasar, 1949: 7.

***Caccobius* (*Caccophilus*) *gallinus*[@] (Arrow, 1907)**

Caccobius (*Caccophilus*) *gallinus*[@] Arrow, 1907, Ann. Mag. Nat. Hist. (7), XIX: 424 (*Onthophagus*); Arrow, 1931: 142, 148; Balthasar, 1949: 14, 33; Balthasar, 1963, II: 136–137.

Distribution: India (Kerala: Nelliampathi, Wayanad; Tamil Nadu: Nilgiri Hills).

***Caccobius* (*Caccophilus*) *meridionalis* Boucomont, 1914**

Caccobius (*Caccophilus*) *meridionalis* Boucomont, 1914, Ann. Mus. Civ. Genova VI (XLVI): 239; Arrow, 1931: 142, 148; Balthasar, 1949: 8, 36; Balthasar, 1963, II: 138.

Distribution: India (Karnataka; Kerala: Erumaiyoor, Mahe, Nelliampathi, Ranipuram, Shendurney, Silent valley, Thekkady, Wayanad; Gujarat; Maharashtr; Tamil Nadu: Anaimalai Hills, Nilgiri Hills), Sri Lanka.

***Caccobius (Caccophilus) ultor* Sharp, 1875**

Caccobius (Caccophilus) ultor Sharp, 1875, Col. Hefte, xiii, 1875: 50, Balthasar, 1963,II: 135.

Distribution: India (Haryana: Kanneri; Karnataka: Budipadaga; Kerala: Nelliampathi, Ranipuram; Maharashtra: Bombay, Khandesh; Punjab, Rajasthan, Uttar Pradesh).

***Onthophagus* Latreille, 1802**

Onthophagus Latreille, 1802, Hist. Nat. Crust. Ins. III: 141; Mulsant, 1842: 102; Erichson, 1848. III: 762; Lacordaire, 1856. Gen. Col. III: 107; Mulsant-rey, 1871: 78; Reitter, 1892 (1893): 47; d'Oribgny, 1898: 132;

d'Oribgny, 1900: 289; Peringuey, 1900 (1901): 168; Peringuey, 1908: 560; Reitter, 1909: 325; Bedel, 1911; 25; d'Oribgny, 1913: 49;1915: 378 (Suppl.); Boucomont, 1914: 238; Boucomont and Gillet, 1921: 1; Boucomont, 1924a: 669; Arrow, 1930: 159; Portevin, 1931:42; Porta, 1932: 408; Balthasar, 1935d: 303; Savcenko, 1938; 46, 136; Paulian, 1941:66; Paulian, 1945: 85; Endrödi, 1956:94; Tesař, 1957: 127; Balthasar, 1963, II: 153.

-*Monapus* Erichson, 1848, Naturg. Ins. Deutschl. Col. III: 763.

-*Psilax* Erichson, 1848, 1.c..

-*Matashia* Matsumura, 1938, Ins. Matsum. XII: 63.

-subg. *Proagoderus* Lansberge, 1883, Not. Leyd. Mus. V: 14; d'Oribgny, 1913: 493; Boucomont, 1914: 261; Marcus, 1917,A (1919): 1; Marcus, 1920, D. Ent. Zeitschr.: 177, 1921, ibid. 163; Balthasar, 1963, II: 158.

-*Tauronthophagus* Shipp, 1895, Entomologist XXVIII: 179.

-subg. *Serrophorus* Balthasar, 1935, Fol. Zool. Hydrob. VIII: 306; Paulian, 1945: 86; Balthasar, 1963, II: 160.

-subg. *Colobonthophagus* Balthasar, 1935, 1.c.: 308; Paulian, 1945, 87; Balthasar, 1963, II: 164.

-subg. *Digitonthophagus* Balthasar, 1959, 1.c.: 464; Balthasar, 1963, II: 159.

-subg. *Paraphanaeomorphus* Balthasar, 1959, 1.c.: 465; Balthasar, 1963, II: 162.

***Onthophagus* (s.str.) *amphicoma*@ Boucomont, 1914**

Onthophagus (s.str.) *amphicoma*@ Boucomont, 1914, Ann. Mus. Civ. Genova, 3, VI (XLVI):239; Arrow, 1931:262; Balthasar, 1963, II: 269.

Distribution: India (Kerala: Mahe, Malabar, Nelliampathi, Travancore; Tamil Nadu: Nilgiri Hills).

***Onthophagus* (s.str.) *andrewesi*[@] Arrow, 1931**

Onthophagus (s.str.) *andrewesi*[@] Arrow, 1931, Fauna Brit. India, Lamell. III: 321, 324; Balthasar, 1963, II: 273–274.

Distribution: India (Karnataka: Kanara; Kerala: Nelliampathi, Wayanad; Tamil Nadu: Anamalai Hills, Nilgiri Hills).

***Onthophagus* (s.str.) *bronzeus*[@] Arrow, 1907**

Onthophagus (s.str.) *bronzeus*[@] Arrow, 1907, Ann. Mag. Nat. Hist. (7), XIX: 429; Arrow, 1931: 184, 192; Balthasar, 1963, II: 299.

Distribution: India (Karnataka; Kerala: Nelliampathi, Wayanad; Tamil Nadu: Nilgiri Hills).

***Onthophagus* (s.str.) *castetsi* Lansberge, 1867**

Onthophagus (s. str.) *castetsi* Lansberge, 1867, Not. Leyden Mus., IX: 163; Arrow, 1931: 210, 215; Balthasar, 1963, II: 304.

Distribution: India (Kerala: Nelliampathi, Travancore, Trivandrum, Wayanad; Tamil Nadu: Kodaikanal (Shembaganur), Madura, Palni Hills; Uttar Pradesh).

***Onthophagus* (*Micronthophagus*) *cavia* Boucomont, 1914**

Onthophagus (*Micronthophagus*) *cavia* Boucomont, 1914, Ann. Mus. Civ. Genova, XLVI : 237 ; Arrow, 1931 :163,166; Balthasar, 1963, II: 305.

Distribution: India (Bombay; Karnataka: Nandidroog; Kerala : Nelliampathi; Tamil Nadu: Conoor, Nilgiri Hills).

***Onthophagus* (s.str.) *centricornis* (Fabricius, 1798)**

Onthophagus (s.str.) *centricornis* Fabricius, 1798, Ent. Syst. Suppl.: 33 (*Copris*); Boucomont, 1914a: 235; Arrow, 1931: 327, 343; Balthasar, 1963, II: 305–306.

-*luteipennis* Weidemann, 1823, Zool. Mag. II, 1: 20 (*Copris*).

-*minutus* Motschulsky, 1858, Etud. Ent. VII: 54.

Distribution: Afghanistan, India (Karnataka; Kerala: Nelliampathi, Wayanad; Maharashtra; Tamil Nadu: Nilgiri Hills), Sri Lanka.

***Onthophagus* (s.str.) *deflexicollis*# Lansberge, 1883**

Onthophagus (s.str.) *deflexicollis*# Lansberge, 1883, Not. Leyden Mus. V: 72; Boucomont,1914 : 311 ; Boucomont and Gillet,1921: 59,60 ; Arrow,1931: 327, 331 ; Balthasar,1935d : 340; Paulian, 1945: 90,118. Balthasar, 1963, II: 327.

-*mutabilis* Lansberge, 1883, 1.c.: 148.

Distribution: Burma, India (Assam; Arunachal Pradesh; Bengal; Kerala: Nelliampathi; Uttaranchal; Sikkim), Indonesia (Sumatra), Malay-Peninsula, Myanmar, Tonkin.

***Onthophagus* (s. str.) *ensifer* Boucomont, 1914**

Onthophagus (s. str.) *ensifer* Boucomont, 1914, Ann. Mus.Civ. Genova, XLVI: 220; Arrow, 1931: 327, 334; Balthasar, 1963, II: 342.

Distribution: India (Arunachal Pradesh; Gujarat; Kerala: Nelliampathi, Ranipuram, Thekkady, Wayanad; Tamil Nadu: Madhura, Nilgiri Hills).

***Onthophagus* (s.str.) *fasciatus* Boucomont, 1914**

Onthophagus (s.str.) *fasciatus* Boucomont, 1914, Ann. Mus. Civ. Genova, XLVI: 231; Arrow, 1931: 310, 311; Balthasar, 1963, II: 347.

Distribution: India (Karnataka; Kerala: Nelliampathi, Ranipuram, Thekkady, Wayanad; Madhya Pradesh; Mumbai; Uttaranchal; W. Bengal; Tamil Nadu: Anaimalai Hills, Madhura, Nilgiri Hills).

***Onthophagus* (s.str.) *favrei* Boucomont, 1914**

Onthophagus (s.str.) *favrei* Boucomont, 1914, Ann. Mus. Civ. Genova, XLVI: 225; Arrow, 1931: 311, 315; Balthasar, 1963, II: 347–348.

Distribution: India (Karnataka; Kerala: Nelliampathi, Wayanad; Tamil Nadu: Coimbatore, Nilgiri Hills), Sri Lanka.

***Onthophagus* (s.str.) *furcillifer* Bates, 1891**

Onthophagus (s.str.) *furcillifer* Bates, 1891, Entomologist XIV, Suppl.: 11; Arrow, 1931: 270, 273; Balthasar, 1963, II: 360.

Distribution: India (Assam; Kashmir; Kerala: Ranipuram, Thekkady, Wayanad; Punjab; Uttaranchal).

***Onthophagu*s (s.str.) *insignicollis* Frey, 1954**

*Onthophagu*s (s.str.) *insignicollis* Frey, 1954, Arb. Mus. Frey, 5:744; Balthasar, 1963, II: 393-394.

Distribution: India (Bihar; Kerala: Nelliampathi, Wayanad).

***Onthophagus* (*Serrotophorous*) *laevis* Harold, 1880**

Onthophagus (s.str.) *laevis* Harold, 1880, Not. Leyden Museum II: 194; Harold, 1886, apud Ritsema, Col. Midden Sumatra: 26; Boucomont, 1914: 276; Boucomont and Gillet, 1921; 51; Arrow, 1931; 171; Paulian, 1945: 89, 109; Balthasar, 1963, II: 412–413.

Distribution: Borneo, China, India (Kerala: Nelliampathi, Wayanad; Sikkim; Uttaranchal, W. Bengal), Indonesia (Java; Sumatra), Myanmar, Thailand.

***Onthophagus* (*macroonthophagus*) *manipurensis*# Arrow, 1907**

Onthophagus (*Digitonthophagus*) *manipurensis*# Arrow, 1907, Ann. Mag. Nat.Hist.7, XIX: 426; Arrow, 1931:230,242;-diabolicus (rubricollis Hope) var manipurensis Arr. Apud Boucomont and Gillet, 1921:31; -nilgirensis Gillet, 1922, Ann. Soc. Sci. Brux. LI; 128,(ex parte); Arrow, 1931:242(ex parte) ; Balthasar, 1963, II: 431.

Distribution: Burma; India (Arunachal Pradesh; Assam; Kerala: Nelliampathi; Manipur).

***Onthophagus* (s.str.) *pacificus* Lansberge, 1885**

Onthophagus (s.str.) *pacificus* Lansberge, 1885, not. Leyden Mus. VII: 17; Boucomont, 1914: 280; Boucomont and Gillet, 1921: 34, 53; Arrow, 1931: 171, 172.

Distribution: China, Bangladesh, Borneo, India (Assam; Karnataka; Kerala: Wayanad, Nelliampathi; Tamil Nadu: Nilgiri Hills; Uttaranchal; W. Bengal), Indonesia (Java; Sumatra), Myanmar, Malaysia, Sunda Islands, Thailand, Laos, Vietnam.

***Onthophagus* (s.str.) *porcus* Arrow, 1931**

Onthophagus (s.str.) *porcus* Arrow, 1931, Fauna Brit. India, Lamell. III: 321, 325; Balthasar, 1963, II: 482.

Distribution: India (Arunachal Pradesh; Kerala: Nelliampathi, Wayanad; W. Bengal).

Onthophagus (Serrophorous) rectecornutus **Lansberge, 1883**

Onthophagus (Serrophorous) rectecornutus Lansberge, 1883, Not. Leyden Mus. V: 49 (female); Arrow, 1907: 421 (male); Boucomont, 1914: 293; Boucomont, 1914a: 228; Boucomont and Gillet, 1921: 55; Arrow, 1931: 229, 233; Balthasar, 1935 d; 342; Paulian, 1945: 90, 119; Balthasar, 1963, II: 498–499.

-*luridus* Paulian, 1933, Bull. Soc. Zool. France LVII: 98; Paulian, 1945: 119.

Distribution: China, India (Assam; Bihar; Karnataka; Kerala: Malabar, Nelliampathi; Tamil Nadu: Nilgiri Hills; W. Bengal), Sri Lanka, Sunda Islands, Thailand.

Onthophagus **(s.str.)** ***turbatus*** **Walker, 1858**

Onthophagus (s.str.) *turbatus* Walker, 1858, Ann. Mag. Nat. Hist. (3), II: 209; Boucomont, 1914a: 222; Boucomont and Gillet, 1921: 54; Arrow, 1931: 327, 329; Balthasar, 1963, II: 569.

Distribution: India (Karnataka; Kerala: Mahe, Malabar, Nelliampathi; Maharashtra; Puducherry; Tamil Nadu: Nilgiri Hills), Sri Lanka.

Onthophagus **(s.str.)** ***vladimiri*****[@] Frey, 1957**

Onthophagus (s.str.) *vladimiri* [@] Frey, 1957, Ent. Arb. Mus. Frey, VIII: 687; Balthasar, 1963, II: 237, 585.

Distribution: India (Kerala: Nelliampathi, Wayanad; Tamil Nadu: Anamalai Hills).

ONITINI

***Onitis* Fabricius, 1798**

Onitis Fabricius, 1798, Suppl. Ent. Syst.: 2; Fabricius, 1801, Syst. Eleuth. I: 26; Castelnau, 1840: 88; Lacordaire, 1856, Gen. Coleopt. III: 103; Lansberge, 1875: 14, 49; Bedel, 1892, Abeille XXVII: 251; Reitter, 1892 (1893): 96; Peringuey, 1900 (1901): 108, 118; Arrow, 1931: 386; Balthasar, 1935: 87; Janssens, 1937: 15; Paulian, 1945: 140; Balthasar, 1963, II: 26.

***Onitis subopacus* Arrow, 1931**

Onitis subopacus Arrow, 1931, Fauna Brit. India, Copr.: 395; Balthasar, 1935: 94; Janssens, 1937: 51; Balthasar, 1963, II: 38–39.

-*philemon* Lansberge (nec Fabricius), 1875, Ann. Soc. Ent. Belg. XVIII: 133; Boucomont, 1914: 336; Boucomont and Gillet, 1921: 19.

Distribution: Afghanistan, China, India (Assam; Bihar; Kashmir; Kerala: Nelliampathi, Wayanad; Madhya Pradesh; Tamil Nadu: Anamalai Hills; Uttaranchal; W. Bengal), Myanmar, Nepal, Sri Lanka, Sunda Islands, Thailand, Vietnam.

ONITICELLINI

***Tibiodrepanus* Kirby, 1828**

Tibiodrepanus Krikken, 2009, Haroldius 4:1–30; Kirby, 1828, Zool. Journ. III: 521(*Drepanocerus*); Castelnau, 1840: 92; Lacordaire, 1856, Gen. Col. II: 105, III; Péringuey, 1900 (1901): 108, 110; Boucomont and Gillet 1921: 19; Boucomont, 1921b: 200; Arrow, 1931: 380; Balthasar, 1935: 97; Paulian, 1945: 50, 137; Janssens, 1953: 9. 12; Balthasar, 1963, II: 61.

-*Ixodina* Roth, 1851, Arch. Naturg. XVII, I: 128.

-*Cyptochirus* Lesne, 1900, apud Ch. Michel, Vers Fachoda: 499.

-*Drepanochirus* Peringuey, 1900 (1901), Trans. S. Afr. Phil. Soc. XII: 17;

Boucomont, 1921b: 199.

***Tibiodrepanus setosus* (Wiedemann, 1823)**

Tibiodrepanus setosus Wiedemann, 1823, Zool. Mag. II, 1: 19 (*Copris*); Arrow, 1931: 381; Janssens, 1953: 19, 31; Balthasar, 1963, II: 68-69 (*Drepanocerus*); Krikken, 2009, Haroldius 4: 1–30.

-*setosa* Motschulsky, 1863, Bull. Soc. Nat. Moscou, XXXVI, II: 459 (*Ixodina*).

Distribution: India (Kerala: Nelliampathi, Wayanad; Tamil Nadu: Anamalai Hills, Nilgiri Hills).

***Tibiodrepanus sinicus*# (Harold 1868)**

Tibiodrepanus sinicus # Harold, 1868, Col. Hefte IV: 104; Arrow, 1931: 381, 383; Balthasar, 1935: 99; Paulian, 1945: 138,139; Janssens, 1953: 20, 31.

-*setosus* Boheman (nec Wiedmann), 1858, Eugenies Resa, Col.: 50; Balthasar, 1963, II: 67–68 (*Drepanocerus*); Krikken, 2009, Haroldius 4: 1–30.

Distribution: Burma, India (Central and Northern India; Kerala: Nelliampathi), Laos, North Vietnam, Southern China.

***Liatongus* Reitter, 1892**

Liatongus Reitter, 1892, Bestimmungstab.d. Lucaniden u. copr. Lamell.: 38, 45; d'Oribgny, 1898: 222; Boucomont, 1923; 53; Arrow, 1931: 79, 362; Balthasar, 1935: 26, 103; Janssens, 1953: 10, 62.

***Liatongus* (s.str.) *indicus*[@] (Arrow, 1908)**

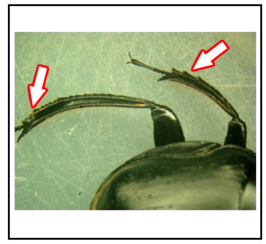
Liatongus (s.str.) *indicus*[@] Arrow, 1908, Ann. Mag. Nat. Hist. (8), 1: 180 (*Oniticellus*); Arrow, 1931: 363, 368; Janssens, 1953; 75, 95, Balthasar, 1963, II: 101–102.

Distribution: India (Kerala: Nelliampathi, Wayanad; Tamil Nadu: Anamalai Hills, Nilgiri Hills).

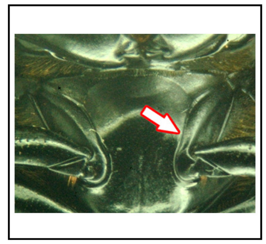
4.1.2. Pictorial key to the dung beetles of Nelliampathi region

KEY TO THE TRIBES AND SUBTRIBES OF SUBFAMILY SCARABAEINAE

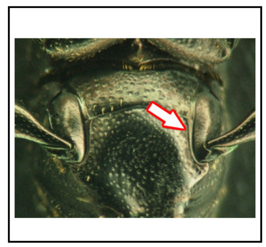
1 (6) Middle and hind tibiae elongate, slender, not or very little widened towards the apex



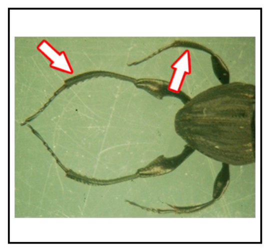
2 (3) Midle coxa not widely separated, strongly oblique- **Gymnopleurini**



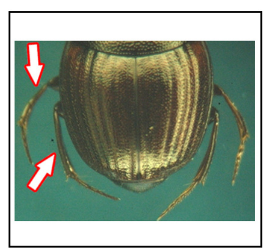
3 (2) Middle coxa widely separated, parallel or only little converging



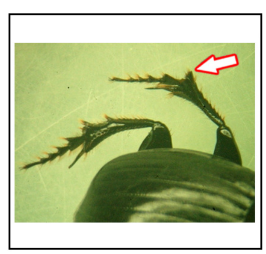
4 (5) Middle and hind legs remarkably long and slender and the hind tibia more or less strongly curved- **Sisyphini**



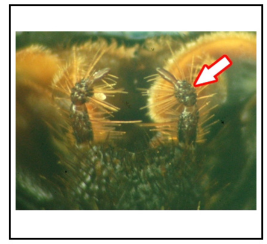
5 (4) Middle and hind legs not remarkably long, hind tibia not strongly curved- **Canthonini**



6 (1) Middle and hind tibia short, widened towards the apex and triangular

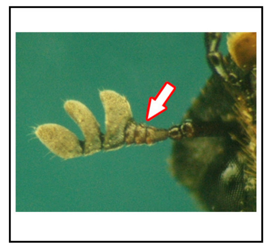


7 (8) Second segment of the labial palpi shorter than the first, third well developed- **Coprini**



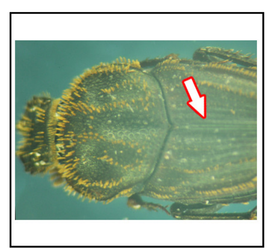
8 (7) Second segment of the labial palpi longer than the first, third very rudimentary or absent

9 (10) Antennae 8 segmented- **Oniticellini**

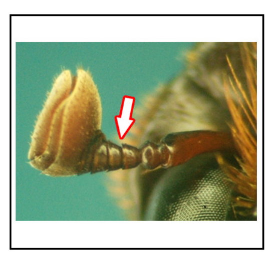


i (ii) Upper surface smooth or with fine hairs- subtribe **Oniticellina**

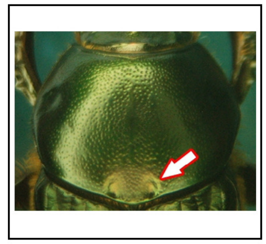
ii (i) Upper surface with coarse erect hairs- subtribe **Drepanocerina**



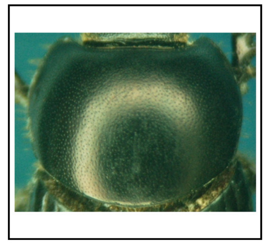
10 (9) Antennae 9 segmented



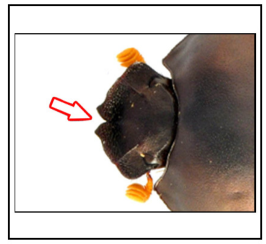
11 (12) Pronotum with two basal impressions near the middle- **Onitini**



12 (11) Pronotum without two basal impressions near the middle- **Onthophagini**



KEY TO THE GENERA

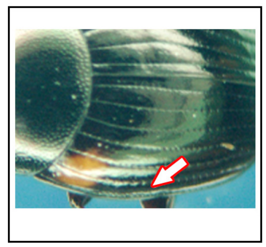


Gymnopleurini

Clypeus with two teeth- ***Paragymnopleurus*** **Shipp**

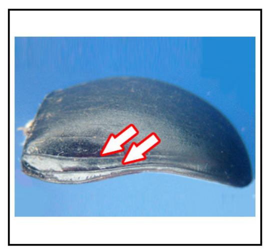
Sisyphini

Body round with disproportionately long legs, clothed above with short, erect, hooked setae- ***Sisyphus*** **Latreille**



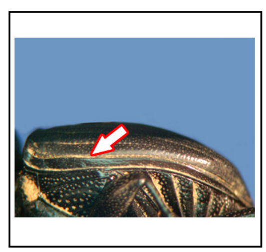
Canthonini

Elytra with six dorsal striae, seventh stria bordering the edge of the elytra- ***Ochicanthon*** **Vaz-de-Mello**

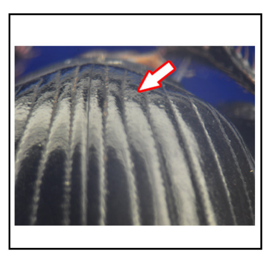


Coprini

1 (2) Elytra with two lateral carina- ***Catharsius*** **Hope**

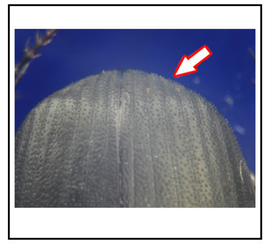


2 (1) Elytra with one lateral carina



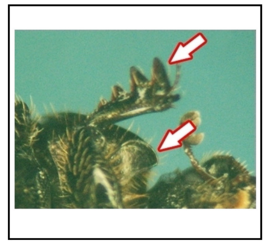
3(4) Punctures at the apex and sides of the elytra without hairs- ***Copris*** **Geoffroy**

4(3) Punctures at the apex and sides of the elytra bearing short stiff hairs- ***Paracopris* Balthasar**



Onthophagini

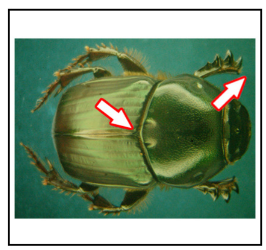
1 (2) Terminal margin of the front tibia at right angles to the inner margin and anterior angles of the prothorax hollowed beneath- ***Caccobius* Thomson**



2 (1) Either one or none of the above characters present- ***Onthophagus* Latreille**

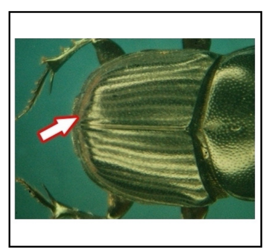
Onitini

Scutellum very minute, front tarsi absent- ***Onitis* Fabricius**

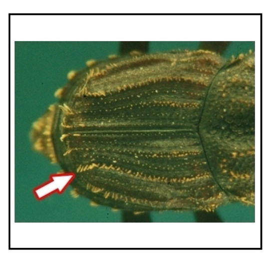


Oniticellini

1 (2) Elytra not fringed before the hind margin- ***Liatongus* Reitter**



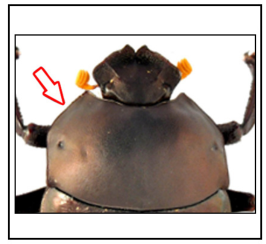
2 (1) Elytra fringed before the hind margin- ***Tibiodrepanus* Krikken**



KEY TO THE SPECIES

Paragymnopleurus

Pronotum strongly angulate at the sides-
***sinuatus* (Olivier)**



Sisyphus

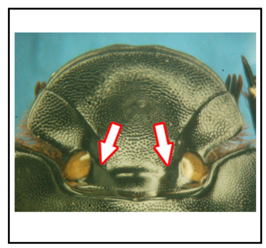
Metasternum feebly punctured in front-
***araneolus* Arrow**

Ochicanthon

Elytral strias narrow with chains of oval depressions joined by straight sulci- ***mussardi* Cuccodoro**

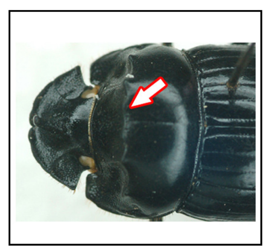
Catharsius

Head with small smooth area adjoining each eye-
***molossus* (Linnaéus)**



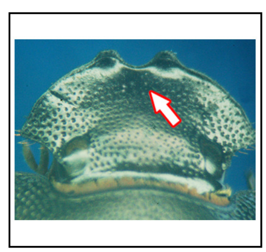
Copris

Pronotum with sharply defined anterior declivity-
***repertus* Walker**

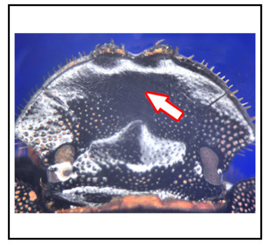


Paracopris

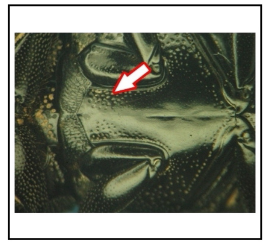
1 (2) Clypeus strongly punctured- ***cribratus* Gillet**



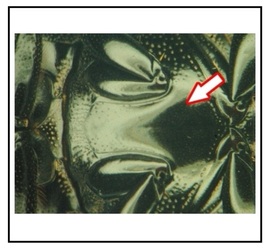
2 (1) Clypeus rather smooth



3 (4) Metasternal shield punctured in front-
davisoni **Waterhouse**

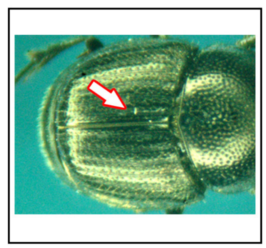


4 (3) Metasternal shield not punctured in front-
signatus **Walker**

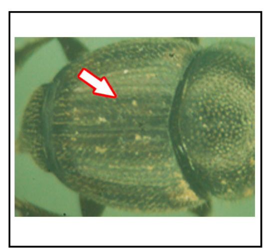


Caccobius

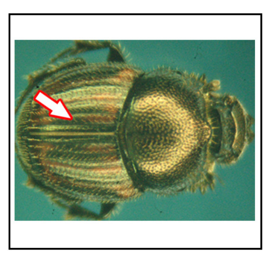
1 (2) Elytra very shining- ***gallinus*** **Arrow**



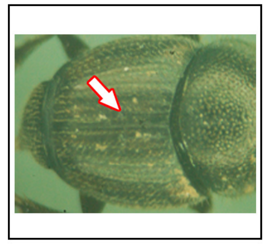
2 (1) Elytra not shining



3 (4) Elytra brown, variegated- ***meridionalis*** **Boucomont**

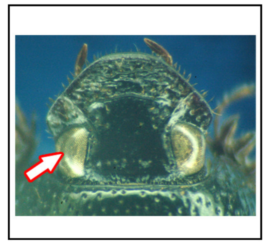


4 (3) Elytra entirely black- ***ultor*** **Sharp**

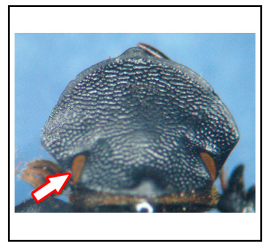


Onthophagus

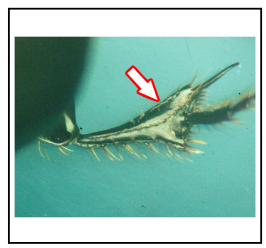
1(2) Eyes large, separated by distinctly less than three times their length- ***cavia*** **Boucomont**



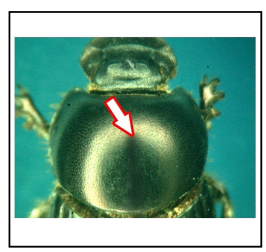
2 (1) Eyes small, separated by at least three times their length



3 (6) Hind tibia extremely short, triangular, as broad at the end as metatarsus is long

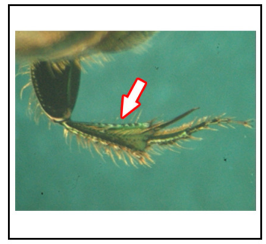


4 (5) Pronotum grooved, vertex bearing a median tubercle- ***laevis*** **Harold**

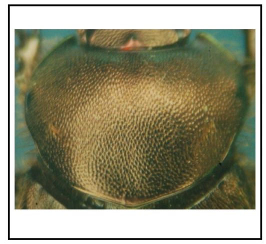


5 (4) Pronotum not grooved, vertex without a median tubercle- ***pacificus*** **Lansberge**

6 (3) Hind tibia not extremely short, triangular not as broad at the end as metatarsus is long

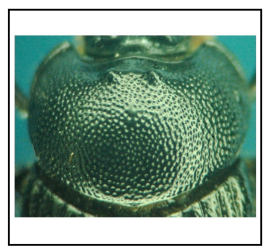


7 (14) Pronotum wholly or partly granular or rugose

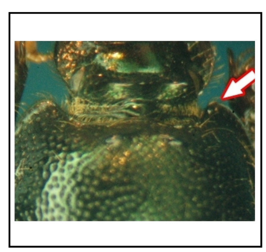


8 (9) Pronotum entirely granular or rugose without distinct punctures- ***bronzeus* Arrow**

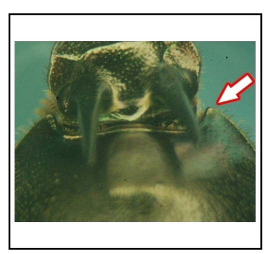
9 (8) Pronotum partly granular or rugose, with some punctures or smooth areas



10 (11) Front angles of pronotum not produced, very blunt- ***castetsi* Lansberge**



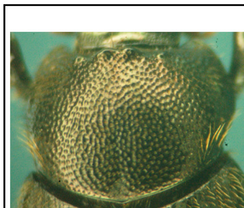
11(10) Front angles of pronotum more or less produced



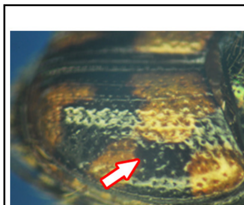
12 (13) Pronotum light brown- ***rectecornutus*** **Lansberge**

13 (12) Pronotum black- ***manipurensis*** **Arrow**

14 (7) Pronotum punctured, without granules, asperities, or rugosity

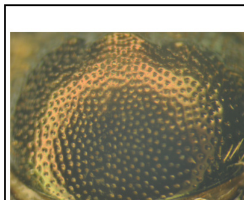


15(16) 7th elytral stria indistinct- ***amphicoma*** **Boucomont**

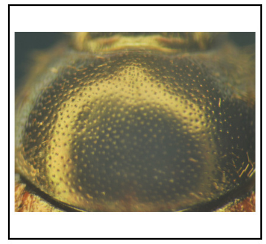


16 (15) 7th elytral stria distinct

17(18) Punctures of the pronotum large, close, umbilicate- ***furcillifer*** **Bates**

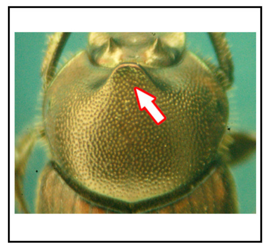


18 (17) Punctures of the pronotum not large, close, umbilicate

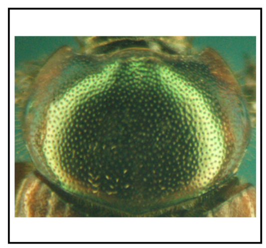


19 (24) Pronotum pale at the sides

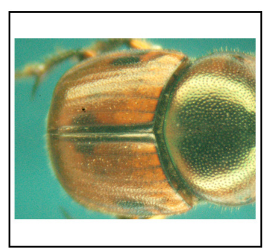
20 (21) Pronotum with an elongated process- ***vladimiri*** **Frey**



21 (20) Pronotum without an elongated process

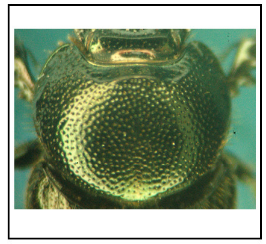


22 (23) Base, apex and sides of the elytra pale-
fasciatus **Boucomont**

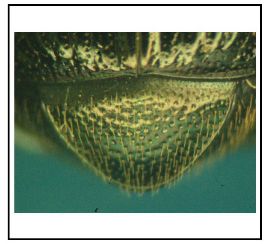


23 (22) Base, apex and sides of the elytra not entirely pale-
favrei **Boucomont**

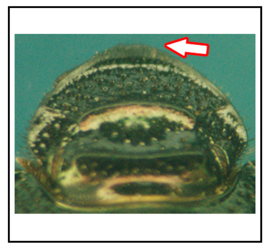
24 (19) Pronotum uniformly coloured



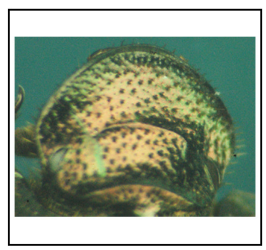
25 (28) Pygidium without a basal ridge



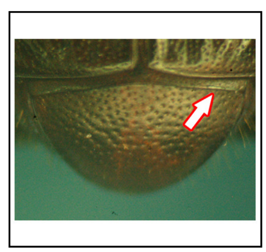
26 (27) Clypeus produced in front, sides of head strongly rounded- ***andrewesi* Arrow**



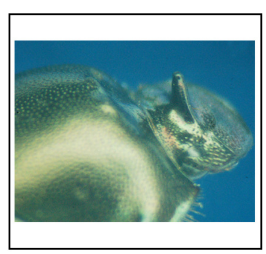
27 (26) Clypeus not produced in front, sides of head feebly rounded- ***porcus* Arrow**



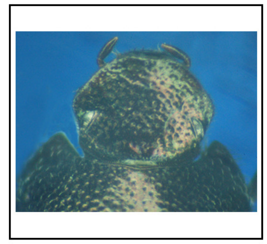
28 (25) Pygidium with a basal ridge



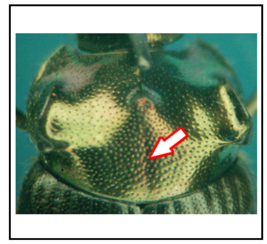
29 (30) Head horned or ridged- ***turbatus* Walker**



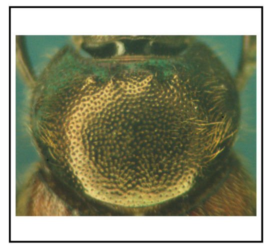
30 (29) Head not horned or ridged- ***deflexicollis* Lansberge**



31 (32) Pronotum with a median longitudinal groove

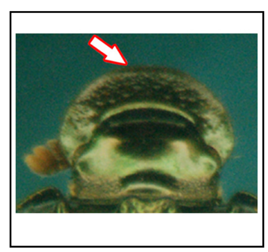


32 (31) Pronotum without a median longitudinal groove- ***insignicollis* Frey**



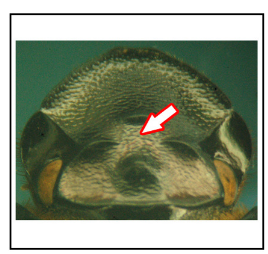
33 (34) Clypeus notched or lobed- ***centricornis* Frey**

34 (33) Clypeus not notched or lobed- ***ensifer* Boucomont**



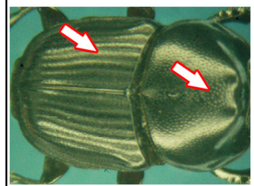
Onitis

Clypeo-frontal carina broadly interrupted- ***subopacus* Arrow**



Liatongus

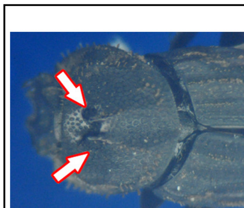
Pronotum well punctured, elytral intervals convex- ***indicus*** **Arrow**



Tibiodrepanus

1 (2) Male with single thoracic horn- ***setosus*** **Wiedemann**

2 (1) Male with two thoracic horns- ***sinicus*** **Harold**



4.2. Ecology

4.2.1. Forest habitat

4.2.1.1. Abundance, species richness and diversity

A total of 622 beetles belonging to 21 species, seven genera namely, *Catharsius*, *Copris, Onthophagus, Paracopris, Paragymnopleurus*, *Sisyphus* and *Tibiodrepanus* and six tribes such as Coprini, Gymnopleurini, Onthophagini, Oniticellini, Paracoprini and Sisyphini, were recorded from the forest habitat during the study period. List of species and their abundance are given in Table 1.

Onthophagus pacificus (37.78%) and *Onthophagus furcillifer* (24.92%) dominated the assemblage and together constituted 62.70% of the total abundance (Plate 5; Table 1). Other major species in the forest habitat were *Paracopris cribratus* and *Sisyphus araneolus*. *Copris repertus, Onthophagus andrewesi O. bronzeus, O. castetsi, O. ensifer, O. favrei, O. laevis, O. manipurensis, O. turbatus,* and *O. vladimiri,* were the minor species. Seven species namely, *Catharsius molossus, Onthophagus amphicoma, O. cavia, O. centricornis, O. insignicollis, Paragymnopleurus sinuatus* and *Tibiodrepanus setosus,* were represented by only one individual each (0.16% of total abundance) and is considered rare (Table1). Rank of each species based on relative abundance is represented in Figure 1.

Five endemics to the Western Ghats namely, *Onthophagus amphicoma*, *O. andrewesi*, *O. bronzeus*, *O. vladimiri* and *Sisyphus araneolus* and one first report (*Onthophagus manipurensis*) were reported from the forest habitat

(Table 1; Plate 3 & 4). The assemblage diversity (H') of the forest habitat was 1.967, Margalef's richness index value (d) was 3.109, dominance (λ) was 0.221 and evenness ($1-\lambda$) was 0.781. Taxonomic diversity and evenness of dung beetle assemblage of the forest were $\Delta+ = 49.524$ and $\Lambda+ = 618.821$ respectively. Small species (represented by 16 species; 85.70% of total abundance) dominated the assemblage when compared to large species (represented by only five species; 14.30% of total abundance) (Table 2).

4.2.1.2. Functional guild composition

Dung beetles belonging to all three functional guilds namely, dwellers, rollers and tunnelers were present in the assemblage (Table 3). Functional guilds showed significant variation in abundance (tunnelers > rollers > dwellers) (Table 4). Tunnelers were the most abundant (93.41% of total abundance) and with 18 species most speciose. Rollers were represented by two species which included *Paragymnopleurus sinuatus* and *Sisyphus araneolus* and were the second most abundant functional guild (6.43% of total abundance). Dwellers represented by one species namely, *Tibiodrepanus setosus* (0.16% of the total abundance) was the least dominant guild (Figure 3).

4.2.1.3. Temporal guild composition

Temporal guild of the forest was made up of diurnal, nocturnal and generalist species (Table 1). Temporal guilds showed significant variation in abundance (nocturnal > diurnal > generalist) (Table 4). Nocturnal guild was the most abundant and consisted of seven species (60% of total abundance), diurnal guild comprised of three species (27% of total abundance) and generalists of nine species (12% of total abundance) (Figure 4). Dominant nocturnal species was *Onthophagus pacificus* and diurnal species was *O. furcillifer*.

4.2.1.4. Seasonality

Overall abundance of dung beetles showed significant variations with seasons (Table 6). Pair wise comparisons of abundance between seasons showed significantly higher abundance in presummer and monsoon over summer. The seasonal abundance varied as follows: monsoon= presummer > summer. Seventeen species were present during the presummer season. Ten species each were recorded during summer and monsoon seasons.

Tunnelers dominated the presummer, summer and monsoon seasons, with 15 species (85.33% of total abundance) in presummer, seven species (96.81% of total abundance) in summer and ten species (100% of total abundance) in monsoon. Rollers were represented by one species (14.67% of total abundance) in presummer, two species (2.13% of total abundance) in summer and none in monsoon. Dwellers were represented by one species in summer (1.06% of total abundance) and none in presummer and monsoon (Figure 3; Table 5). Tunnelers (presummer= monsoon> summer) and rollers (presummer= summer> monsoon) showed significant variations in abundance with seasons (Table 6).

Nine species comprising eight tunnelers and one roller showed significant seasonality. *Onthophagus andrewesi*, *O. bronzeus*, *O. laevis*, *O. manipurensis*, *O. pacificus*, *O. turbatus*, *O. vladimiri* and *Paracopris cribratus* were the seasonal tunnelers and *Sisyphus araneolus* was the seasonal roller (Table 5).

Seasonal species showed higher abundance during different seasons, tunnelers namely, *Onthophagus pacificus* in presummer and monsoon*;* *Onthophagus bronzeus*, *O. laevis*, *O. manipurensis* and *Paracopris cribratus* in monsoon; *Onthophagus andrewesi*, *O. vladimiri* and *O. turbatus* during presummer and roller *Sisyphus araneolus* in presummer. Five species, all tunnelers were aseasonal. Seasonality in seven species could not be determined due to rarity in collection (Figure 5; Table 5).

Nocturnal guild was most abundant in the three seasons: presummer (nocturnal> diurnal> generalist), summer (nocturnal> diurnal> generalist) and monsoon (nocturnal> diurnal= generalist) (Figure 4). Abundance of generalist (presummer> monsoon> summer) and nocturnal guild (monsoon> presummer> summer) varied significantly with seasons (Table 6). Rank of each species based on relative abundance for the three seasons is given in Figure 2.

4.2.2. Agriculture habitat

4.2.2.1. Abundance, species richness and diversity

A total of 343 beetles belonging to 25 species, eight genera namely, *Caccobius, Catharsius*, *Copris, Liatongus, Onitis, Onthophagus, Paracopris* and *Tibiodrepanus,* and four tribes namely, Coprini, Oniticellini, Onitini and Onthophagini, were recorded from the agriculture habitat during the study period. List of species and their abundance are given in Table 7.

Caccobius meridionalis (25.66%) and *Onthophagus fasciatus* (21.57%) dominated the assemblage and together constituted 46.23% of the total abundance (Plate 5; Table 7). Other major species of the agriculture habitat were *Copris repertus* and *Onthophagus furcillifer*. Minor species included *Caccobius gallinus*, *Caccobius ultor*, *Catharsius molossus*, *Onthophagus amphicoma*, *O. bronzeus*, *O. ensifer*, *O. favrei*, *O. insignicollis*, *O. laevis*, *O. manipurensis*, *O. pacificus*, *O.turbatus*, *Paracopris cribratus*, *P. davisoni* and *Tibiodrepanus setosus.* Six species namely, *Liatongus indicus*, *Onitis subopacus*, *Onthophagus andrewesi*, *O. porcus*, *O. rectecornutus* and *Tibiodrepanus sinicus* were represented by only one individual each (0.29% of total abundance) and is considered rare (Table 7). Rank of each species based on relative abundance is represented in Figure 6.

Six endemics to the Western Ghats namely, *Caccobius gallinus*, *Liatongus indicus*, *Onthophagus amphicoma*, *O. andrewesi*, *O.bronzeus* and *Paracopris davisoni* and two first reports (*Onthophagus manipurensis* and *Tibiodrepanus sinicus*) were reported from the habitat (Table 7; Plate 3 & 4). The assemblage diversity was H'= 2.380, Margalef's richness index (d=4.111), dominance (λ= 0.143) and evenness (1-λ= 0.859). Taxonomic diversity and evenness of dung beetle assemblage of the agriculture habitat were $\Delta+$ = 54.750, $\Lambda+$ = 504.521 respectively. Small species represented by 19 species (82.22% of total abundance) dominated the assemblage compared to large species represented by only five species (17.78% of total abundance) (Table 8).

4.2.2.2. Functional guild composition

Dung beetles belonging to only two functional guilds namely, dwellers and tunnelers were present in the assemblage (Table 9). Temporal guild showed significant variation in abundance (Table 10). Tunnelers, represented by 22 species were the most speciose and abundant (96.50% of total abundance) functional guild. Dwellers represented by three species *Liatongus indicus, Tibiodrepanus setosus* and *T. sinicus* (3.50% of total abundance) was the second dominant guild (Figure 8; Table 9).

4.2.2.3. Temporal guild composition

Temporal guild of agriculture field was made up of diurnal, nocturnal and generalist species (Table 7). Temporal guilds showed significant variation in abundance (diurnal> nocturnal> generalist) (Table 10). Diurnal guild comprising of six species (66% of total abundance) was the most abundant, followed by nocturnal guild of six species (23% of total abundance) and generalists of eight species (11% of total abundance) (Figure 9). The dominant diurnal species were *Caccobius meridionalis* and *Onthophagus fasciatus*.

4.2.2.4. Seasonality

Abundance of dung beetles showed significant variation with seasons (summer= monsoon> presummer) (Table 12). Monsoon and summer seasons had 17 species each. Eight species were recorded during presummer.

Tunnelers dominated the seasons with six species (91% of total abundance) in presummer, 16 species (96% of total abundance) in summer and 16 species (99% of total abundance) in monsoon. Rollers were absent in the presummer, summer and monsoon collections. Dwellers were represented in presummer by two species namely, *Tibiodrepanus setosus* and *Liatongus indicus* (9% of total abundance), one species in summer namely, *Tibiodrepanus setosus* (4% of total abundance) and one species in monsoon namely, *Tibiodrepanus sinicus* (1% of total abundance) (Figure 8; Table 11). Tunnelers showed significant variations in abundance with seasons (summer> monsoon> presummer) (Table 12).

Eight species, all tunnelers showed significant seasonality namely, *Caccobius meridionalis*, *Catharsius molossus*, *Copris repertus*, *Onthophagus furcillifer*, *O. laevis*, *O. manipurensis*, *O. pacificus* and *Paracopris davisoni* (Table 11).

Caccobius meridionalis and *Onthophagus furcillifer* showed highest abundance in summer; *Copris repertus* and *Onthophagus pacificus* showed highest abundance in monsoon. *Catharsius molossus* was absent in presummer; *Onthophagus laevis* and *Paracopris davisoni* were present only in monsoon; *O. manipurensis* was present only in summer. Eleven species were aseasonal tunnelers. Seasonality in six species could not be determined due to rarity in collection (Figure 10; Table 11).

Abundance of temporal guilds varied with seasons as follows: presummer (diurnal> generalist, nocturnal guild was absent); summer (diurnal> nocturnal> generalist) and monsoon (nocturnal> diurnal> generalist) (Figure 9). Abundance of diurnal (summer> monsoon= presummer), generalist (monsoon= summer; monsoon= presummer; summer> presummer) and nocturnal guild (summer= monsoon> presummer) varied significantly with seasons (Table 12). Rank of each species based on relative abundance for the three seasons is represented in Figure 7.

4.2.3. Edge

4.2.3.1. Abundance, species richness and diversity

A total of 460 beetles belonging to 25 species, eight genera namely, *Caccobius, Catharsius*, *Copris*, *Ochicanthon*, *Onthophagus*, *Paracopris Sisyphus* and *Tibiodrepanus* and five tribes namely, Coprini, Canthonini, Oniticellini, Onthophagini and Sisyphini, were recorded from the edge. List of species and their abundance are given in Table 13.

Onthophagus pacificus (20.65%) and *Onthophagus furcillifer* (19.78%) dominated the assemblage and together constituted 40.43% of total abundance (Plate 5; Table 13). *Copris repertus, Onthophagus bronzeus, O. manipurensis* and *O. turbatus,* constituted the other major species. *Caccobius gallinus, Catharsius molossus*, *Ochicanthon mussardi*, *Onthophagus amphicoma*, *O. andrewesi*, *O. castetsi*, *O. ensifer*, *O. favrei*, *O. insignicollis*, *O. laevis*, *O. vladimiri*, *Paracopris cribratus*, *P. davisoni* and *Sisyphus araneolus* were the minor species. Four species namely, *Onthophagus cavia, O. fasciatus, Paracopris signatus* and *Tibiodrepanus setosus* were represented by only one individual each (0.22% of total abundance) and is considered rare. (Table13). Rank of each species based on relative abundance is represented in Figure 11.

Eight endemics to the Western Ghats namely, *Caccobius gallinus*, *Ochicanthon mussardi*, *Onthophagus amphicoma*, *O. andrewesi*, *O. bronzeus*, *O. vladimiri*, *Paracopris davisoni* and *Sisyphus araneolus* and two first reports (*Onthophagus deflexicollis* and *O. manipurensis*) were reported from the habitat (Plate 3 & 4; Table 13). The assemblage diversity was H'= 2.545, Margalef's richness index (d=3.914), dominance (λ= 0.113) and evenness (1-λ= 0.889).) Taxonomic diversity and evenness of dung beetle assemblage of the edge were $\Delta+$ = 52.333, $\Lambda+$ = 577.889 respectively. Small species represented by 19 species (86.29% of total abundance) dominated the assemblage compared to large species represented by six species (13.71% of total abundance) (Table 14).

4.2.3.2. Functional guild composition

Dung beetles belonging to all three functional guilds namely, tunnelers, rollers and dwellers were present in the assemblage. Tunnelers showed significantly high abundance (tunnelers> rollers= dwellers) (Table 16). Tunnelers were the most speciose represented by 22 species (95.87% of total abundance). Rollers represented by two species which included *Ochicanthon mussardi* and *Sisyphus araneolus* were the second most abundant functional guild (3.91% of total abundance). Dwellers represented by one species namely, *Tibiodrepanus setosus* (0.22% of the total abundance) was the least dominant guild (Figure 13; Table 15).

4.2.3.3. Temporal guild composition

Temporal guild of the edge was made up of diurnal, nocturnal and generalist species (Table 13). Nocturnal guild consisting of eight species (48% of total abundance) was the most abundant followed by generalists consisting of 11 species (27% of total abundance) and diurnal guild of five species (25% of total abundance) (Figure14). Temporal guilds did not show significant variation in abundance (Table 16). Dominant nocturnal species was *Onthophagus pacificus*.

4.2.3.4. Seasonality

Abundance of dung beetles showed significant variation with seasons (presummer= monsoon> summer) (Table 18). Eighteen species were present during presummer and monsoon seasons; eleven species were recorded during summer.

Tunneler dominated during all the seasons represented by 16 species (90.36% of total abundance) in presummer, 11 species (100% of total abundance) in summer and 17 species (98.65% of total abundance) in monsoon. Rollers were represented by one species (9.04% of total abundance) in presummer, none in summer and one species (1.35% of total abundance) in monsoon; and dwellers by one species (0.60% of total abundance) in presummer and none in monsoon and summer (Figures 13). Tunnelers (summer< presummer= monsoon) and rollers (summer< presummer= monsoon) showed significant variation in abundance with seasons (Table 18).

Nine species comprising eight tunnelers and one roller showed significant seasonality. *Onthophagus amphicoma*, *O. bronzeus*, *O. insignicollis*, *O. laevis*, *O. manipurensis*, *O. pacificus*, *O. turbatus* and *Paracopris davisoni* were the seasonal tunnelers and *Sisyphus araneolus* was the seasonal roller (Table 17).

Tunnelers such as *Paracopris davisoni* and *Onthophagus laevis* were recorded only in monsoon season; *O. insignicollis* and *O. amphicoma* only in presummer; *O. bronzeus, O. pacificus* and *O. turbatus* showed higher abundance in monsoon; *O. manipurensis* showed higher abundance in summer. Roller species *Sisyphus araneolus* was collected only in presummer. Twelve species, 11 tunnelers and one roller were aseasonal. Seasonality in four species could not be determined due to rarity in collection (Figure 15; Table 17).

Abundance of temporal guilds varied with seasons as follows: presummer (nocturnal> diurnal> generalist), summer (diurnal> generalist> nocturnal) and monsoon (nocturnal> generalist> diurnal) (Figure 14). Abundance of diurnal guild and generalist did not vary significantly with seasons but abundance of nocturnal guild varied with seasons (monsoon> presummer= summer) (Table 18). Rank of each species based on relative abundance for the three seasons is represented in Figure 12.

4.2.4. Comparative analysis of dung beetle assemblages of semi-evergreen forest, agriculture habitat and ecotone of Nelliampathi region

A total of 1425 beetles belonging to 34 species, 11 genera namely, *Caccobius*, *Catharsius*, *Copris*, *Liatongus*, *Ochicanthon*, *Onitis*, *Onthophagus*, *Paracopris*, *Paragymnopleurus*, *Tibiodrepanus* and *Sisyphus* and seven tribes namely, Coprini, Canthonini, Gymnopleurini, Onitini, Oniticellini, Onthophagini and Sisyphini were captured during the study period from the three habitats. Onthophagini and Coprini were the most speciose tribes in the three habitats. Genus *Onthophagus* was the most abundant and diverse genera in all the three habitats (Tables 1, 7, 13).

Nine species endemic to the Western Ghats were collected from the region which included *Caccobius gallinus, Liatongus indicus, Ochicanthon mussardi, Onthophagus amphicoma*, *O. andrewesi*, *O. bronzeus*, *O. vladimiri*, *Paracopris davisoni* and *Sisyphus araneolus*. *Onthophagus andrewesi*, *O. amphicoma*, *O. bronzeus*, *O. vladimiri* and *Sisyphus araneolus* were collected from the forest. *Caccobius gallinus*, *Liatongus indicus*, *Onthophagus andrewesi*, *O. amphicoma*, *O. bronzeus* and *Paracopris davisoni* were collected from agriculture habitat. *Caccobius gallinus*, *Ochicanthon mussardi*, *Onthophagus andrewesi*, *O. amphicoma*, *O. bronzeus*, *O. vladimiri*, *Paracopris davisoni* and *Sisyphus araneolus* were collected from ecotone (Plates 3 & 4; Tables 1, 7, 13).

Dung beetle abundance varied between habitats (agriculture< forest= ecotone) and diversity did not vary between habitats (Figure 16; Table 19). Highest taxonomic diversity and evenness was observed in agriculture habitat followed by edge and forest.

Four species exhibited strong habitat associations. They were *Caccobius meridionalis* and *Onthophagus fasciatus* in agriculture habitat; *O. amphicoma* in edge and *O. furcillifer* in forest. *Onthophagus centricornis* and *Paragymnopleurus sinuatus* were recorded only from forest. *Copris signatus, Ochicanthon mussardi, Onthophagus deflexicollis* were collected only from edge. *Caccobius ultor*, *C. meridionalis*, *Liatongus indicus*, *Onitis subopacus*, *Onthophagus porcus*, *O. rectecornutus* and *Tibiodrepanus sinicus* were recorded only from the agriculture habitat.

Three species namely, *Caccobius gallinus, Onthophagus fasciatus* and *Paracopris davisoni* were shared between only agriculture and edge habitat; four species were shared between only forest and edge namely, *Onthophagus castetsi*, *O. cavia*, *O. vladimiri* and *Sisyphus araneolus*. Fifteen species were shared between the three habitats. Eight species were singletons or rare species from the Nelliampathi region of which one was from edge namely, *Paracopris signatus*; two were from forest namely, *Onthophagus centricornis* and *Paragymnopleurus sinuatus* and five were from agriculture habitat namely, *Liatongus indicus, Onthophagus porcus, O. rectecornutus, Onitis subopacus* and *Tibiodrepanus sinicus* (Tables1, 7, 13).

Rank abundance plot of all the three habitats showed a steep initial slope with two dominant species namely, *Onthophagus pacificus* and *Onthophagus furcillifer* in forest, *Caccobius meridionalis* and *Onthophagus fasciatus* in agriculture habitat and *Onthophagus pacificus* and *Onthophagus furcillifer* in edge (Figures 1, 6, 11; Plate 5). Forest had a longer tail of seven rare species, agriculture habitat had six rare species and edge had four rare species (Figures 1, 6, 11). Small dung beetles dominated the assemblages in the three habitats (Tables 2, 8, 14).

Bray Curtis similarity coefficient showed highest similarity between the dung beetle assemblages of forest and ecotone followed by ecotone and agriculture habitat and least similarity between agriculture habitat and forest (Figure 17; Table 20).

Percentage contribution of each species towards dissimilarity between habitats is provided in Table 21. 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%). Edge 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%).

Indicator species for forest were *Onthophagus furcillifer* and *O. pacificus;* ecotone was *O. furcillifer* and agriculture habitat was *O. fasciatus* (Plate 6; Table 22). Detector species in forest were *Copris repertus* and *Paracopris cribratus*; in edge were *Onthophagus bronzeus, O.pacificus* and *Copris repertus* and in agriculture habitat were *Caccobius meridionalis* and *Onthophagus furcillifer* (Table 22).

Tunnelers and rollers showed significant variation in abundance across habitats. Tunnelers were the most dominant functional guild in the three habitats. Dominance of tunnelers varied between habitats as follows, (forest= ecotone; ecotone= agriculture habitat; forest> agriculture habitat). Rollers were the second dominant guild in forest and edge and not recorded from agriculture habitat (ecotone= forest> agriculture habitat). Dwellers were the second dominant guild in agriculture habitat and least abundant functional guild in the forest and edge habitats (Figures 3, 8, 13; Table 19).

Temporal guild abundance varied for generalist (ecotone> agriculture= forest) and nocturnal guilds (ecotone> forest> agriculture) (Table 19). Nocturnal guild dominated in forest and edge assemblage while diurnal guild dominated in agriculture habitat (Figures 4, 9, 14).

Patterns of rarefaction curves differed for the habitats (Figure 18). Rarefaction curve for agriculture and edge habitat reached asymptote whereas the rarefaction curve for the forest did not reach an asymptote.

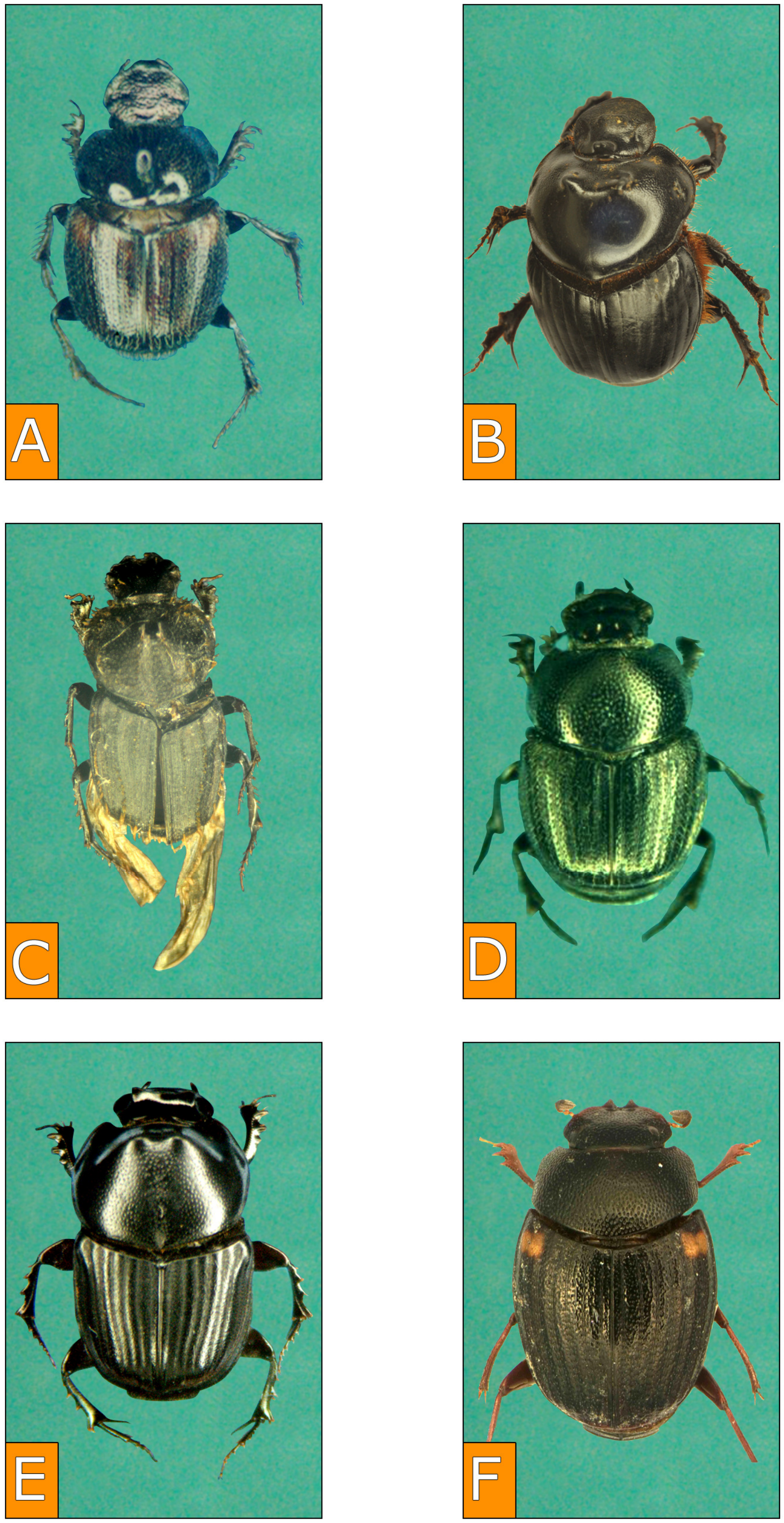


Plate 3: Dung Beetle species- First report from South India (A) *Onthophagus deflexicollis,* (B) *O. manipurensis* and (C) *Tibiodrepanus sinicus*. Endemics to the Western Ghats (D) *Caccobius gallinus* (E) *Liatongus indicus* (F) *Ochicanthon mussardi*.

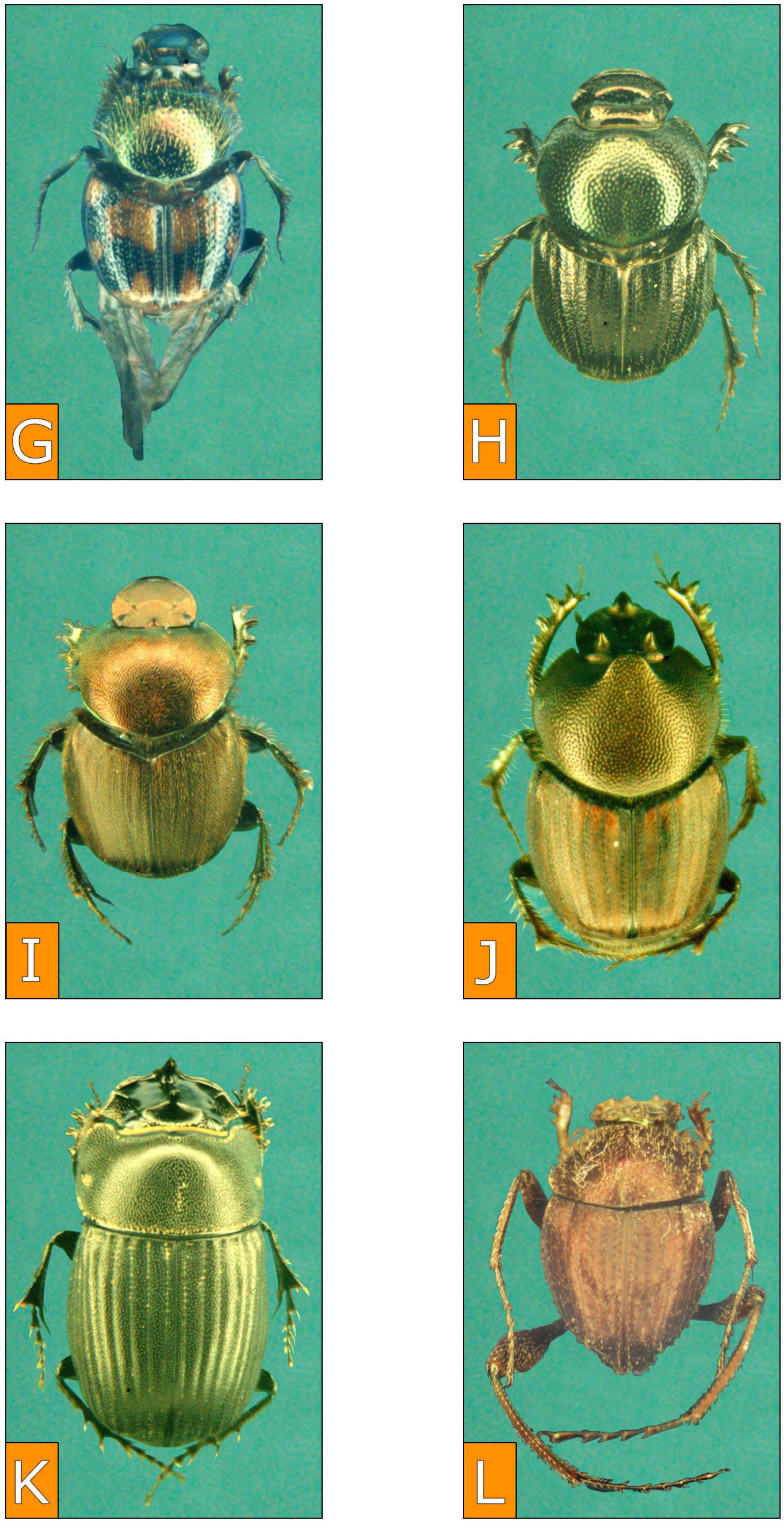


Plate 4: Dung Beetle species- Endemics to the Western Ghats (cont.) (G) *Onthophagus amphicoma*, (H) *O. andrewesi*, (I) *O. bronzeus*, (J) *O. vladimiri*, (K) *Paracopris davisoni* and (L) *Sisyphus araneolus*.

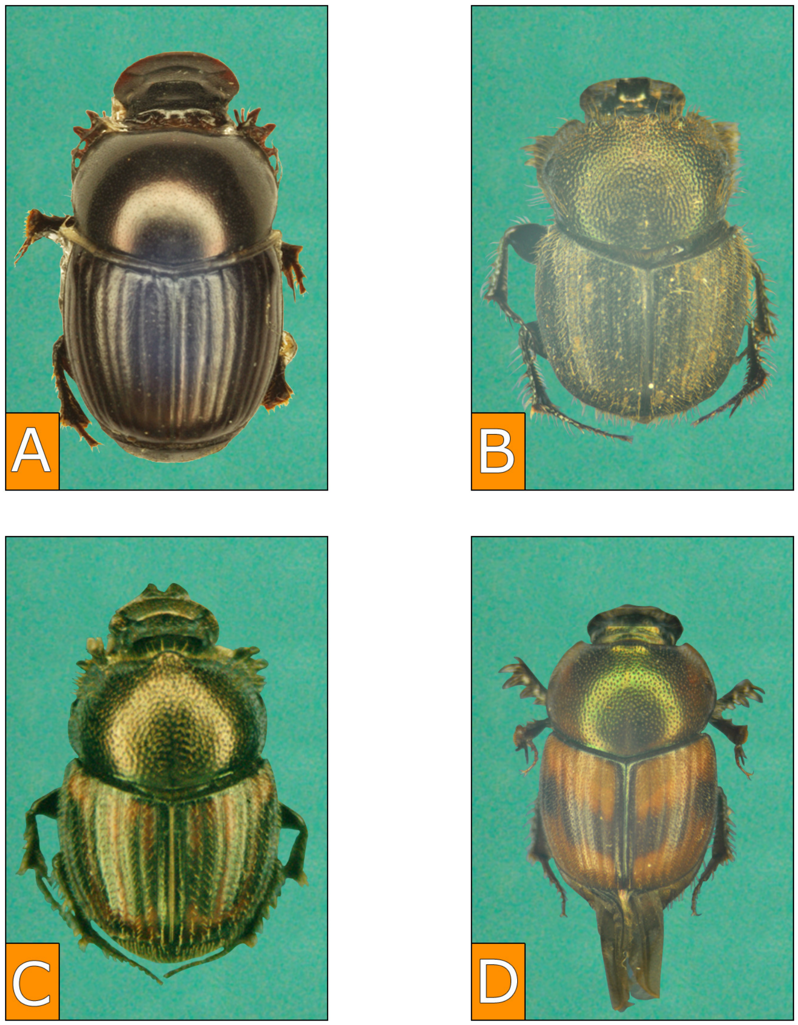


Plate 5: Dominant dung beetle species associated with Forest and Ecotone (A) *Onthophagus pacificus*, (B) *O. furcillifer*; Agriculture habitat (C) *Caccobius meridionalis*, (D) *Onthophagus fasciatus*.

Plate 6: Indicator species associated with Forest (A) *Onthophagus pacificus*; Forest and Ecotone (B) *Onthophagus furcillifer* and Agriculture habitat (C) *Onthophagus fasciatus*.

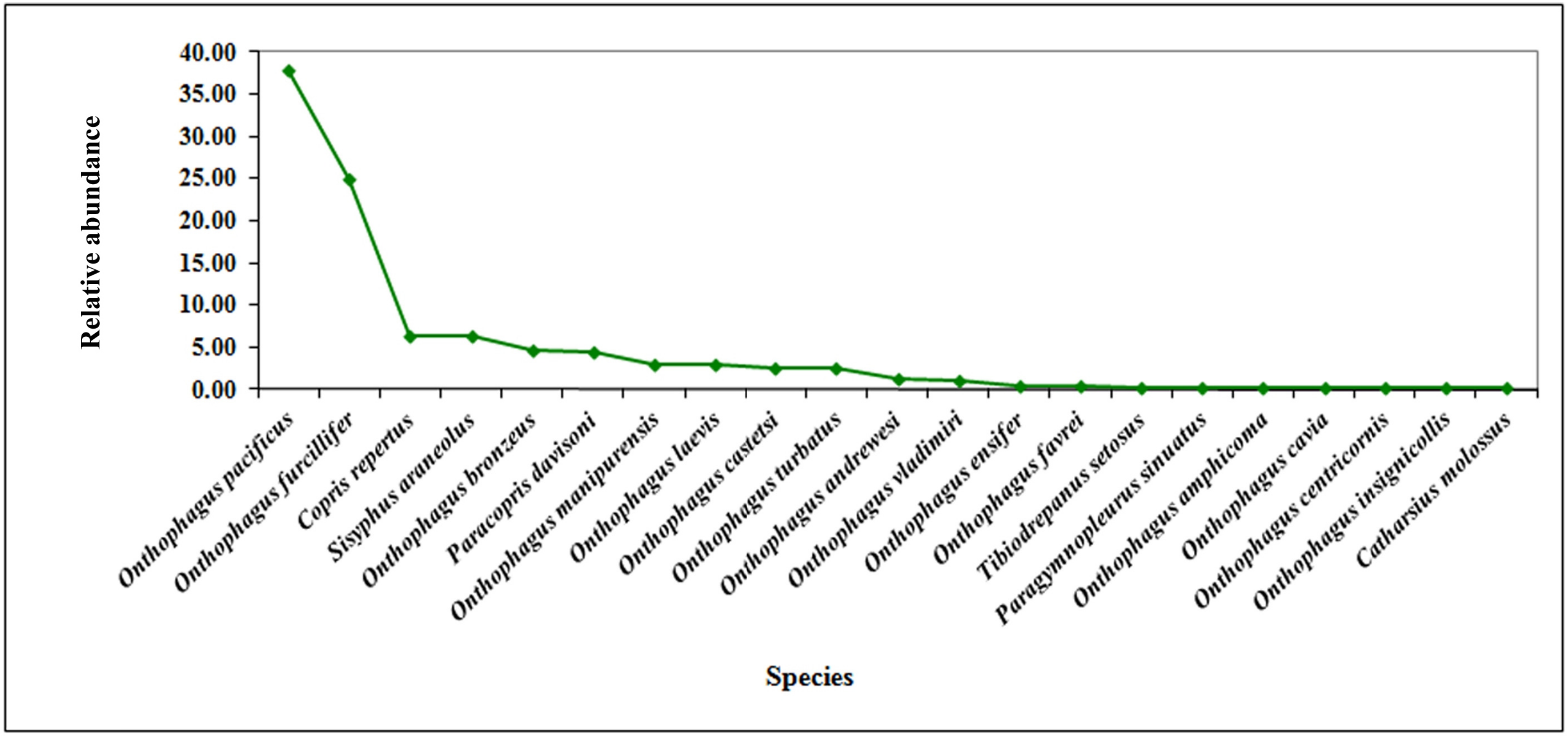


Figure 1: Overall rank abundance plot of dung beetles in a semi- evergreen forest habitat at Nelliampathi during 2007-08 study period.

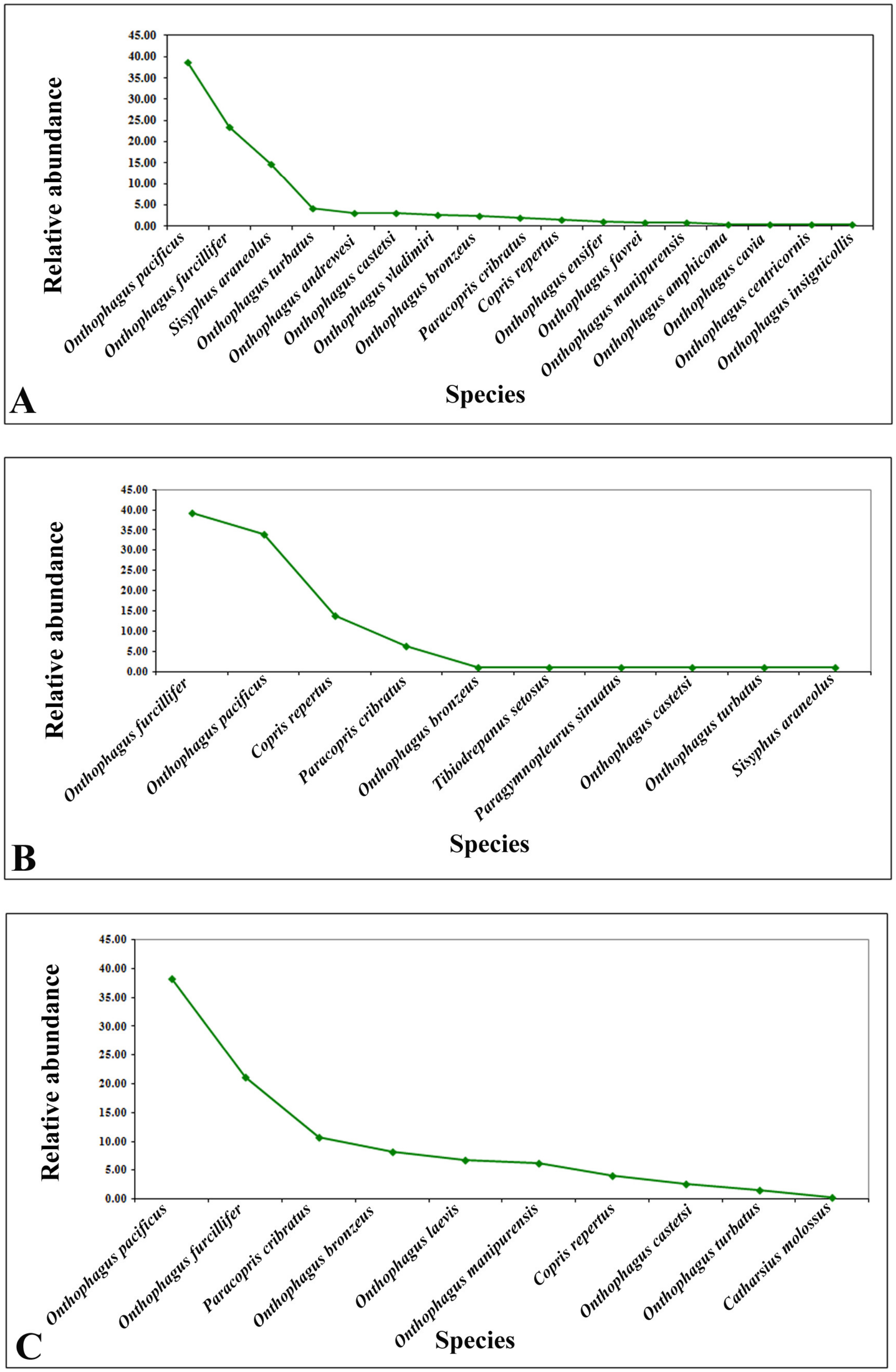


Figure 2: Rank abundance plot of dung beetles in a semi- evergreen forest habitat at Nelliampathi during 2007-08 study period (A- Presummer, B- Summer, C- Monsoon).

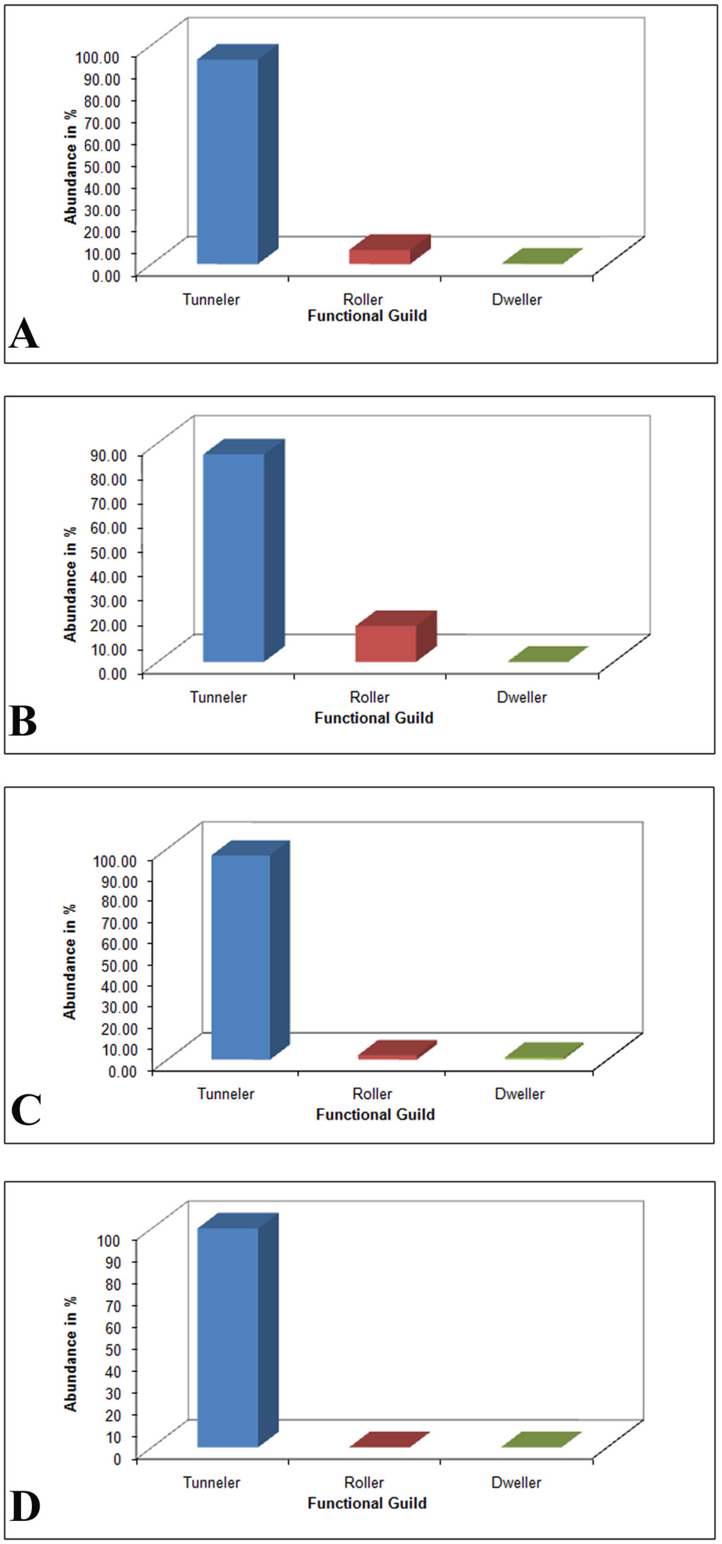


Figure 3: Functional guild composition and abundance of dung beetles in a semi-evergreen forest habitat at Nelliampathi during 2007-08 study period (A- Overall, B- Presummer, C- Summer, D- Monsoon).

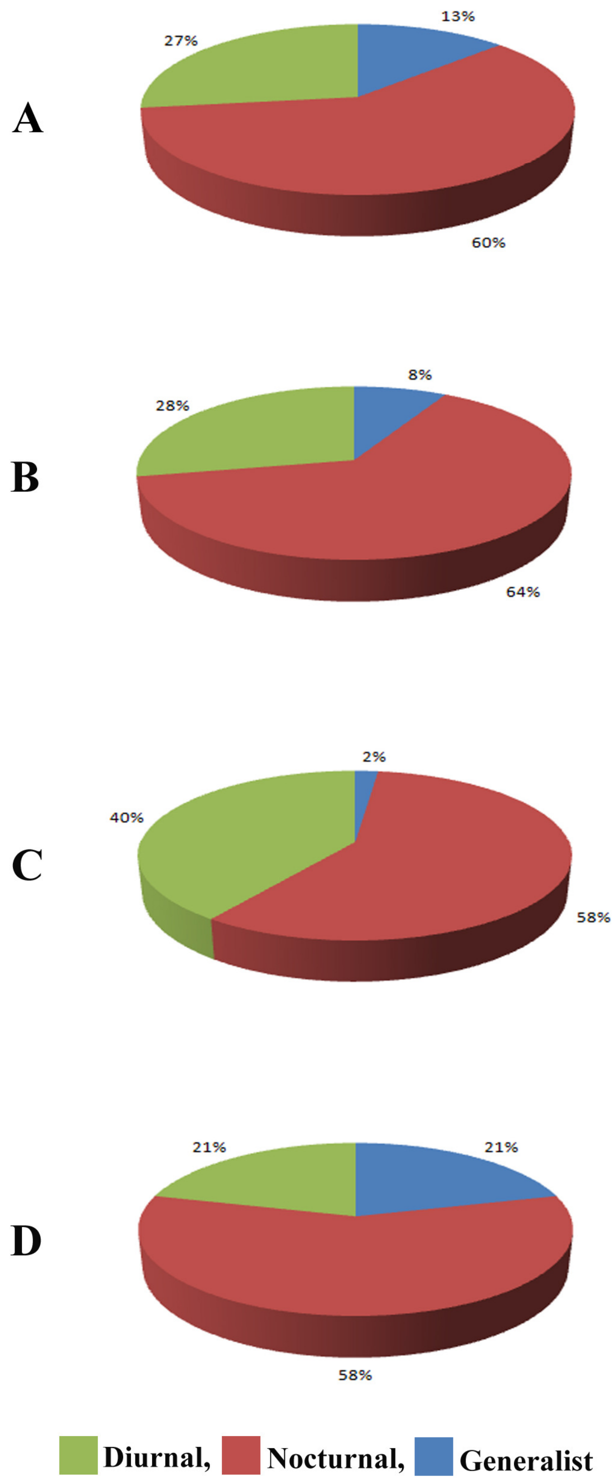


Figure 4: Temporal guild composition and abundance of dung beetles in a semi-evergreen forest habitat at Nelliampathi during 2007-08 study period (A- Overall, B- Presummer, C- Summer, D- Monsoon).

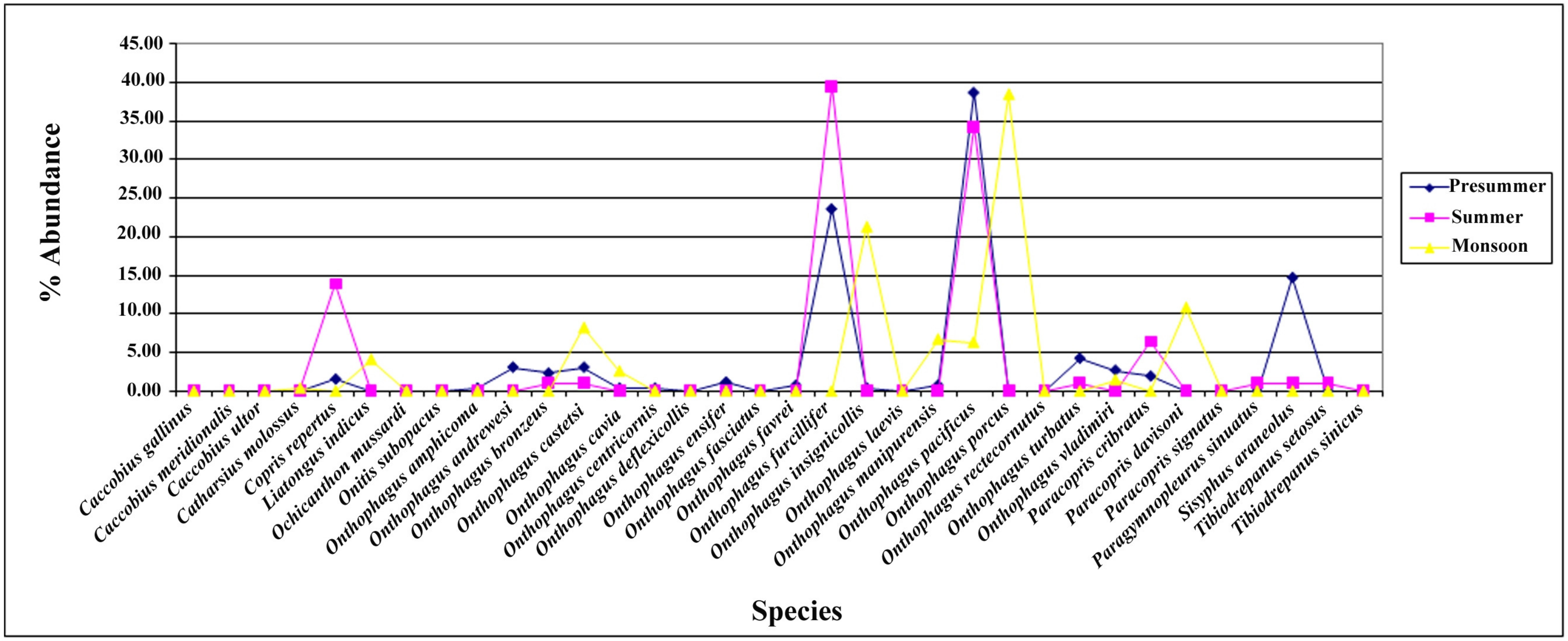


Figure 5: Seasonal abundance of dung beetles in a semi- evergreen forest habitat at Nelliampathi during the 2007-2008 study period.

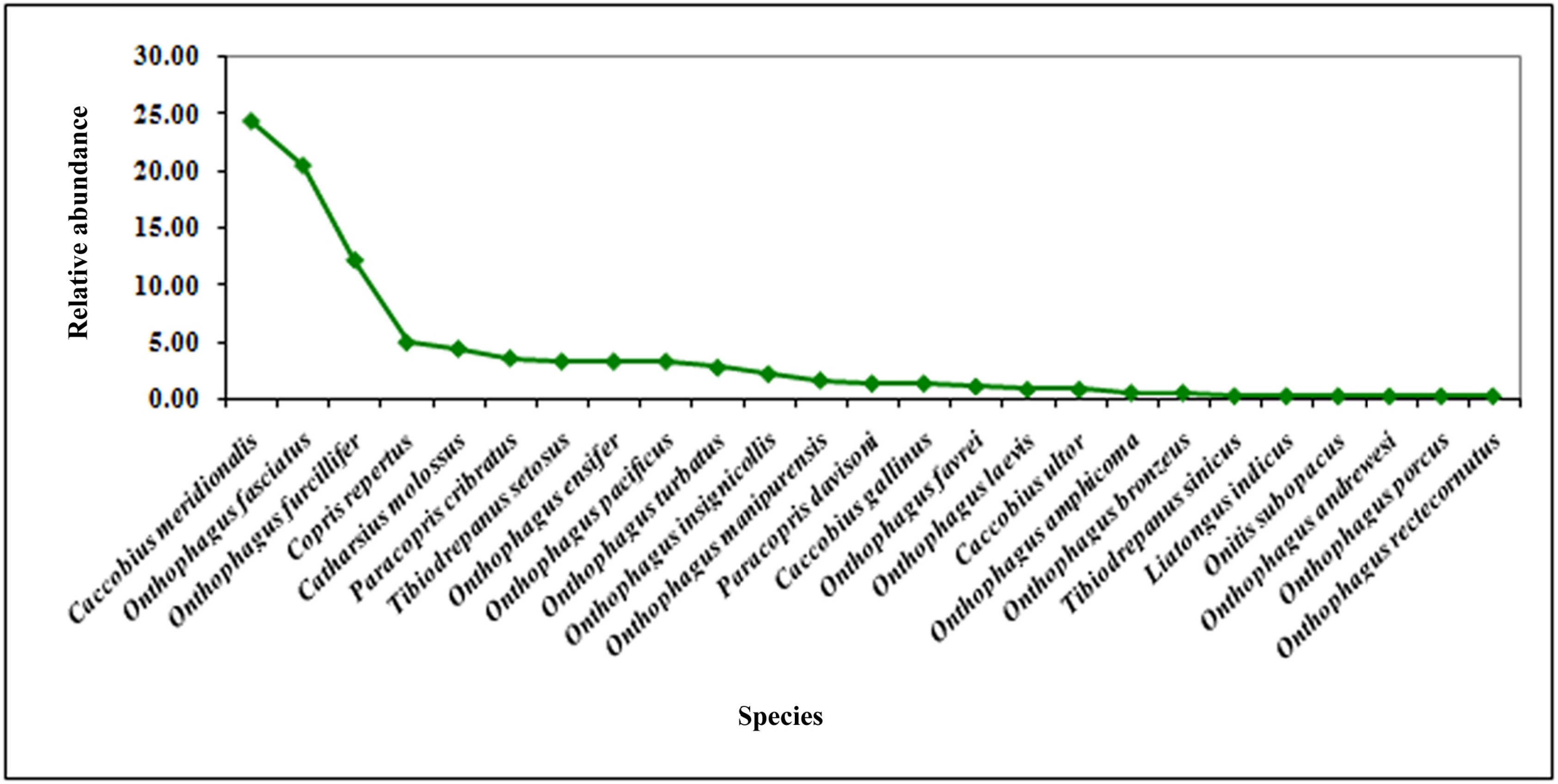


Figure 6: Overall rank abundance plot of dung beetles in an agriculture habitat at Nelliampathi during 2007-08 study period.

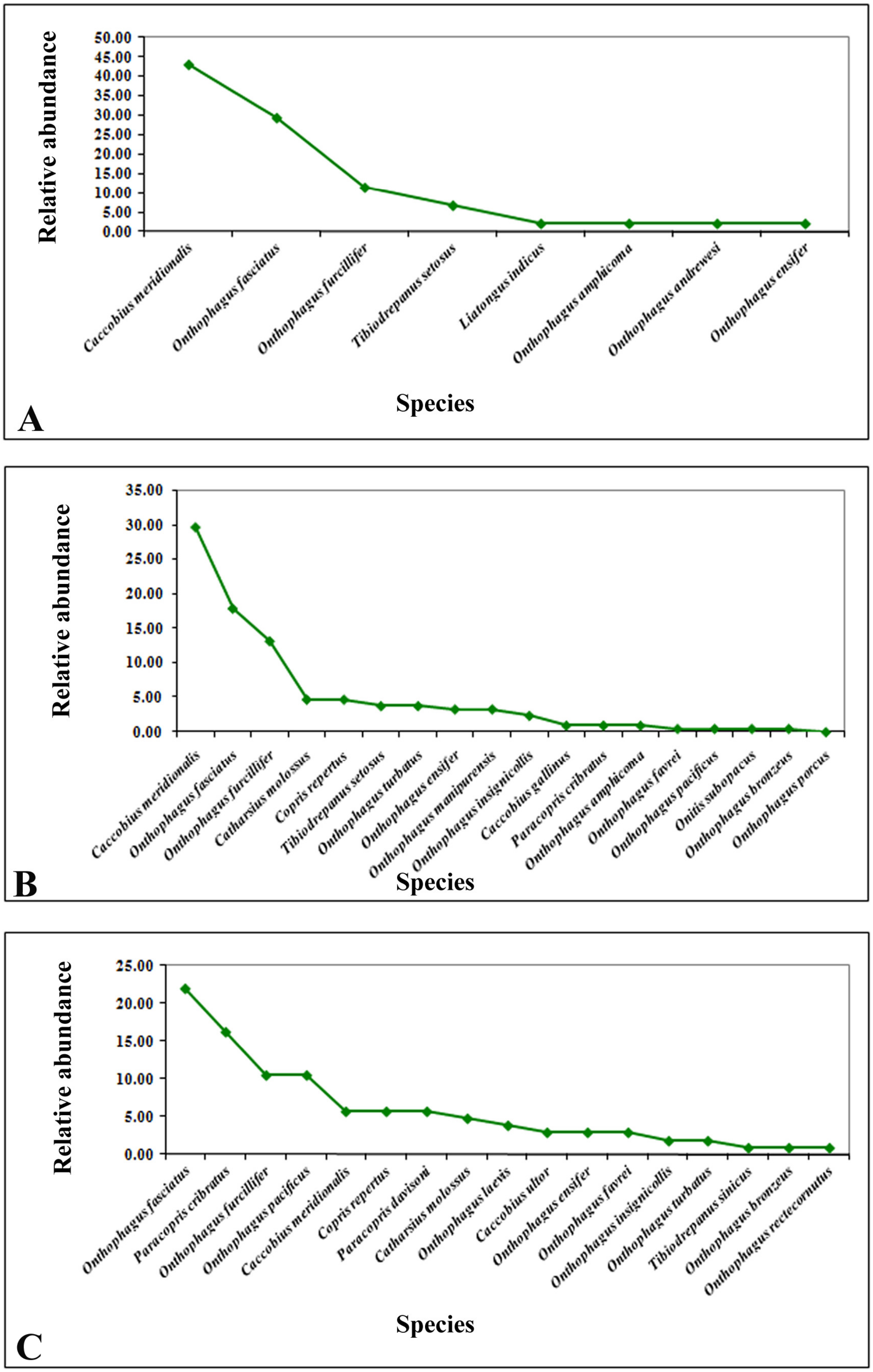


Figure 7: Rank abundance plot of dung beetles in an agriculture habitat at Nelliampathi during 2007-08 study period (A- Presummer, B-Summer, C- Monsoon).

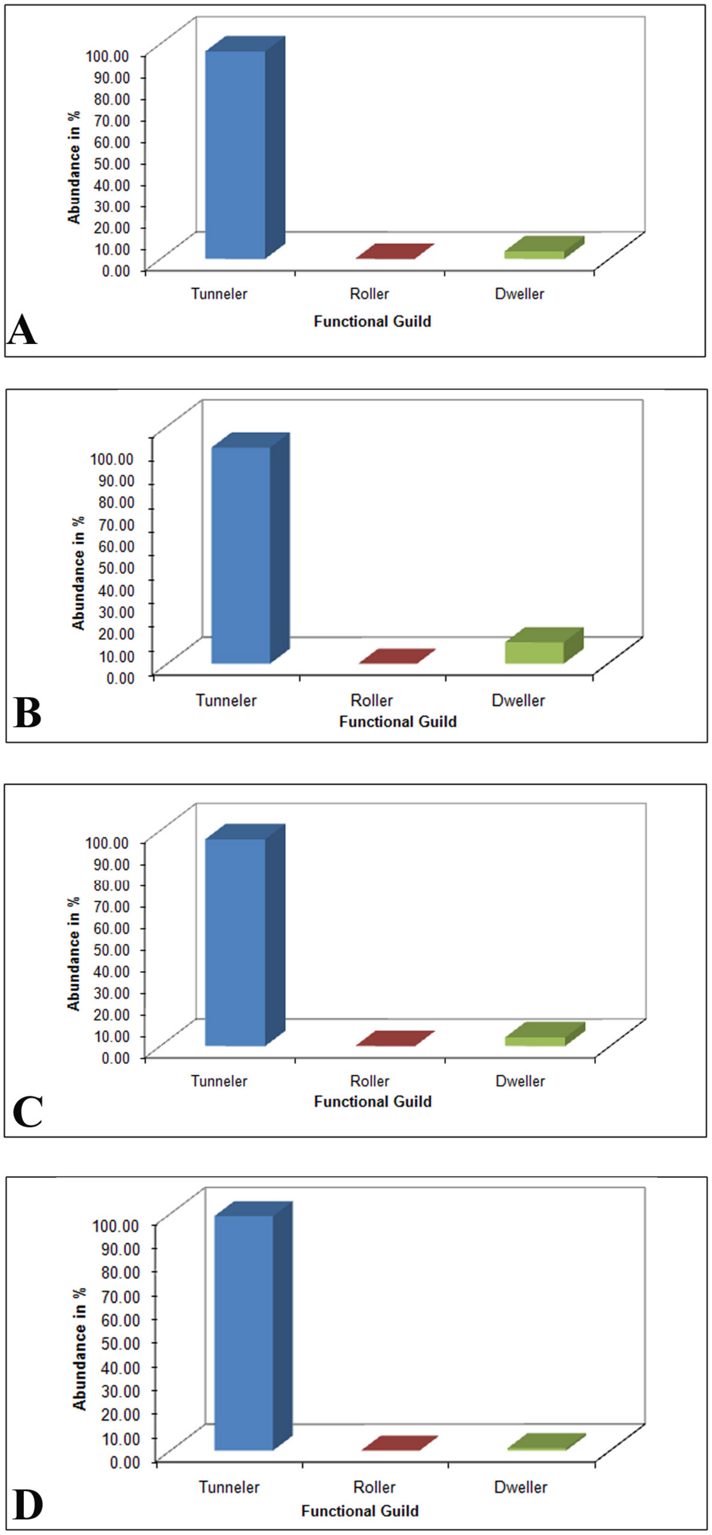


Figure 8: Functional guild composition and abundance of dung beetles in an agriculture habitat at Nelliampathi during 2007-08 study period (A- Overall, B- Presummer, C- Summer, D- Monsoon).

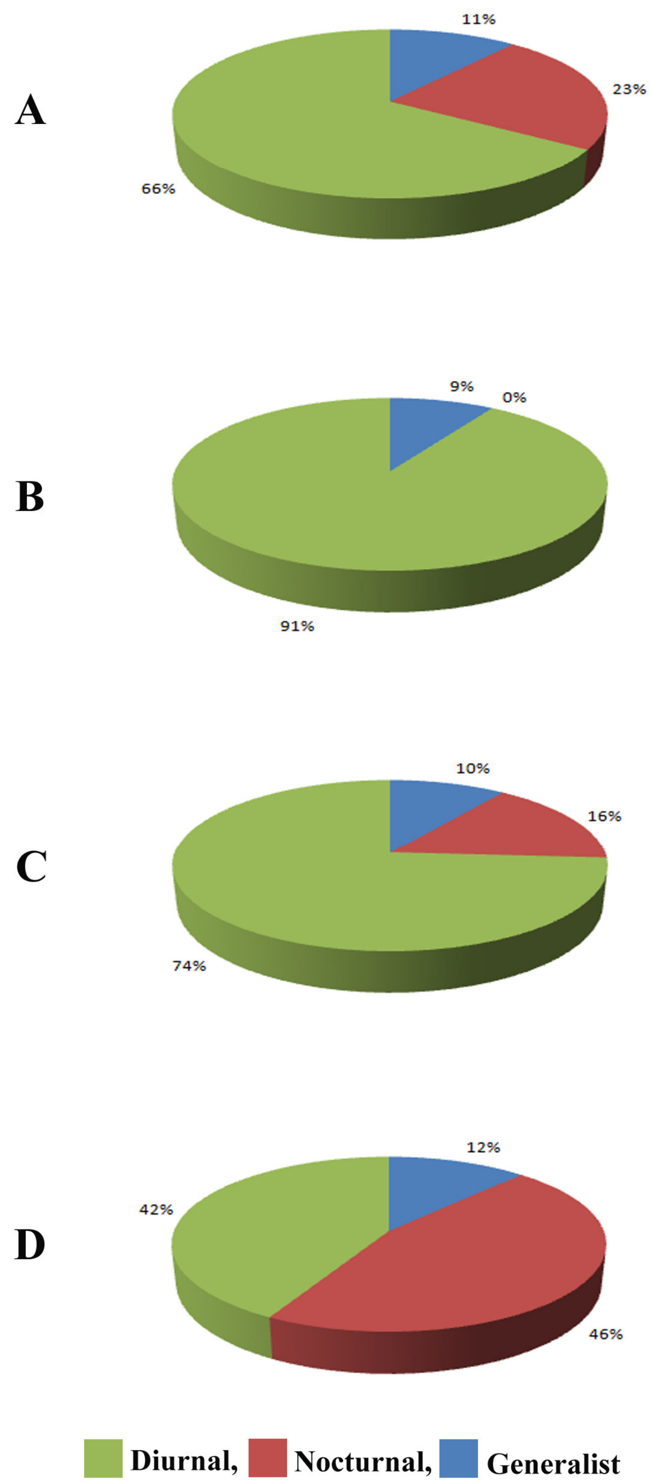


Figure 9: Temporal guild composition and abundance of dung beetles in an agriculture habitat at Nelliampathi during 2007-08 study period (A- Overall, B- Presummer, C- Summer, D- Monsoon).

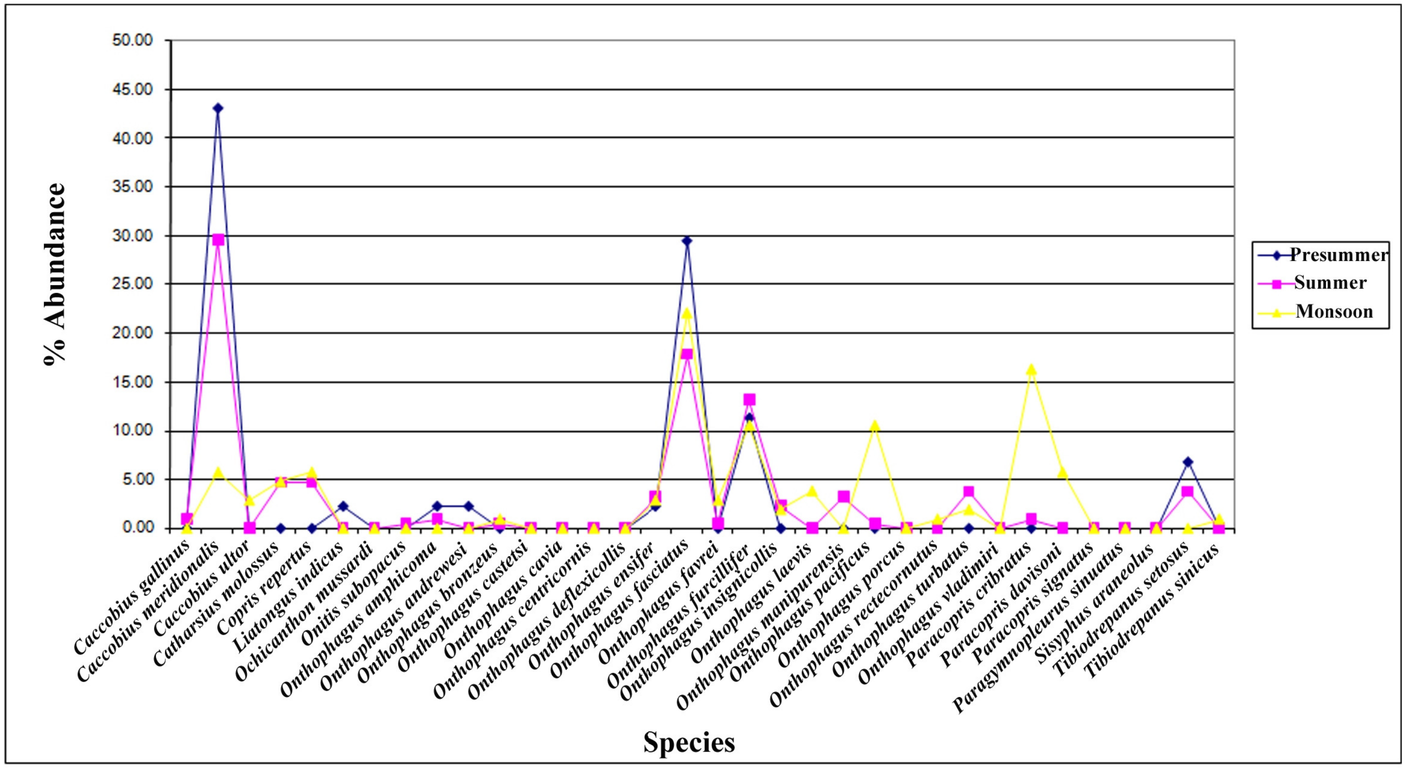


Figure 10: Seasonal abundance of dung beetles in an agriculture habitat at Nelliampathi during the 2007-2008 study period.

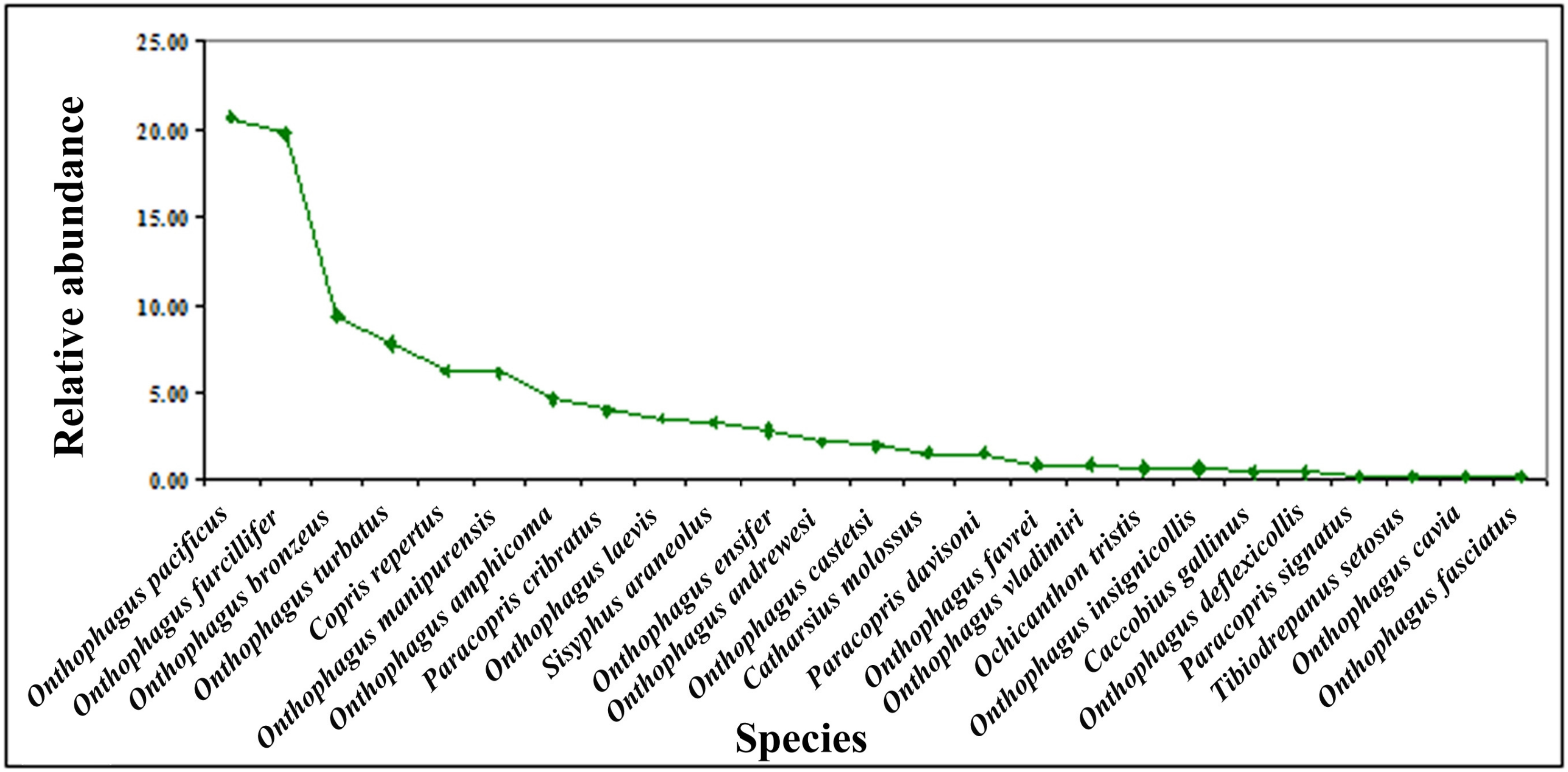


Figure 11: Overall rank abundance plot of dung beetles in an ecotone between a semi-evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period.

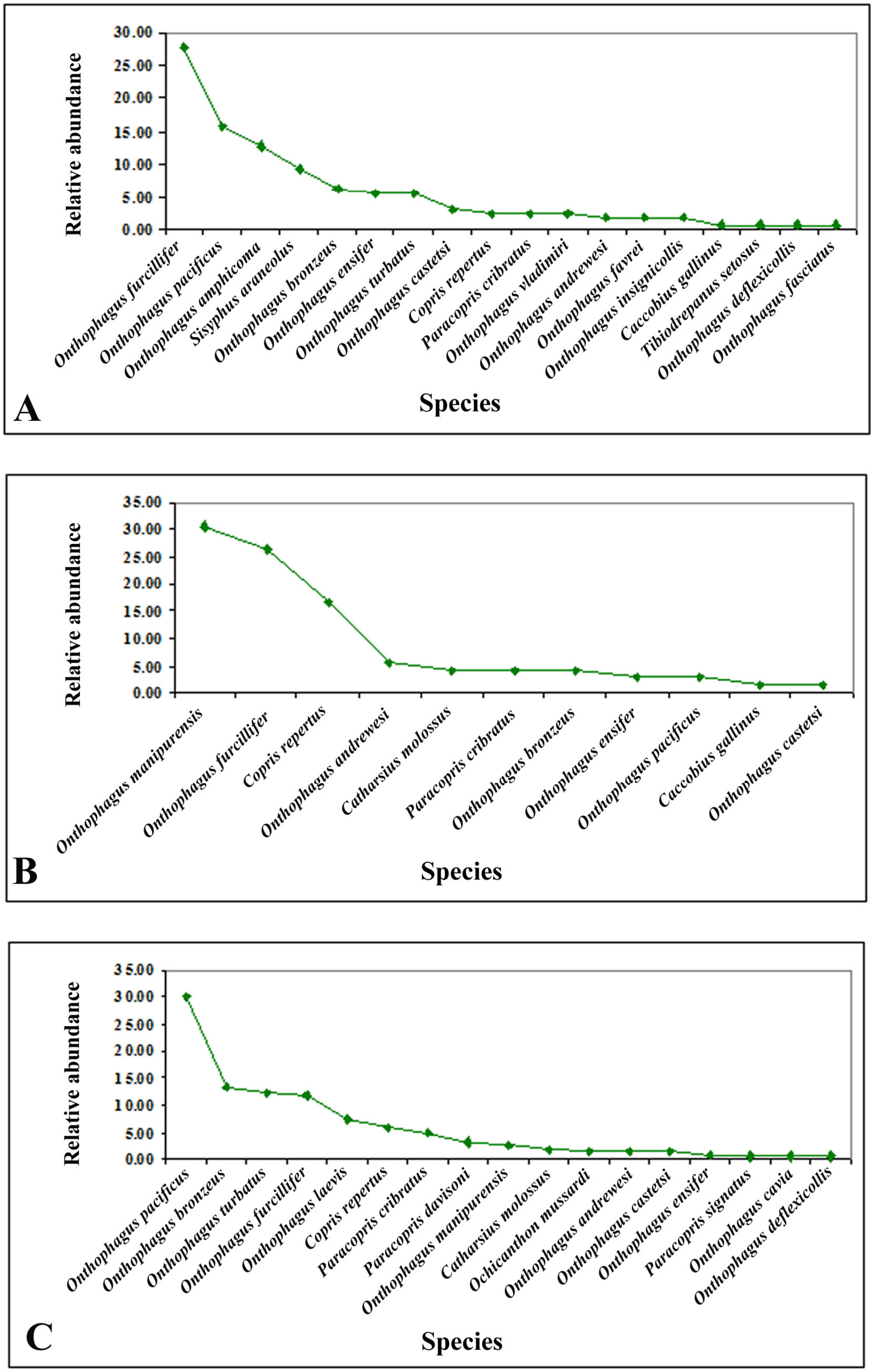


Figure 12: Rank abundance plot of dung beetles in an ecotone between a semi-evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period (A- Presummer, B- Summer, C- Monsoon).

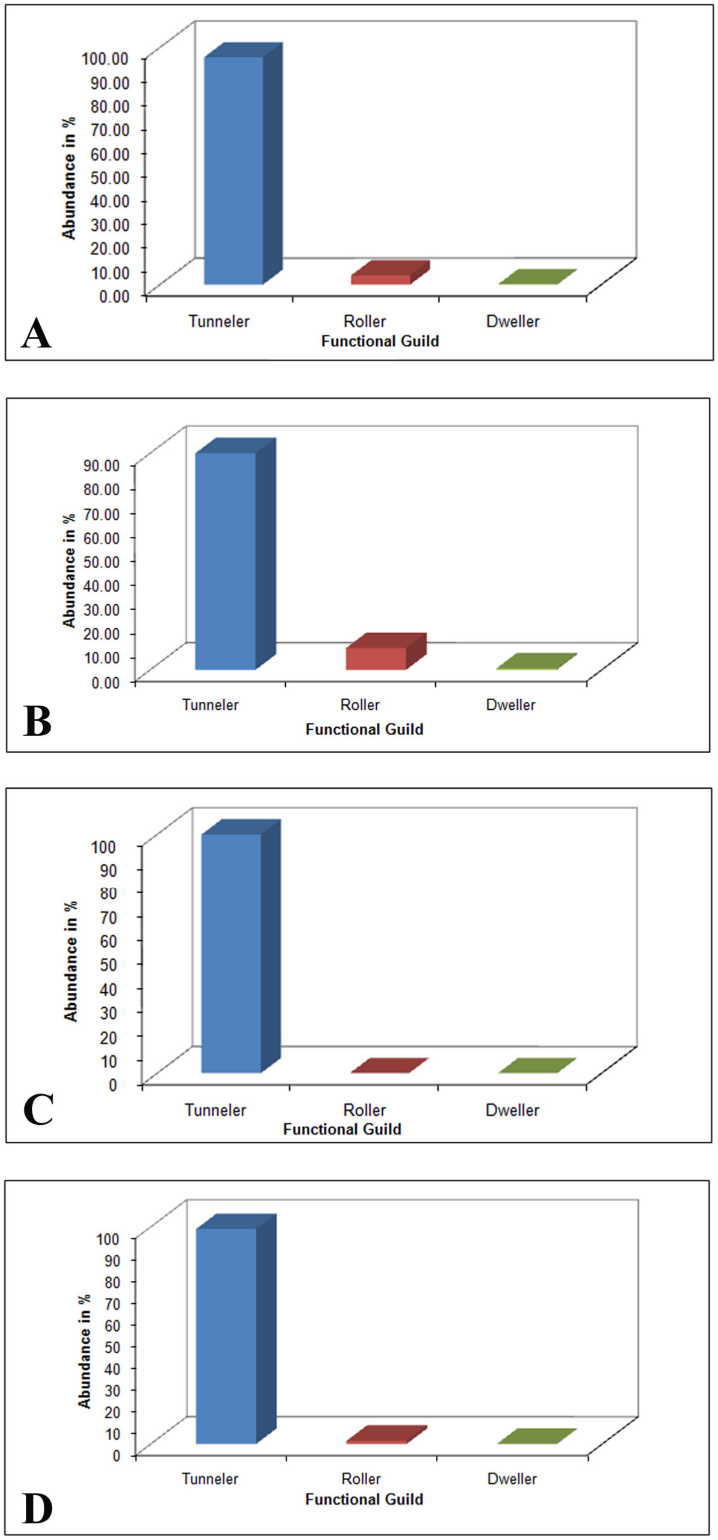


Figure 13: Functional guild composition and abundance of dung beetles in an ecotone between a semi-evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period (A- Overall, B- Presummer, C- Summer, D- Monsoon).

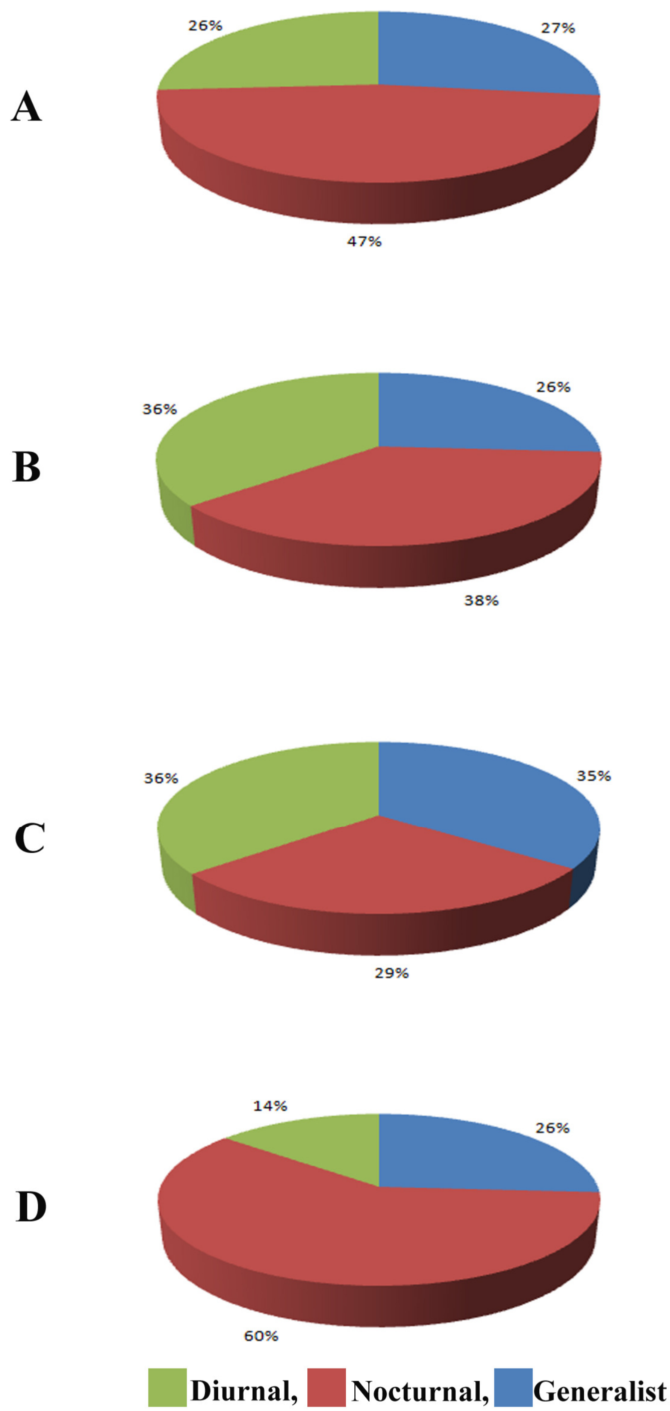


Figure 14: Temporal guild composition and abundance of dung beetles in an ecotone between a semi- evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period (A- Overall, B- Presummer, C- Summer, D- Monsoon).

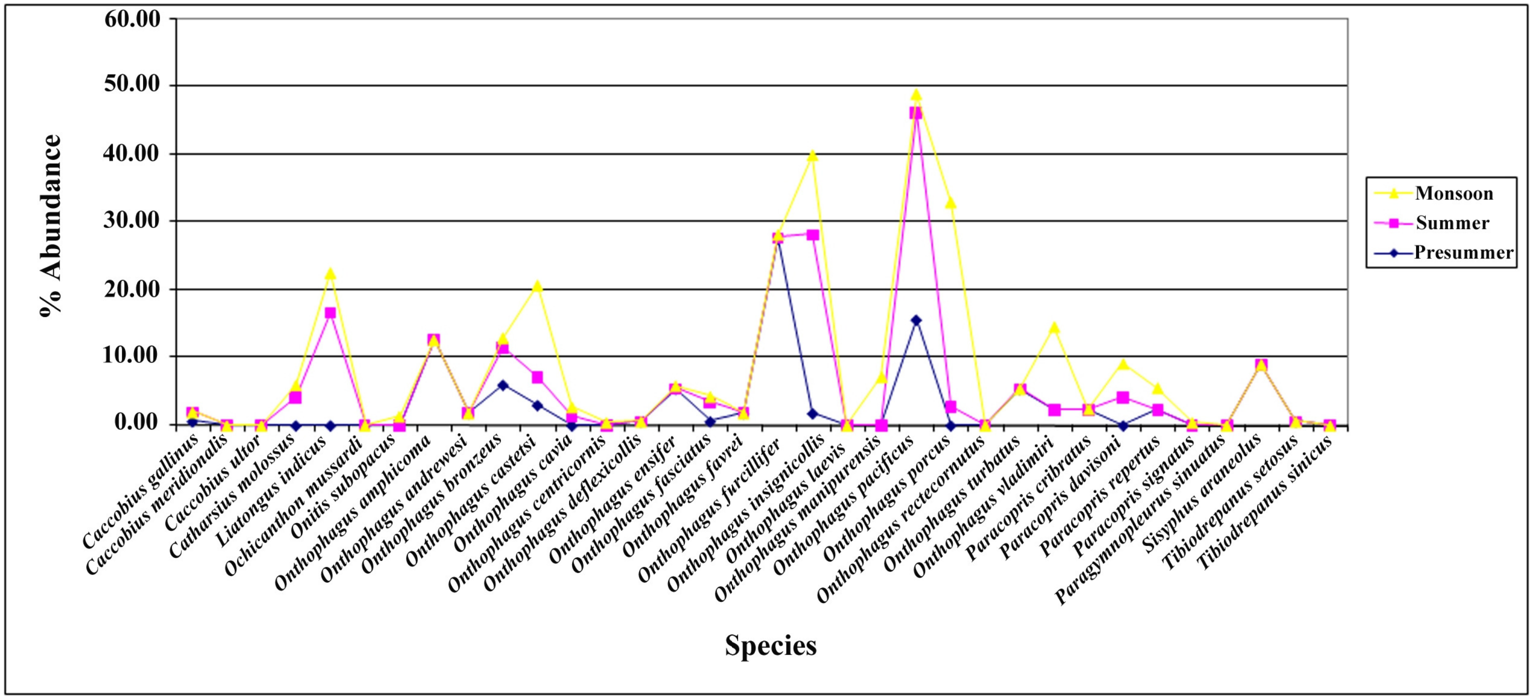


Figure 15: Seasonal abundance of dung beetles in an ecotone between a semi- evergreen forest and an agriculture habitat at Nelliampathi during 2007-2008 study period.

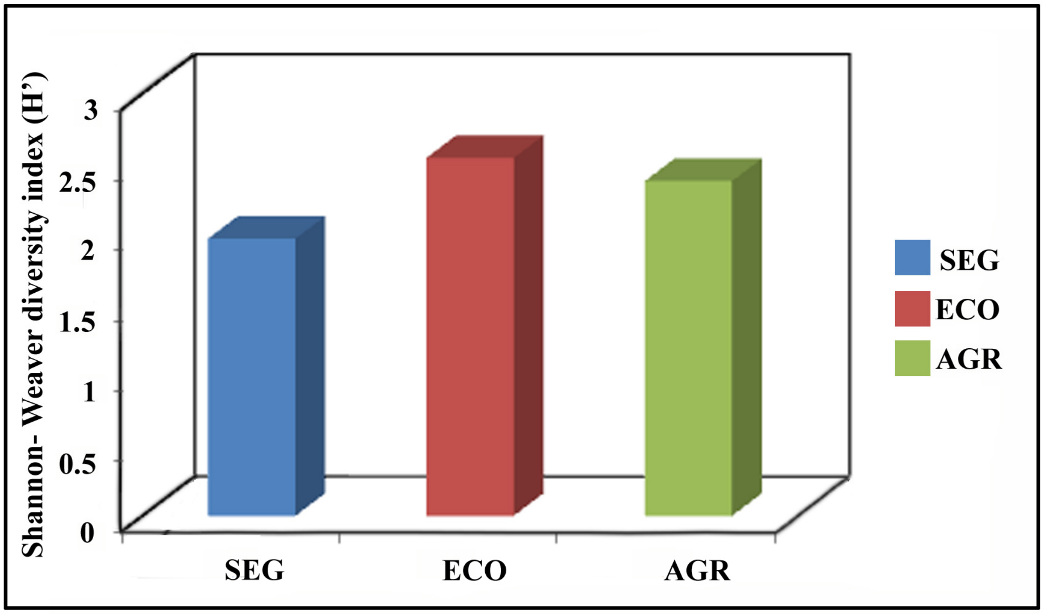


Figure 16: Diversity of dung beetles between a semi-evergreen forest (SEG), ecotone (ECO) and agriculture habitat (AGR) at Nelliampathi during 2007-08 study period.

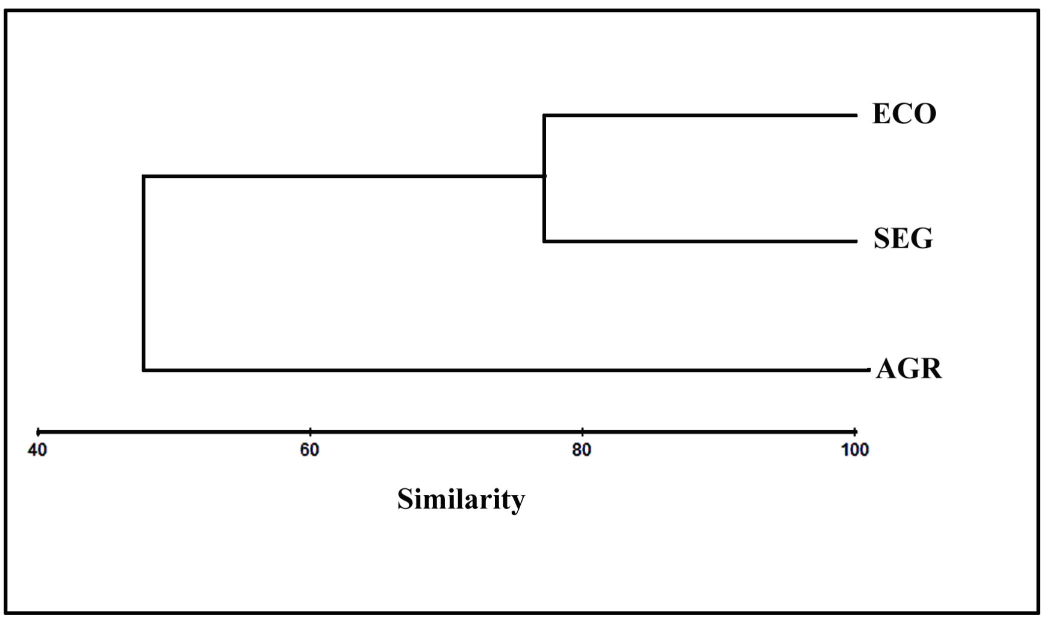


Figure 17: Dendrogram based on hierarchical clustering (group-average linking) of dung beetles in a semi- evergreen forest (SEG), ecotone (ECO) and agriculture habitat (AGR) at Nelliampathi during 2007-08 study period.

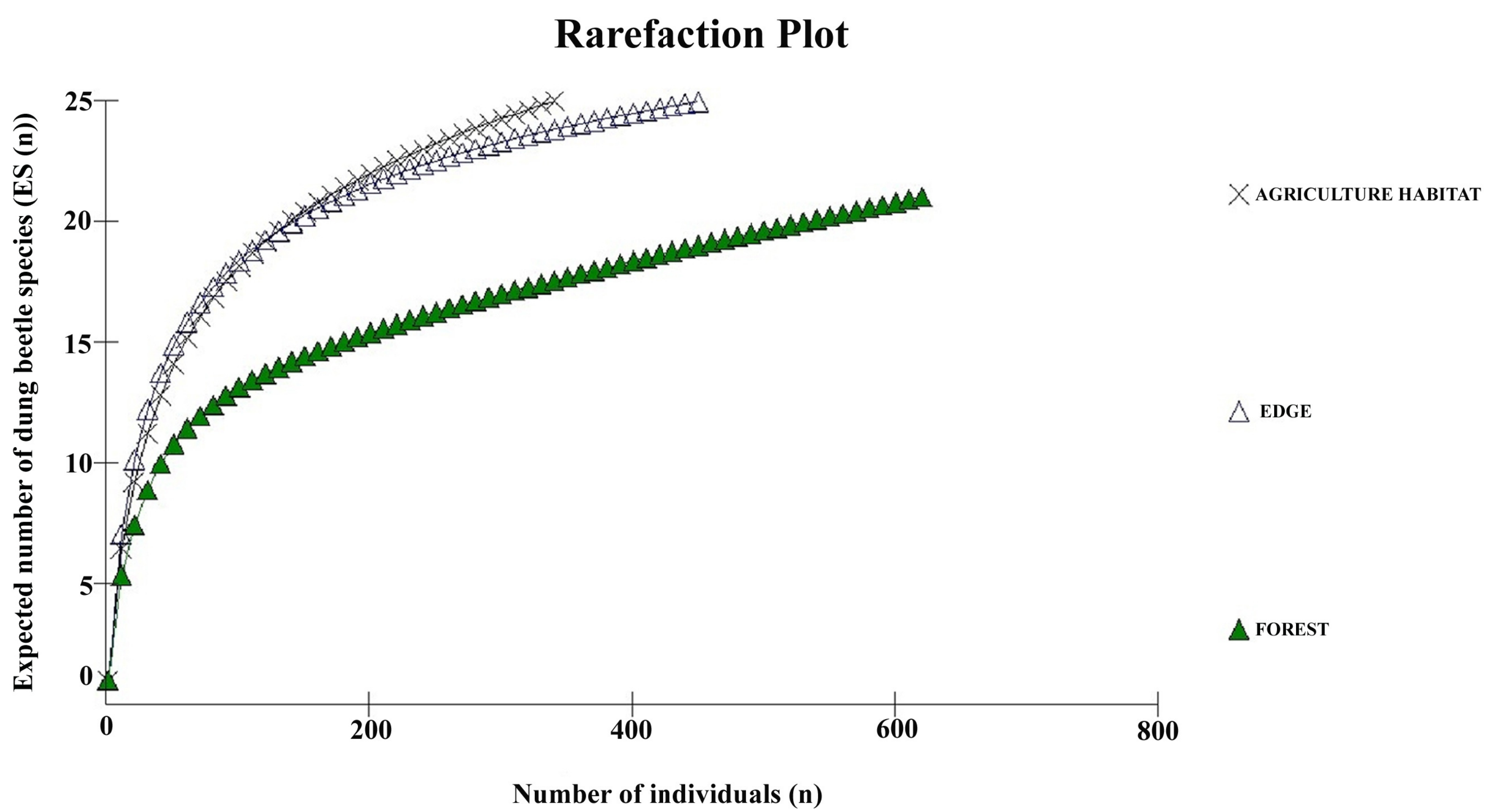


Figure 18: Rarefaction curves (expected species accumulation curves) showing the expected number of dung beetle species (ES(n)) plotted on Y axis as a function of the accumulated number of the individuals (n) of agriculture habitat, ecotone and semi-evergreen forest at Nelliampathi during 2007-08 study period.

Table 1: Abundance (mean ± SD and percentage), temporal and functional guild composition and seasonality of dung beetle assemblage associated with a semi-evergreen forest at Nelliampathi during 2007-08 study period.

No.	Species	Mean ± SD	%	Temporal guild	Functional guild	Seasonality
1	*Onthophagus pacificus*	7.83 ± 5.88	37.78	N	T	SE
2	*Onthophagus furcillifer*	5.17 ± 3.04	24.92	Di	T	AS
3	*Paracopris cribratus*	1.33 ± 1.86	6.43	N	T	SE
4	*Sisyphus araneolus*[@]	1.30 ± 3.42	6.27	N	R	SE
5	*Onthophagus bronzeus*[@]	0.97 ± 1.43	4.66	G	T	SE
6	*Copris repertus*	0.93 ± 1.11	4.50	N	T	AS
7	*Onthophagus manipurensis*	0.63 ± 1.03	3.05	G	T	SE
8	*Onthophagus laevis*	0.60 ± 1.10	2.89	G	T	SE
9	*Onthophagus turbatus*	0.53 ± 0.94	2.57	N	T	SE
10	*Onthophagus castetsi*	0.53 ± 0.90	2.57	N	T	AS
11	*Onthophagus andrewesi*[@]	0.27 ± 0.94	1.29	Di	T	SE
12	*Onthophagus vladimiri*[@]	0.23 ± 0.63	1.13	G	T	SE
13	*Onthophagus ensifer*	0.10 ± 0.31	0.48	Di	T	AS
14	*Onthophagus favrei*	0.07 ± 0.25	0.32	G	T	AS
15	*Catharsius molossus*	0.03 ± 0.18	0.16	N	T	*
16	*Onthophagus amphicoma*[@]	0.03 ± 0.18	0.16	G	T	*
17	*Onthophagus cavia*	0.03 ± 0.18	0.16	G	T	*
18	*Onthophagus centricornis*[$]	0.03 ± 0.18	0.16	*	T	*
19	*Onthophagus insignicollis*	0.03 ± 0.18	0.16	G	T	*
20	*Paragymnopleurus sinuatus*[$]	0.03 ± 0.18	0.16	*	R	*
21	*Tibiodrepanus setosus*	0.03 ± 0.18	0.16	G	Dw	*

Table 2: Abundance of small and large dung beetle species associated with a semi-evergreen forest at Nelliampathi during 2007-08 study period.

No.	Species	Mean ± SD	%	Size
	Small species			
1	*Onthophagus pacificus*	7.83 ± 5.88	37.78	S
2	*Onthophagus furcillifer*	5.17 ± 3.04	24.92	S
3	*Sisyphus araneolus*	1.30 ± 3.42	6.27	S
4	*Onthophagus bronzeus*	0.97 ± 1.43	4.66	S
5	*Onthophagus laevis*	0.60 ± 1.10	2.89	S
6	*Onthophagus turbatus*	0.53 ± 0.94	2.57	S
7	*Onthophagus castetsi*	0.53 ± 0.90	2.57	S
8	*Onthophagus andrewesi*	0.27 ± 0.94	1.29	S
9	*Onthophagus vladimiri*	0.23 ± 0.63	1.13	S
10	*Onthophagus ensifer*	0.10 ± 0.31	0.48	S
11	*Onthophagus favrei*	0.07 ± 0.25	0.32	S
12	*Onthophagus amphicoma*	0.03 ± 0.18	0.16	S
13	*Onthophagus cavia*	0.03 ± 0.18	0.16	S
14	*Onthophagus centricornis*	0.03 ± 0.18	0.16	S
15	*Onthophagus insignicollis*	0.03 ± 0.18	0.16	S
16	*Tibiodrepanus setosus*	0.03 ± 0.18	0.16	S
	Total %		**85.70%**	
No.	**Large species**			
1	*Paracopris cribratus*	1.33 ± 1.86	6.43	L
2	*Copris repertus*	0.93 ± 1.11	4.50	L
3	*Onthophagus manipurensis*	0.63 ± 1.03	3.05	L
4	*Catharsius molossus*	0.03 ± 0.18	0.16	L
5	*Paragymnopleurus sinuatus*	0.03 ± 0.18	0.16	L
	Total %		**14.30%**	

Table 3: Functional guild composition of dung beetles associated with a semi-evergreen forest at Nelliampathi during 2007-08 study period.

No.	Species	Mean ± SD	%	Functional guild	Seasonality
	Tunnelers				
1	*Onthophagus pacificus*	7.83 ± 5.88	37.78	T	SE
2	*Onthophagus furcillifer*	5.17 ± 3.04	24.92	T	AS
3	*Paracopris cribratus*	1.33 ± 1.86	6.43	T	SE
4	*Onthophagus bronzeus*	0.97 ± 1.43	4.66	T	SE
5	*Copris repertus*	0.93 ± 1.11	4.50	T	AS
6	*Onthophagus manipurensis*	0.63 ± 1.03	3.05	T	SE
7	*Onthophagus laevis*	0.60 ± 1.10	2.89	T	SE
8	*Onthophagus turbatus*	0.53 ± 0.94	2.57	T	SE
9	*Onthophagus castetsi*	0.53 ± 0.90	2.57	T	AS
10	*Onthophagus andrewesi*	0.27 ± 0.94	1.29	T	SE
11	*Onthophagus vladimiri*	0.23 ± 0.63	1.13	T	SE
12	*Onthophagus ensifer*	0.10 ± 0.31	0.48	T	AS
13	*Onthophagus favrei*	0.07 ± 0.25	0.32	T	AS
14	*Catharsius molossus*	0.03 ± 0.18	0.16	T	*
15	*Onthophagus amphicoma*	0.03 ± 0.18	0.16	T	*
16	*Onthophagus cavia*	0.03 ± 0.18	0.16	T	*
17	*Onthophagus centricornis*	0.03 ± 0.18	0.16	T	*
18	*Onthophagus insignicollis*	0.03 ± 0.18	0.16	T	*
	Total %		**93.41%**		

Table 3. Continued

	Dwellers				
1	*Tibiodrepanus setosus*	0.03 ± 0.18	0.16	Dw	AS
	Total %		**0.16%**		
	Rollers				
1	*Sisyphus araneolus*	1.30 ± 3.42	6.27	R	SE
2	*Paragymnopleurus sinuatus*	0.03 ± 0.18	0.16	R	AS
	Total %		**6.43%**		

Table 4: Statistical analysis of functional and temporal guild composition of dung beetle species in a semi- evergreen forest at Nelliampathi during 2007-08 study period.

Parameters	**Kruskal-Wallis H test**			**Wilcoxon-Mann/Whitney Test (*P* value)**		
	H	**DF**	***P***	**T-R**	**R-Dw**	**T-Dw**
Functional guild	63.77	2	<0.05	<0.05	<0.05	<0.05
	H	**DF**	***P***	**Di-N**	**N-G**	**Di-G**
Temporal guild	30.96	2	<0.05	<0.05	<0.05	<0.05

Table 5: Seasonal abundance (mean ± SD) of dung beetle species associated with a semi- evergreen forest at Nelliampathi during 2007-08 study period.

No.	Species	Seasonality	Presummer	Summer	Monsoon	Wilcoxon-Mann/Whitney Test (*P* value)		
			Mean ± SD	**Mean ± SD**	**Mean ± SD**	**PS-SU**	**SU-M**	**PS-M**
1	*Onthophagus pacificus*	SE	10.00±6.55	3.20±4.10	10.30±4.00	<0.05	<0.05	>0.05
2	*Onthophagus furcillifer*	AS	6.10±2.56	3.70±3.13	5.70±3.13	*	*	*
3	*Paracopris cribratus*	SE	0.50±0.70	0.60±0.97	2.90±2.38	>0.05	<0.05	>0.05
4	*Sisyphus araneolus*	SE	3.80±5.20	0.10±0.32	0.00±0.00	<0.05	>0.05	<0.05
5	*Onthophagus bronzeus*	SE	0.60±1.07	0.10±0.32	2.20±1.62	>0.05	<0.05	<0.05
6	*Copris repertus*	AS	0.40±0.52	1.30±1.64	1.10±0.74	*	*	*
7	*Onthophagus manipurensis*	SE	0.20±0.42	0.00±0.00	1.70±1.16	>0.05	<0.05	<0.05
8	*Onthophagus laevis*	SE	0.00±0.00	0.00±0.00	1.80±1.23	*	<0.05	<0.05
9	*Onthophagus turbatus*	SE	1.10±1.29	0.10±0.32	0.40±0.70	<0.05	>0.05	>0.05
10	*Onthophagus castetsi*	AS	0.80±1.03	0.10±0.32	0.70±1.06	*	*	*
11	*Onthophagus andrewesi*	SE	0.80±1.55	0.00±0.00	0.00±0.00	<0.05	*	<0.05
12	*Onthophagus vladimiri*	SE	0.70±0.95	0.00±0.00	0.00±0.00	<0.05	*	<0.05

Table 5. Continued

13	*Onthophagus ensifer*	AS	0.30±0.48	0.00±0.00	0.00±0.00	*	*	*
14	*Onthophagus favrei*	AS	0.20±0.42	0.00±0.00	0.00±0.00	*	*	*
15	*Catharsius molossus*	*	0.00±0.00	0.00±0.00	0.10±0.32	*	*	*
16	*Tibiodrepanus setosus*	*	0.00±0.00	0.10±0.32	0.00±0.00	*	*	*
17	*Paragymnopleurus sinuatus*	*	0.00±0.00	0.10±0.32	0.00±0.00	*	*	*
18	*Onthophagus amphicoma*	*	0.10±0.32	0.00±0.00	0.00±0.00	*	*	*
19	*Onthophagus cavia*	*	0.10±0.32	0.00±0.00	0.00±0.00	*	*	*
20	*Onthophagus centricornis*	*	0.10±0.32	0.00±0.00	0.00±0.00	*	*	*
21	*Onthophagus insignicollis*	*	0.10±0.32	0.00±0.00	0.00±0.00	*	*	*

Table 6: Statistical analysis of seasonal variation in overall abundance and abundance of functional and temporal guild of dung beetle species in a semi- evergreen forest at Nelliampathi during 2007-08 study period.

Parameters	Kruskal Wallis Test			Wilcoxon-Mann/Whitney Test (P value)		
	H	DF	P	PS-SU	SU-M	PS-M
Overall abundance	14.98	2	<0.05	<0.05	<0.05	>0.05
Abundance of dwellers	2.00	2	>0.05	*	*	*
Abundance of rollers	7.62	2	<0.05	>0.05	>0.05	<0.05
Abundance of tunnelers	14.97	2	<0.05	<0.05	<0.05	>0.05
Abundance of diurnal guild	5.19	2	>0.05	*	*	*
Abundance of generalist	21.31	2	<0.05	<0.05	<0.05	<0.05
Abundance of nocturnal guild	11.34	2	<0.05	<0.05	<0.05	>0.05

Table 7: Abundance (mean ± SD and percentage), temporal and functional guild composition and seasonality of dung beetle assemblage associated with an agriculture habitat at Nelliampathi during 2007-08 study period.

No.	Species	Mean ± SD	%	Temporal guild	Functional guild	Seasonality
1	*Caccobius meridionalis*	2.93 ± 5.27	25.66	Di	T	SE
2	*Onthophagus fasciatus*	2.47 ± 2.78	21.57	Di	T	AS
3	*Onthophagus furcillifer*	1.47 ± 1.81	12.83	Di	T	SE
4	*Copris repertus*	0.90 ± 1.18	7.87	N	T	SE
5	*Onthophagus pacificus*	0.43 ± 0.77	3.79	N	T	SE
6	*Catharsius molossus*	0.40 ± 0.56	3.50	N	T	SE
7	*Onthophagus ensifer*	0.40 ± 0.81	3.50	Di	T	AS
8	*Onthophagus turbatus*	0.40 ± 0.89	3.50	N	T	AS
9	*Tibiodrepanus setosus*	0.33 ± 0.88	2.92	G	Dw	AS
10	*Onthophagus manipurensis*	0.27 ± 0.64	2.33	G	T	SE
11	*Paracopris cribratus*	0.23 ± 0.63	2.04	N	T	SE
12	*Paracopris davisoni*@	0.20 ± 0.55	1.75	N	T	SE
13	*Caccobius gallinus*@	0.17 ± 0.59	1.46	Di	T	SE
14	*Onthophagus favrei*	0.17 ± 0.59	1.46	G	T	AS
15	*Onthophagus laevis*	0.13 ± 0.34	1.17	G	T	SE
16	*Caccobius ultor*	0.10 ± 0.54	0.87	G	T	AS
17	*Onthophagus amphicoma*@	0.10 ± 0.40	0.87	G	T	AS
18	*Onthophagus bronzeus*@	0.07 ± 0.25	0.58	G	T	AS
19	*Onthophagus insignicollis*	0.07 ± 0.25	0.58	G	T	AS
20	*Liatongus indicus*@$	0.03 ± 0.18	0.29	*	Dw	*

Table 7. Continued

21	*Onthophagus andrewesi*[@]	0.03 ± 0.18	0.29	Di	T	*
22	*Onthophagus porcus*[$]	0.03 ± 0.18	0.29	*	T	*
23	*Onthophagus rectecornutus*[$]	0.03 ± 0.18	0.29	*	T	*
24	*Onitis subopacus*[$]	0.03 ± 0.18	0.29	*	T	*
25	*Tibiodrepanus sinicus*[$]	0.03 ± 0.18	0.29	*	Dw	*

Table 8: Abundance of small and large dung beetle species associated with an agriculture habitat at Nelliampathi during 2007-08 study period.

No.	Species	Mean ± SD	%	Size
	Small species			
1	*Caccobius meridionalis*	2.93 ± 5.27	25.66	S
2	*Onthophagus fasciatus*	2.47 ± 2.78	21.57	S
3	*Onthophagus furcillifer*	1.47 ± 1.81	12.83	S
4	*Onthophagus pacificus*	0.43 ± 0.77	3.79	S
5	*Onthophagus ensifer*	0.40 ± 0.81	3.5	S
6	*Onthophagus turbatus*	0.40 ± 0.89	3.5	S
7	*Tibiodrepanus setosus*	0.33 ± 0.88	2.92	S
8	*Caccobius gallinus*	0.17 ± 0.59	1.46	S
9	*Onthophagus favrei*	0.17 ± 0.59	1.46	S
10	*Onthophagus laevis*	0.13 ± 0.35	1.17	S
11	*Caccobius ultor*	0.10± 0.55	0.87	S
12	*Onthophagus amphicoma*	0.10 ± 0.40	0.87	S
13	*Onthophagus bronzeus*	0.07 ± 0.25	0.58	S
14	*Onthophagus insignicollis*	0.07 ± 0.25	0.58	S
15	*Liatongus indicus*	0.03 ± 0.18	0.29	S
16	*Onthophagus andrewesi*	0.03 ± 0.18	0.29	S
17	*Onthophagus porcus*	0.03 ± 0.18	0.29	S
18	*Onthophagus rectecornutus*	0.03 ± 0.18	0.29	S
19	*Tibiodrepanus sinicus*	0.03 ± 0.18	0.29	S
	Total %		**82.22%**	

Table 8. Continued

	Large species			
1	*Copris repertus*	0.90 ± 1.18	7.87	L
2	*Catharsius molossus*	0.40 ± 0.56	3.50	L
3	*Onthophagus manipurensis*	0.27 ± 0.64	2.33	L
4	*Paracopris cribratus*	0.23 ± 0.63	2.04	L
5	*Paracopris davisoni*	0.20 ± 0.55	1.75	L
6	*Onitis subopacus*	0.03 ± 0.18	0.29	L
	Total %		**17.78%**	

Table 9: Functional guild composition of dung beetle species associated with an agriculture habitat at Nelliampathi during 2007-2008 study period.

No.	Species	Mean ± SD	%	Functional guild	Seasonality
	Tunnelers				
1	*Caccobius meridionalis*	2.93 ± 5.27	25.66	T	SE
2	*Onthophagus fasciatus*	2.47 ± 2.78	21.57	T	AS
3	*Onthophagus furcillifer*	1.47 ± 1.81	12.83	T	SE
4	*Copris repertus*	0.90 ± 1.18	7.87	T	SE
5	*Onthophagus pacificus*	0.43 ± 0.77	3.79	T	SE
6	*Catharsius molossus*	0.40 ± 0.56	3.50	T	SE
7	*Onthophagus ensifer*	0.40 ± 0.81	3.50	T	AS
8	*Onthophagus turbatus*	0.40 ± 0.89	3.50	T	AS
9	*Onthophagus manipurensis*	0.27 ± 0.63	2.33	T	SE
10	*Paracopris cribratus*	0.23 ± 0.62	2.04	T	AS
11	*Paracopris davisoni*	0.20 ± 0.55	1.75	T	SE

Table 9. Continued

12	*Caccobius gallinus*	0.17 ± 0.59	1.46	T	AS
13	*Onthophagus favrei*	0.17 ± 0.59	1.46	T	AS
14	*Onthophagus laevis*	0.13 ± 0.34	1.17	T	SE
15	*Caccobius ultor*	0.10 ± 0.54	0.87	T	AS
16	*Onthophagus amphicoma*	0.10 ± 0.40	0.87	T	AS
17	*Onthophagus bronzeus*	0.07 ± 0.25	0.58	T	AS
18	*Onthophagus insignicollis*	0.07 ± 0.25	0.58	T	AS
19	*Onthophagus andrewesi*	0.03 ± 0.18	0.29	T	*
20	*Onthophagus porcus*	0.03 ± 0.18	0.29	T	*
21	*Onthophagus rectecornutus*	0.03 ± 0.18	0.29	T	*
22	*Onitis subopacus*	0.03 ± 0.18	0.29	T	*
	Total %		**96.50%**		
	Dwellers				
1	*Tibiodrepanus setosus*	0.33 ± 0.88	2.92	Dw	AS
2	*Liatongus indicus*	0.03 ± 0.18	0.29	Dw	*
3	*Tibiodrepanus sinicus*	0.03 ± 0.18	0.29	Dw	*
	Total %		**3.50%**		

Table 10: Statistical analysis of functional and temporal guild composition of dung beetles in an agriculture habitat at Nelliampathi during 2007-08 study period.

Parameters	**Kruskal-Wallis H test**			**Wilcoxon-Mann/ Whitney Test (*P* value)**		
	H	**DF**	***P***	**T-R**	**R-Dw**	**T-Dw**
Functional guild	74.32	2	<0.05	<0.05	<0.05	<0.05
	H	**DF**	***P***	**Di-N**	**N-G**	**Di-G**
Temporal guild	25.46	2	<0.05	<0.05	<0.05	<0.05

Table 11: Seasonal abundance (mean ± SD) of dung beetle species associated with an agriculture habitat at Nelliampathi during 2007-2008 study period.

No.	Species	Seasonality	Presummer	Summer	Monsoon	Wilcoxon-Mann/Whitney Test (*P* value)		
			Mean ± SD	Mean ± SD	Mean ± SD	PS-SU	SU-M	PS-M
1	*Caccobius meridionalis*	SE	1.90±1.66	6.30±8.08	0.6±1.26	>0.05	<0.05	<0.05
2	*Onthophagus fasciatus*	AS	1.30±1.16	3.80±3.12	2.30±3.20	*	*	*
3	*Onthophagus furcillifer*	SE	0.50±0.71	2.80±2.35	1.10±1.20	<0.05	>0.05	>0.05
4	*Copris repertus*	SE	0.00±0.00	1.00±1.05	1.70±1.30	<0.05	>0.05	<0.05
5	*Onthophagus pacificus*	SE	0.00±0.00	0.20±0.42	1.10±0.99	>0.05	>0.05	<0.05
6	*Catharsius molossus*	SE	0.00±0.00	0.70±0.67	0.50±0.53	<0.05	>0.05	<0.05
7	*Onthophagus ensifer*	AS	0.10±0.32	0.80±1.14	0.30±0.67	*	*	*
8	*Onthophagus turbatus*	AS	0.00±0.00	1.00±1.25	0.20±0.63	*	*	*
9	*Tibiodrepanus setosus*	AS	0.30±0.95	0.70±1.16	0.00±0.00	*	*	*
10	*Onthophagus manipurensis*	SE	0.00±0.00	0.80±0.92	0.00±0.00	<0.05	<0.05	*
11	*Paracopris cribratus*	AS	0.00±0.00	0.10±0.32	0.60±0.97	*	*	*

Table 11. Continued

12	*Paracopris davisoni*	SE	0.00±0.00	0.00±0.00	0.60±0.84	<0.05	>0.05	<0.05
13	*Caccobius gallinus*	AS	0.00±0.00	0.50±0.97	0.00±0.00	*	*	*
14	*Onthophagus favrei*	AS	0.00±0.00	0.20±0.42	0.30±0.95	*	*	*
15	*Onthophagus laevis*	SE	0.00±0.00	0.00±0.00	0.40±0.52	*	<0.05	<0.05
16	*Caccobius ultor*	AS	0.00±0.00	0.00±0.00	0.30±0.95	*	*	*
17	*Onthophagus amphicoma*	AS	0.10±0.32	0.20±0.63	0.00±0.00	*	*	*
18	*Onthophagus bronzeus*	AS	0.00±0.00	0.10±0.32	0.10±0.32	*	*	*
19	*Onthophagus insignicollis*	AS	0.00±0.00	0.00±0.00	0.20±0.42	*	*	*
20	*Tibiodrepanus sinicus*	*	0.00±0.00	0.00±0.00	0.10±0.32	*	*	*
21	*Liatongus indicus*	*	0.10±0.32	0.00±0.00	0.00±0.00	*	*	*
22	*Onthophagus andrewesi*	*	0.10±0.32	0.00±0.00	0.00±0.00	*	*	*
23	*Onthophagus porcus*	*	0.00±0.00	0.10±0.32	0.00±0.00	*	*	*
24	*Onthophagus rectecornutus*	*	0.00±0.00	0.00±0.00	0.10±0.32	*	*	*
25	*Onitis subopacus*	*	0.00±0.00	0.10±0.32	0.00±0.00	*	*	*

Table 12: Statistical analysis of seasonal variation in overall abundance and abundance of functional and temporal guild of dung beetle species in an agriculture habitat at Nelliampathi during 2007-08 study period.

Parameters	Kruskal Wallis Test			Wilcoxon-Mann/Whitney Test (P value)		
	H	**DF**	**P**	**PS-SU**	**SU-M**	**PS-M**
Overall abundance	15.92	2	<0.05	<0.05	>0.05	<0.05
Abundance of dwellers	1.86	2	>0.05	*	*	*
Abundance of rollers	*	*	*	*	*	*
Abundance of tunnelers	16.79	2	<0.05	<0.05	<0.05	<0.05
Abundance of diurnal guild	12.24	2	<0.05	<0.05	<0.05	>0.05
Abundance of generalist	8.17	2	<0.05	<0.05	>0.05	>0.05
Abundance of nocturnal guild	20.69	2	<0.05	<0.05	>0.05	<0.05

Table 13: Abundance (mean ± SD and percentage) and percentage, temporal and functional guild composition and seasonality of dung beetle assemblage associated with an ecotone between a semi- evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period.

No.	Species	Mean ± SD	%	Temporal guild	Functional guild	Seasonality
1	*Onthophagus pacificus*	3.17 ± 4.47	20.65	N	T	SE
2	*Onthophagus furcillifer*	3.03 ± 2.70	19.78	Di	T	AS
3	*Onthophagus bronzeus*@	1.43 ± 2.24	9.35	G	T	SE
4	*Onthophagus turbatus*	1.2 ± 1.83	7.83	N	T	SE
5	*Copris repertus*	0.97 ± 1.03	6.30	N	T	AS
6	*Onthophagus manipurensis*	0.93 ± 1.55	6.09	G	T	SE
7	*Onthophagus amphicoma*@	0.7 ± 1.49	4.57	G	T	AS
8	*Paracopris cribratus*	0.6 ± 0.81	3.91	N	T	AS
9	*Onthophagus laevis*	0.53 ± 1.04	3.48	G	T	SE
10	*Sisyphus araneolus*@	0.50 ± 1.53	3.26	N	R	SE
11	*Onthophagus ensifer*	0.43 ± 0.94	2.83	Di	T	AS
12	*Onthophagus andrewesi*@	0.33 ± 0.66	2.17	Di	T	AS
13	*Onthophagus castetsi*	0.30 ± 0.53	1.96	N	T	AS
14	*Catharsius molossus*	0.23 ± 0.43	1.52	N	T	AS
15	*Paracopris davisoni*@	0.23 ± 0.68	1.52	N	T	SE
16	*Onthophagus favrei*	0.13 ± 0.43	0.87	G	T	AS
17	*Onthophagus vladimiri*@	0.13 ± 0.43	0.87	G	T	AS
18	*Ochicanthon mussardi*@	0.10±0.55	0.65	G	R	AS
19	*Onthophagus insignicollis*	0.10±0.31	0.65	G	T	SE

Table 13. Continued

20	*Caccobius gallinus*[@]	0.07 ± 0.18	0.43	Di	T	AS
21	*Onthophagus deflexicollis*	0.07 ± 0.25	0.43	G	T	AS
22	*Onthophagus cavia*	0.03 ± 0.18	0.22	G	T	*
23	*Onthophagus fasciatus*	0.03 ± 0.18	0.22	Di	T	*
24	*Paracopris signatus*[$]	0.03 ± 0.18	0.22	*	T	*
25	*Tibiodrepanus setosus*	0.03 ± 0.18	0.22	G	Dw	*

Table 14: Abundance of large and small dung beetle species associated with an ecotone between a semi- evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period.

No.	Species	Mean ± SD	%	Size
	Small species			
1	*Onthophagus pacificus*	2.93 ± 5.27	25.66	S
2	*Onthophagus furcillifer*	2.47 ± 2.78	21.57	S
3	*Onthophagus bronzeus*	1.47 ± 1.81	12.83	S
4	*Onthophagus turbatus*	0.90 ± 1.18	7.87	S
5	*Onthophagus amphicoma*	0.40 ± 0.81	3.5	S
6	*Onthophagus laevis*	0.33 ± 0.88	2.92	S
7	*Sisyphus araneolus*	0.27 ± 0.64	2.33	S
8	*Onthophagus ensifer*	0.23 ± 0.63	2.04	S
9	*Onthophagus andrewesi*	0.20 ± 0.55	1.75	S
10	*Onthophagus castetsi*	0.17 ± 0.59	1.46	S
11	*Onthophagus favrei*	0.10 ± 0.54	0.87	S
12	*Onthophagus vladimiri*	0.10 ± 0.40	0.87	S
13	*Ochicanthon mussardi*	0.07 ± 0.25	0.58	S
14	*Onthophagus insignicollis*	0.07 ± 0.25	0.58	S
15	*Caccobius gallinus*	0.03 ± 0.18	0.29	S
16	*Onthophagus deflexicollis*	0.03 ± 0.18	0.29	S
17	*Onthophagus cavia*	0.03 ± 0.18	0.29	S
18	*Onthophagus fasciatus*	0.03 ± 0.18	0.29	S
19	*Tibiodrepanus setosus*	0.03 ± 0.18	0.29	S
	Total %		**86.29%**	

Table 14. Continued

	Large species			
1	*Copris repertus*	0.43 ± 0.77	3.79	L
2	*Onthophagus manipurensis*	0.40 ± 0.56	3.5	L
3	*Paracopris cribratus*	0.40 ± 0.89	3.5	L
4	*Catharsius molossus*	0.17 ± 0.59	1.46	L
5	*Paracopris davisoni*	0.13 ± 0.34	1.17	L
6	*Paracopris signatus*	0.03 ± 0.18	0.29	L
	Total %		**13.71%**	

Table 15: Functional guild composition of dung beetle species associated with an ecotone between a semi- evergreen forest and an agriculture habitat at Nelliampathi during 2007-2008 study period.

No.	Species	Mean ± SD	%	Functional guild	Seasonality
	Tunnelers				
1	*Onthophagus pacificus*	3.17 ± 4.47	20.65	T	SE
2	*Onthophagus furcillifer*	3.03 ± 2.70	19.78	T	AS
3	*Onthophagus bronzeus*	1.43 ± 2.24	9.35	T	SE
4	*Onthophagus turbatus*	1.2 ± 1.83	7.83	T	SE
5	*Copris repertus*	0.97 ± 1.03	6.30	T	AS
6	*Onthophagus manipurensis*	0.93 ± 1.55	6.09	T	SE
7	*Onthophagus amphicoma*	0.7 ± 1.49	4.57	T	SE
8	*Paracopris cribratus*	0.6 ± 0.81	3.91	T	AS
9	*Onthophagus laevis*	0.53 ± 1.04	3.48	T	SE
10	*Onthophagus ensifer*	0.43 ± 0.94	2.83	T	AS
11	*Onthophagus andrewesi*	0.33 ± 0.66	2.17	T	AS
12	*Onthophagus castetsi*	0.30 ± 0.53	1.96	T	AS
13	*Catharsius molossus*	0.23 ± 0.43	1.52	T	AS
14	*Paracopris davisoni*	0.23 ± 0.68	1.52	T	SE
15	*Onthophagus favrei*	0.13 ± 0.43	0.87	T	AS
16	*Onthophagus vladimiri*	0.13 ± 0.43	0.87	T	AS
17	*Onthophagus insignicollis*	0.10±0.31	0.65	T	SE
18	*Caccobius gallinus*	0.07 ± 0.18	0.43	T	AS
19	*Onthophagus deflexicollis*	0.07 ± 0.25	0.43	T	AS
20	*Paracopris signatus*	0.03 ± 0.18	0.22	T	*

Table 15. Continued

21	*Onthophagus cavia*	0.03 ± 0.18	0.22	T	*
22	*Onthophagus fasciatus*	0.03 ± 0.18	0.22	T	*
	Total %		**95.87%**		
	Dwellers				
1	*Tibiodrepanus setosus*	0.03 ± 0.18	0.22	Dw	AS
	Total %		**0.22%**		
	Rollers				
1	*Sisyphus araneolus*	0.5 ± 1.53	3.26	R	SE
2	*Ochicanthon mussardi*	0.1 ± 0.55	0.65	R	*
	Total %		**3.91%**		

Table 16: Statistical analysis of functional and temporal guild composition of dung beetle species associated with an ecotone between a semi- evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period.

Parameters	**Kruskal-Wallis H test**			**Wilcoxon-Mann/Whitney Test (*P* value)**		
	H	**DF**	***P***	**T-R**	**R-Dw**	**T-Dw**
Functional guild	70.31	2	<0.05	<0.05	>0.05	<0.05
	H	**DF**	***P***	**Di-N**	**N-G**	**Di-G**
Temporal guild	1.98	2	>0.05	*	*	*

Table 17: Seasonal abundance (mean ± SD) of dung beetle species associated with an ecotone between a semi- evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period.

No.	Species	Seasonality	Presummer	Summer	Monsoon	Wilcoxon-Mann/Whitney Test (*P* value)		
			Mean ± SD	**Mean ± SD**	**Mean ± SD**	**PS-SU**	**SU-M**	**PS-M**
1	*Onthophagus pacificus*	SE	2.60±3.53	0.20±0.42	6.70±5.27	<0.05	<0.05	<0.05
2	*Onthophagus furcillifer*	AS	4.60±3.53	1.90±1.45	2.60±2.12	*	*	*
3	*Onthophagus bronzeus*	SE	1.00±0.94	0.30±0.48	3.00±3.27	>0.05	<0.05	>0.05
4	*Onthophagus turbatus*	SE	0.90±1.29	0.00±0.00	2.70±2.21	<0.05	<0.05	>0.05
5	*Copris repertus*	AS	0.40±0.84	1.20±1.03	1.30±1.06	*	*	*
6	*Onthophagus manipurensis*	SE	0.00±0.00	2.20±1.99	0.60±0.97	<0.05	<0.05	<0.05
7	*Onthophagus amphicoma*	SE	2.10±1.97	0.00±0.00	0.00±0.00	<0.05	*	<0.05
8	*Paracopris cribratus*	AS	0.40±0.52	0.30±0.48	1.10±1.10	*	*	*
9	*Onthophagus laevis*	SE	0.00±0.00	0.00±0.00	1.60±1.26	*	<0.05	<0.05
10	*Sisyphus araneolus*	SE	1.50±2.42	0.00±0.00	0.00±0.00	<0.05	*	<0.05
11	*Onthophagus ensifer*	AS	0.90±1.45	0.20±0.42	0.20±0.42	*	*	*
12	*Onthophagus andrewesi*	AS	0.30±0.48	0.40±0.52	0.30±0.95	*	*	*

Table 17. Continued

13	*Onthophagus castetsi*	AS	0.50±0.53	0.10±0.32	0.30±0.67	*	*	*
14	*Catharsius molossus*	AS	0.00±0.00	0.30±0.48	0.40±0.52	*	*	*
15	*Paracopris davisoni*	SE	0.00±0.00	0.00±0.00	0.70±1.06	*	<0.05	<0.05
16	*Onthophagus favrei*	AS	0.30±0.67	0.00±0.00	0.10±0.32	*	*	*
17	*Onthophagus vladimiri*	AS	0.40±0.70	0.00±0.00	0.00±0.00	*	*	*
18	*Ochicanthon mussardi*	AS	0.00±0.00	0.00±0.00	0.30±0.95	*	*	*
19	*Onthophagus insignicollis*	SE	0.30±0.48	0.00±0.00	0.00±0.00	>0.05	*	>0.05
20	*Caccobius gallinus*	AS	0.10±0.32	0.10±0.32	0.00±0.00	*	*	*
21	*Onthophagus deflexicollis*	AS	0.10±0.32	0.00±0.00	0.10±0.32	*	*	*
22	*Paracopris signatus*	*	0.00±0.00	0.00±0.00	0.10±0.32	*	*	*
23	*Tibiodrepanus setosus*	*	0.10±0.32	0.00±0.00	0.00±0.00	*	*	*
24	*Onthophagus cavia*	*	0.00±0.00	0.00±0.00	0.10±0.32	*	*	*
25	*Onthophagus fasciatus*	*	0.10±0.32	0.00±0.00	0.00±0.00	*	*	*

Table 18: Statistical analysis of seasonal variation in overall abundance, functional guild and temporal guild of dung beetle species in an ecotone between a semi-evergreen forest and an agriculture habitat at Nelliampathi during 2007-2008 study period.

Parameters	**Kruskal Wallis Test**			**Wilcoxon-Mann/Whitney Test (P value)**		
	H	**DF**	**P**	**PS-SU**	**SU-M**	**PS-M**
Overall abundance	12.82	2	<0.05	<0.05	<0.05	>0.05
Abundance of dwellers	2.00	2	>0.05	*	*	*
Abundance of rollers	6.11	2	<0.05	<0.05	>0.05	>0.05
Abundance of tunnelers	14.28	2	<0.05	<0.05	<0.05	>0.05
Abundance of diurnal guild	4.02	2	>0.05	*	*	*
Abundance of generalist	3.79	2	>0.05	*	*	*
Abundance of nocturnal guild	14.03	2	<0.05	>0.05	<0.05	<0.05

Table 19: Statistical analysis of variation in overall abundance, diversity, functional guild and temporal guild of dung beetle species across a semi- evergreen forest, agriculture habitat and ecotone at Nelliampathi during 2007-2008 study period.

Parameters	**Kruskal Wallis Test**			**Wilcoxon-Mann/Whitney Test (P value)**		
	H	**DF**	**P**	**SEG-ECO**	**ECO-AGR**	**SEG-AGR**
Overall abundance	11.31	2	<0.05	>0.05	>0.05	<0.05
Overall diversity	3.24	2	>0.05	*	*	*
Abundance of dwellers	5.22	2	>0.05	*	*	*
Abundance of rollers	7.45	2	<0.05	>0.05	<0.05	<0.05
Abundance of tunnelers	10.74	2	<0.05	>0.05	>0.05	<0.05
Abundance of diurnal guild	4.70	2	>0.05	*	*	*
Abundance of generalist	17.59	2	<0.05	<0.05	<0.05	>0.05
Abundance of nocturnal guild	24.49	2	<0.05	<0.05	<0.05	<0.05

Table 20: Analysis of the similarity of dung beetle assemblage across a semi-evergreen forest, agriculture habitat and ecotone at Nelliampathi during 2007-2008 study period.

Habitat	**SEG**	**ECO**	**AGR**
SEG			
ECO	77.30		
AGR	45.80	56.59	

Table 21: Percentage contribution of species towards dissimilarity between a semi-evergreen forest, agriculture habitat and ecotone at Nelliampathi during 2007-08 study period.

No.	Species	Semi-evergreen Forest v/s Ecotone	Ecotone v/s Agriculture habitat	Semi-evergreen forest v/s Agriculture habitat
1	*Caccobius gallinus*	3.63	1.17	2.63
2	*Caccobius meridionalis*	0.00	13.32	11.03
3	*Caccobius ultor*	0.00	2.46	2.04
4	*Catharsius molossus*	4.22	1.16	2.90
5	*Copris repertus*	0.24	0.27	0.11
6	*Liatongus indicus*	0.00	1.42	1.18
7	*Ochicanthon mussardi*	4.44	2.46	0.00
8	*Onitis subopacus*	0.00	1.42	1.18
9	*Onthophagus amphicoma*	9.19	4.05	0.86
10	*Onthophagus andrewesi*	0.86	3.07	2.15
11	*Onthophagus bronzeus*	3.01	7.30	4.67
12	*Onthophagus castetsi*	2.56	4.26	4.70
13	*Onthophagus cavia*	0.00	1.42	1.18
14	*Onthophagus centricornis*	2.56	0.00	1.18
15	*Onthophagus deflexicollis*	3.63	2.01	0.00
16	*Onthophagus ensifer*	4.80	0.20	2.04
17	*Onthophagus fasciatus*	2.56	10.80	10.12
18	*Onthophagus favrei*	1.50	0.34	0.97
19	*Onthophagus furcillifer*	7.46	4.13	6.84
20	*Onthophagus insignicollis*	1.88	0.45	0.49
21	*Onthophagus laevis*	0.62	2.84	2.64

Table 21. Continued

22	*Onthophagus manipurensis*	2.39	3.50	1.80
23	*Onthophagus pacificus*	14.32	8.72	13.79
24	*Onthophagus porcus*	0.00	1.42	1.18
25	*Onthophagus rectecornutus*	0.00	1.42	1.18
26	*Onthophagus turbatus*	5.13	3.60	0.63
27	*Onthophagus vladimiri*	1.66	2.84	3.11
28	*Paracopris cribratus*	5.34	2.27	4.33
29	*Paracopris davisoni*	6.79	0.28	2.88
30	*Paracopris signatus*	2.56	1.42	0.00
31	*Paragymnopleurus sinuatus*	2.56	0.00	1.18
32	*Sisyphus araneolus*	6.08	5.50	7.34
33	*Tibiodrepanus setosus*	0.00	3.07	2.54
34	*Tibiodrepanus sinicus*	0.00	1.42	1.18

Table 22: Indicator value of species collected from a semi- evergreen forest, ecotone and agriculture habitat at Nelliampathi during 2007-08 study period.

No.	Species	Semi - evergreen forest	Ecotone	Agriculture habitat
1	*Caccobius gallinus*	0.00	6.67	10.00
2	*Caccobius meridionalis*	0.00	0.00	56.67
3	*Caccobius ultor*	0.00	0.00	3.33
4	*Catharsius molossus*	3.33	23.33	36.67
5	*Copris repertus*	60.00	53.33	46.67
6	*Liatongus indicus*	0.00	0.00	3.33
7	*Ochicanthon mussardi*	0.00	3.33	0.00
8	*Onitis subopacus*	0.00	0.00	3.33
9	*Onthophagus amphicoma*	3.33	23.33	6.67
10	*Onthophagus andrewesi*	13.33	26.67	3.33
11	*Onthophagus bronzeus*	43.33	56.67	6.67
12	*Onthophagus castetsi*	30.00	26.67	0.00
13	*Onthophagus cavia*	3.33	3.33	0.00
14	*Onthophagus centricornis*	3.33	0.00	0.00
15	*Onthophagus deflexicollis*	0.00	6.67	0.00
16	*Onthophagus ensifer*	10.00	26.67	23.33
17	*Onthophagus fasciatus*	0.00	3.33	76.67
18	*Onthophagus favrei*	6.67	10.00	10.00
19	*Onthophagus furcillifer*	93.33	80.00	60.00
20	*Onthophagus insignicollis*	3.33	10.00	6.67
21	*Onthophagus laevis*	26.67	26.67	13.33
22	*Onthophagus manipurensis*	36.67	40.00	16.67

Table 22. Continued

23	*Onthophagus pacificus*	86.67	56.67	30.00
24	*Onthophagus porcus*	0.00	0.00	3.33
25	*Onthophagus rectecornutus*	0.00	0.00	3.33
26	*Onthophagus turbatus*	33.33	43.33	23.33
27	*Onthophagus vladimiri*	16.67	10.00	0.00
28	*Paracopris cribratus*	53.33	43.33	16.67
29	*Paracopris davisoni*	0.00	13.33	13.33
30	*Paracopris signatus*	0.00	3.33	0.00
31	*Paragymnopleurus sinuatus*	3.33	0.00	0.00
32	*Sisyphus araneolus*	20.00	13.33	0.00
33	*Tibiodrepanus setosus*	3.33	3.33	13.33
34	*Tibiodrepanus sinicus*	0.00	0.00	3.33

DISCUSSION

Latha Mathews “Systematics and ecology of dung beetles (coleoptra: scarabaeidae: scarabaeinae) in the Nelliampathi region of South Western Ghats” Thesis. Department of Zoology, St. Joseph's College Devagiri , University of Calicut, 2013

Chapter 5

DISCUSSION

5.1. Taxonomy

Three first reports for the South Indian region recorded from Nelliampathi which included, *Onthophagus deflexicollis*, *O. manipurensis* and *Tibiodrepanus sinicus* indicates that further studies in Nelliampathi region and similar high elevation montane region in the Western Ghats may disclose new additions to the species list of the South Indian region. Record of nine species endemic to the Western Ghats region from Nelliampathi namely, *Caccobius gallinus*, *Liatongus indicus*, *Ochicanthon mussardi*, *Onthophagus amphicoma*, *O. andrewesi*, *O. bronzeus*, *O. Vladimiri*, *Paracopris davisoni* and *Sisyphus araneolus* highlights the importance of Nelliampathi as a region of conservation priority.

Comparison of dung beetles collected in the present study with collections of Arrow (1931), Balthasar (1963a, b), Paulian (1945, 1980, 1983) and the checklist of dung beetles of the moist western slope of the south Western Ghats (Sabu 2011a) revealed that several species belonging to genus *Ochicanthon* and *Panelus* which were earlier well represented in the Nelliampathi region was not recorded in the present study. Genus *Ochicanthon* was represented by only *Ochicanthon mussardi* (Latha *et al.* 2011) in the present study while earlier collections had reported the presence of *O. gauricola* (Latha *et al.* 2011), *O. laetus* (Arrow 1931) and *O. nitidus* (Paulian 1980). Genus *Panelus* was not recorded in the present study but earlier, *Panelus mussardi* (Paulian 1980) and *P. keralai* (Paulian 1980) were recorded. These are dung beetles preferring pelleted dung and their absence indicate that the habitat degradation of the Nelliampathi region had led to decline in pelleted dung producing mammal in the region thereby affecting the dung beetle composition of the region.

Checklist prepared provides baseline information on the composition of dung beetle fauna of the Nelliampathi region of the Western Ghats. Similar collection efforts done in Wayanad (Vinod 2009), Thekkady (unpublished), Ranipuram (unpublished) will provide an up to date, comprehensive list of dung beetles of the Western Ghats in Kerala region, as no such studies have been done in the region since the work of Arrow (1931). The pictorial key provided will make the identification of dung beetles more accurate and easier. Such studies gains significance in the context of present deterioration of forests in the region due to anthropogenic pressures as adequate information of species in the region is essential for planning conservation strategy for the region.

5.2. Ecology

5.2.1. Forest

5.2.1.1. Abundance, species richness and diversity

Twenty one species were recorded from the forest of Nelliampathi. As this is the first repeatedly sampled study of the region there is no available data for comparison, but when compared with similar forests in Wayanad region of the Western Ghats the species richness and diversity was comparatively low as 56 species were recorded from the Wayanad region of Western Ghats (Anu 2006; Sabu *et al.* 2006; Sabu *et al*. 2007; Vinod & Sabu 2007; Vinod 2009). Global comparison from forests revealed 87 species from Malaysia (Davis

2000b), 76 species from French Guyana (Feer 2000), 75 species from Ivory Coast (Taï) (Cambefort & Walter 1991), 72 species from Pará (Brazilian Amazonia) (Gardner *et al*. 2008), and 60 species from Colombia (Amazonas) (Howden & Nealis 1975). Species richness similar to the results in Nelliampathi was recorded from studies in the evergreen forest of Thekkady with 30 species (unpublished data) and Ranipuram with 21 species (unpublished data).

Abundance and species richness of dung beetle is directly influenced by diversity of habitats, animals and physical factors (Loozada & Lopez 1997). Areas that are rich in mammals and in particular have a significant biomass of large herbivores contain more species of dung beetles than those that have comparatively poor mammalian fauna (Hanski & Cambefort 1991d). Vegetation structure also determines the species richness of dung beetles in tropical habitats (Howden & Nealis 1975; Walter 1978; Peck & Forsyth 1982). Large scale human disturbance over a number of years in the region have affected the nature of the habitats, its physical factors and mammalian fauna in the Nelliampathi region which consequently affected the species richness and abundance of dung beetles in these forests (Joy 1991; Mathew *et al*. 1998; Abraham *et al*. 2006; Sukumar & Easa 2006).

Reduction in species richness of dung beetles in forest patches is a direct response to area loss (Klein 1989; Saunders *et al.* 1991; Wiens 1997) and isolation (distance effect to the nearest forest neighbor through a harsh continuous matrix) as shown by Estrada *et al.* (1998) in tropical sites of

Mexico. Large number of leased estates in the region has fragmented and destroyed the forests (Prabhakaran 2011). Nelliampathi represents a similar habitat with mosaic of forest fragments and plantations (Joy 1991; Nair 1991) which contributed to the low species richness and diversity.

All six tribes recorded from the forest of Nelliampathi represented the Afro-Eurasian centered modern tribes and subtribe namely, Coprini, Gymnopleurini, Oniticellini: Drepanocerina, Onthophagini, Paracoprini and Sisyphini. Absence of the old southern tribe Canthonini, which had retained the Gondwanian distribution until the present (Cambefort 1991) is of significance. Canthonini is generally more common in moist forests and regions with abundant dung pellet producing terrestrial mammals (Davis & Scholtz 2001; Davis *et al.* 2002; Sabu *et al.* 2011b). Absence of Canthonini indicates the disturbed nature of the forests with less dung pellet producing mammals.

Onthophagus pacificus and *O. furcillifer* contributed 62.70% of the total abundance. Forests of Ranipuram located north of the Palghat gap also recorded similar dominance of these two beetles (unpublished data). These are heliophilic species preferring open forests (Sabu 2011) and the presence of heliophilic species indicates the degradation of the once closed forests of Nelliampathi into more open patches which facilitated the colonization of such species. Such decreased equitability in community structure owing to the dominance of few dung beetle species is often associated with disturbed habitats, such as logged forests, plantation forests, forest fragments, and pastures (Klein 1989; Halffter *et al.* 1992; Escobar 1997; Estrada *et al.* 1998;

Davis *et al*. 2001; Halffter & Arellano 2002). High specificity and fidelity of *O. pacificus* and *O. furcillifer* in forest habitat made them the indicator species for the forests of Nelliampathi.

Five endemics recorded from Nelliampathi forest namely, *Onthophagus amphicoma*, *O. andrewesi*, *O. bronzeus*, *O. vladimiri* and *Sisyphus araneolus* were reported from both north and south of the Palghat Gap which is considered as a geographic barrier for faunal movement. Their presence in both sides of the Palghat Gap suggests that these species were already wide spread in the Western Ghats before the formation of the Palghat Gap.

Small beetles dominated the dung beetle assemblage. Similar dominance of small beetles was observed in the forests of Thekkady (unpublished data) and in other forest habitats around the world (Escobar 2004). Size of dung beetles depends on the size of the available dung pads and large beetles prefer large dung pads (Hanski & Cambefort 1991c). This indicates the abundance of small dung pad producing mammals in these forests, opposed to large dung pad producing mammals like elephants, gaur which is a direct result of severe anthropogenic disturbance in the region (Joy 1991; Mathew *et al.* 1998; Abraham *et al*. 2006; Sukumar & Easa 2006). Moreover large species tend to have small populations due to low fecundity and reproductive rate and long life span (Cardillo *et al.* 2005) and this could be another reason for their low abundance.

5.2.1.2. Functional guild composition

Tunnelers represented the most speciose and abundant functional guild. Tunneler guild dominated the assemblage in other forests of Western Ghats also (Sabu *et al*. 2006, 2007; Vinod & Sabu 2007; Sabu *et al*. 2011b; Ranipuram (unpublished); Thekkady (unpublished) and across the globe (Cambefort & Walter 1991; Andresen 2005). Aggressive and superior competitive nature of tunnelers in utilizing the dung resource (Doube 1991; Krell-Westerwalbesloh *et al*. 2004) contributed to their success and dominance in the various habitats.

Rollers were the second most dominant guild in Nelliampathi (6.43%). In the South Western Ghats, roller abundance in the various forests is as follows, Thirunelly (3.19%) (Vinod 2009), Thekkady (3.30%) (unpublished data), Ranipuram 1% (unpublished data). Low abundance of rollers in these forests is attributed to the specific requirement in the nature of dung they can utilize. Rollers require firm (less liquid) dung than the tunnelers because of the need to make them into balls (Halffter & Mathews 1966). The low forest floor temperature and high humidity in these moist forests keeps the dung moist and in a semi fluid state for longer periods which make dung ball making and rolling an energetically costly behaviour (Sabu *et al*. 2007). Moreover their abundance is correlated with temperature of feces and soil (Krell 2003) and the low temperature in these forests could be discouraging rollers. Thick under storey vegetation in these moist forests also act as a hindrance to ball rolling activities (Vinod 2009).

Rollers were represented by only two species namely, large roller *Paragymnopleurus sinuatus* and small roller *Sisyphus araneolus*. High abundance of small roller genus, *Sisyphus* in the forests of Nelliampathi is similar to earlier records from the Wayanad forests of South Western Ghats (Vinod & Sabu 2007; Vinod 2009; Sabu 2011) and Thekkady (unpublished data). High abundance of the genus *Sisyphus* in the moist Western Ghats indicates its adaptation to the vegetation, trophic resource and microclimate of the region. Moreover genus *Sisyphus* is active during most part of the year and feed on a variety of dung resource (Cambefort 1991). Adult *Sisyphus* also lives more than a year and can have upto five generations per year (Paschalidis 1974). *Sisyphus araneolus* recorded from Nelliampathi was not recorded from other forests of moist South Western Ghats. This might be related to its capacity to survive in disturbed habitats. The rarity of the large roller *Paragymnopleurus sinuatus* is related to their seasonal activity as most larvae and adult remain buried in soil for most part of the year (Doube 1991).

Dweller guild was represented by only one species, *Tibiodrepanus setosus* that was rare. Similar results were obtained from Thekkady (1.28%) (unpublished data) and there was none in Ranipuram (unpublished data). Very low abundance of dwellers in the present study is contradictory to the results obtained from the forests of Wayanad (Vinod 2009), where they were the second most dominant guild (19.51% of the total abundance) after the tunnelers. Dwellers are strongly associated with large herbivore dung pads and breeds successfully only in undisturbed dung pads with little competition from competitively superior tunnelers and rollers (Hanski & Cambefort 1991c; Krell *et al*. 2003; Krell-Westerwalbesloh *et al*. 2004). Low abundance of megaherbivores (Sukumar & Easa 2006) and their dung pads in these forests due to extensive human interference (Joy 1991; Mathew *et al.* 1998; Abraham *et al*. 2006; Sukumar & Easa 2006) could be the reason for the very low abundance of dwellers and moreover competition from the competitively superior rollers and tunnelers limits the availability of undisturbed dung pads for use by dwellers (Doube 1991).

5.2.1.3. Temporal guild composition

Nocturnal guild dominated the assemblage in Nelliampathi forests. Dawn and dusk are the two periods when defecation of mammals peak and this corresponds to the increase in activity of dung beetles during these times (Gill 1991). Dominance of nocturnal guild in the forests of Nelliampathi is probably related to this availability of food resource in the night as many mammals void their dung at the end of a feeding day. Similar dominance of nocturnal guild was observed in the forests of Ranipuram (unpublished data).

Diurnal beetles were second most abundant. Diurnal beetles were smaller than nocturnal and generalist species. This is a widespread trend in dung beetles (Cambefort 1991) and is partially related to thermoregulatory constraints (Bartholomew & Heinrich 1978). Large beetles dissipate heat more slowly during the day compared to small beetles and may face the problem of overheating. Predation may also play some role in limiting the size of diurnal beetles (Cambefort & Walter 1991). Small beetles will be less visible to the predator during the day than large beetles. Generalists were the least abundant. Their low abundance is attributed to their dependence on food left over by the more competitive diurnal and nocturnal beetles.

5.2.1.4. Seasonality

Significant seasonal effect on abundance was noticed in the dung beetle population of the forest with monsoon and presummer recording higher abundance. Similar results were observed in forests of Wayanad (Vinod 2009). During both the seasons the tunnelers *Onthophagus pacificus* and *O. furcillifer* were the dominant species. The seasonal activity of dung beetles at a site depends on the temperature and precipitation cycles (Lumaret & Kirk 1991). High abundance in presummer and monsoon in the Nelliampathi forests could be attributed to the optimum conditions prevailing during these seasons with respect to physical parameters, vegetation and trophic resources (Vinod 2009).

Low abundance in the summer period is probably due to the less optimum conditions prevailing during the season (Hanski & Cambefort 1991d; Andresen 2005). In tropical biomes in which temperature fluctuations are small, rainfall is the most important climatic factor affecting dung beetle communities (Hanski & Cambefort 1991d), with lower abundance and often also lower species richness during the dry season (Andresen 2005). Moreover changes in vegetation cover led to differences in mammalian fauna which in turn, affected dung beetle populations (Cambefort & Walter 1991; Estrada *et al*. 1999). Drying up of under storey vegetation and shedding of leaves by the deciduous trees of the semi-evergreen forests in Nelliampathi reduced food availability for herbivores which migrated to other evergreen patches in the region and thereby reduced dung availability. Similar observations were made in forests of Wayand also (Vinod 2009). Moreover dung pads exposed to higher temperatures and light levels may reduce the time interval during which they are available to beetles and increase adult and larval mortality (Klein 1989; Galante *et al.* 1991; Durães *et al.* 2005). Further, rapid surface crust formation in dung pads (Sowig & Wassmer 1994; Horgan 2001) makes it less usable by beetles.

Tunnelers dominated the three seasons followed by rollers. Dwellers were the least dominant guild. Tunnelers are superior competitors capable of utilizing the dung resource rapidly (Doube 1991; Krell-Westerwalbesloh *et al.* 2004). Moreover the tribe Onthophagini which is the dominant tunneler includes small tunnelers with high fecundity and more than one generation per year (Cambefort 1991). This led to the dominance of tunnelers at all seasons.

Tunnelers showed seasonality with low abundance during summer compared to presummer and monsoon seasons. The unfavourable conditions prevailing in summer as mentioned earlier led to their low abundance in summer. Rollers also showed seasonality with presummer and summer showing similar abundance. Rollers require firm dung which can be made into balls and rolled away. The climatic conditions of presummer and summer will allow the dung to dry enabling it to be made into balls unlike monsoon season. Absence of rollers in monsoon is most likely due to the heavy rains which makes dung ball making and rolling difficult and rain might also wash away dung pads. Dweller guild was not represented in the rainy season or presummer but only in summer by the species *Tibiodrepanus setosus* that was rare. The rarity of dwellers in the region is as mentioned previously related to the low presence of undisturbed dung pads in the Nelliampathi forests as it is quickly used up by the activity of tunnelers and rollers.

Nocturnal species represented by tunnelers and rollers dominated the assemblage during presummer, summer and monsoon seasons. As mentioned earlier high availability of dung at the end of a feeding day could be the reason for the high abundance of nocturnal guild (Gill1991).

Peak in abundance of many dung beetle species may correspond to the events in lifecycle such as oviposition period or emergence of immature stages (Doube 1991; Lumaret & Kirk 1991) or it may indicate the preference of these species to the climatic conditions of that particular season. Amongst the seasonal tunnelers *Onthophagus bronzeus*, *O. laevis, O. manipurensis*, *O. pacificus* and *Paracopris cribratus* showed higher abundance during monsoon period which is attributed to their tolerance to heavy rains of the season and this makes them better adapted to the moist forests of Western Ghats. *Onthophagus andrewesi*, *O. turbatus*, *O. vladimiri* and roller *Sisyphus araneolus* showed the general trend with high abundance in presummer which is the most favourable season with respect to climatic factors and trophic availability. Aseasonality in five species, all tunnelers namely, *Copris repertus*, *Onthophagus castetsi*, *O. ensifer*, *O. favrei* and *O. furcillifer* indicates that these species do not show preference towards any particular seasons.

5.2.2. Agriculture habitat

5.2.2.1. Abundance, species richness and diversity

The species richness of 25 recorded from the agriculture habitat of Nelliampathi was lower when compared 55 species recorded from the agriculture habitat of Tanzania (Nielsen 2007) and 28 species from Wayanad (Vinod 2009). However it was high when compared to seven species recorded from shaded coffee plantation in Mexico (Arellano *et al*. 2005), 10 species from cropland in Columbia (Escobar 2004), 10 species from agriculture fields of North India (Mittal & Vadhera 1998), 12 species from agroecosystems of Guatemala (Avendano-Mendoza *et al*. 2005), 13 species from agriculture field in Sulawesi, Indonesia (Shahabuddin *et al*. 2005) and 22 species from agriculture habitat in Mexico (Estrada *et al*. 1998).

Caccobius meridionalis and *Onthophagus fasciatus* both small tunnelers constituted 46.32% of abundance in the agriculture habitat. Due to the strong habitat association, *O. fasciatus* is considered as indicator species for the agriculture habitat in Wayanad (Vinod 2009) and Nelliampathi. Distribution records from the subcontinent reveal that they are widespread species (Arrow 1931). *Caccobius meridionalis* is present in both central and south India and *Onthophagus fasciatus* all over India (Arrow 1931). These are therefore well adapted species capable of surviving in variety of habitats including disturbed habitats like crop fields and may produce several broods per year as common in small tunnelers (Cambefort & Hanski 1991) which led to their high abundance. Similar observations were made in beetle communities from highly modified habitats where hyperabundance of a few small-bodied species was observed (Scheffler 2005; Davis & Philips 2005). *Onthophagus furcillifer*, *Copris repertus*, *Onthophagus ensifer*, *O. turbatus* and *Tibiodrepanus setosus* recorded from Nelliampathi were recorded from Wayanad also indicating their adaptability to modified open habitats (Vinod 2009).

Among the 25 species recorded from the agriculture habitat, six species namely, *Caccobius gallinus*, *Liatongus indicus*, *Onthophagus amphicoma*, *O. andrewesi*, *O. bronzeus* and *Paracopris davisoni* were endemic to the Western Ghats accounting for 24% of the species collected. The presence of these beetles in the agriculture habitat indicates that the habitat modification of the Western Ghats did not affect the survival capacity of these endemic species and they were able to adapt themselves to the newly modified environment. Small beetles dominated the assemblage as opposed to large beetles. Capacity of small beetles to utilize small dung resources (Nealis 1977) and their ability to use greater range of microhabitats and food resources (Jankielsohn *et al.* 2001) must have led to their abundance.

5.2.2.2. Functional guild composition

In Nelliampathi complete absence of rollers from the agriculture habitat is notable**.** Functional guild composition in agroecosystems across the world showed different patterns. Dwellers and rollers were not recorded from the assemblages in the agroecosystems of Indonesia (Shahabuddin *et al.* 2005); dwellers were not recorded in the dung beetle assemblage of Guatemala (Avendano-Mendoza *et al.* 2005); rollers reported as the second dominant guild preceded by tunnelers in the assemblages of Mexico (Estrada *et al*. 1998), Tanzania (Nielsen 2007) and Wayanad (Vinod 2009). Rollers were not recorded in the agroecosystems of Columbia (Escobar 2004) and North India (Mittal & Vadhera 1998). Sensitivity of rollers to changes in vegetation and soil use (Escobar 2004) is probably the reason for the absence of rollers from the agriculture habitat. The change in vegetation, microclimate and land use of the cultivated land make it less suitable for rollers (Nielsen 2007).

Tunnelers were the most dominant guild. Dwellers which were poorly represented included *Liatongus indicus*, *Tibiodrepanus setosus* and *T. sinicus*. Low abundance of dwellers in the agriculture habitat is attributed to the unavailability of undisturbed dung pads. The removal of dung by farmers during agricultural practices like tilling, ploughing, manuring etc., disrupts feeding and breeding activities of dwellers and also rollers (Sabu & Vinod 2005). The competition from superior competitors, the tunnelers which can rapidly remove dung from the pad also affected dweller and roller abundance (Doube 1991; Krell *et al*. 2003).

5.2.2.3. Temporal guild composition

Diurnal guild represented by small tunnelers belonging to the tribe Onthophagini dominated the assemblage followed by nocturnal guild dominated by large tunnelers of the tribe Coprini. Diurnal guild is generally small in size owing to thermoregulatory constraints (Bartholomew & Heinrich 1978).

Dominance of diurnal species (heliophiles) compared to nocturnal species (umbrophiles) was observed in pastures, croplands and areas used for raising cattle in Honduras (Halffter *et al.*1992), Mexico (Horgan 2002) and Colombia (Escobar 2004). Abundance of diurnal guild is probably related to the agricultural practices of the region where the main source of dung is contributed by domestic herbivores which are active during the day and confined to sheds at night.

5.2.2.4. Seasonality

Abundance of dung beetles showed significant variation with seasons. Low abundance during presummer, compared to monsoon and summer is in contrast to results observed in agriculture habitat of Wayanad (Vinod 2009) where highest abundance is recorded in presummer. This is related to the agricultural practices of the region. Cultivation of banana begins toward the end of the rainy season and peaks during presummer and during this period domestic herbivores are not allowed to graze in the agriculture field. This lowers the dung resource availability in presummer leading to the low abundance of dung beetles.

High abundance in summer and monsoon is attributed to the entry of domestic cattle for grazing following the harvesting of banana which leads to greater availability of dung resource for the dung beetles. *Caccobius meridionalis, Onthophagus fasciatus* and *O. furcillifer* were the abundant species during summer and monsoon seasons.

Eight species all tunnelers showed significant seasonality. Species that showed high abundance in summer such as *Caccobius meridionalis, Catharsius molossus*, *Copris repertus, Onthophagus furcillifer* and *O. manipurensis* and in monsoon such as *Catharsius molossus*, *Copris repertus*, *Onthophagus furcillifer*, *O. laevis* and *Paracopris davisoni* were showing the general trend observed in the agriculture habitat of Nelliampathi where highest abundance of dung beetles were recorded during summer and rainy season. This also points to the increased tolerance of such dung beetles to heat of summer or rains of monsoon season.

Tunnelers dominated the assemblages in abundance in all the three seasons, followed by dwellers. Dwellers showed lower abundance in rainy season and it is attributed to the heavy rains of the monsoon season that wash away dung pads. Diurnal guild dominated the assemblage in presummer and summer and nocturnal guild dominated the assemblage in monsoon period. Dominance of diurnal guild was contributed by *Caccobius meridionalis* and *Onthophagus fasciatus*. The abundance of nocturnal guild was contributed by *Catharsius molossus*, *Copris repertus*, *Paracopris cribratus* and *Paracopris davisoni* all large tunellers present in greater abundance in monsoon. Their abundance in monsoon compared to other seasons is probably related to their life history, with emergence of new generation or adults from diapause in the rainy season and their tolerance to the wet conditions of monsoon.

5.2.3. Edge

5.2.3.1. Abundance, species richness and diversity

Twenty five species belonging to eight genera namely, *Caccobius*, *Catharsius*, *Copris*, *Ochicanthon*, *Onthophagus*, *Paracopris*, *Sisyphus* and *Tibiodrepanus* and five tribes namely, Coprini, Canthonini, Oniticellini, Onthophagini and Sisyphini were recorded from the edge. As this is the first such study done on the dung beetle assemblage in an ecotone in South Western Ghats there is no available data for comparison.

Edge had similar species richness to agriculture habitat. Reason being the absence of any forest specialist in the region and the dominance of dry habitat preferring, heliophilic species in the region that are adapted to survive in the open edge and agriculture habitat. Presence of synanthropogenic species in the region such as *Caccobius gallinus*, *Onthophagus fasciatus* and *Paracopris davisoni* preferring ruminant herbivore dung and adapted to survive in anthropogenically modified habitats (Sabu 2011) also might have contributed to the similar species richness in agriculture and edge habitat.

Onthophagus pacificus and *O. furcillifer* contributed 43.43% of abundance in edge. These two species dominated the forests of Nelliampathi also. These are dominant forest species in the South Western Ghats region (Sabu 2011). Their dominance in the open degraded forest of the region and in the unshaded edge points toward their ability to survive in the open edge which lacks the canopy covers. High specificity and fidelity of *O. furcillifer* make it the indicator species for edge habitat. Rank abundance plot showed the dominance of two species and a tail of four rare species which were *Onthophagus cavia, O. fasciatus, Paracopris signatus* and *Tibiodrepanus setosus*. Number of rare species was low in edge compared to forest and agriculture habitat. Reason might be that the open, unshaded conditions of the edge was preferred by the dung beetles of the region and the species present in the edge habitat were represented in greater numbers and were not singletons.

Eight endemics to Western Ghats namely, *Caccobius gallinus, Ochicanthon mussardi, Onthophagus amphicoma, O. andrewesi, O. bronzeus, O. vladimiri, Paracopris davisoni* and *Sisyphus araneolus* were reported from the edge habitat. Higher number of endemics in edge compared to forest and agriculture habitat could be due to the presence of species from both the habitat types in the edge.

Dominance of small dung beetles in the edge habitat is linked to the drier conditions in the edge which are not preferred by the larger bodied beetles that dissipate heat slowly (Bartholomew & Henirich 1978) and are vulnerable to over-heating and desiccation in drier habitats (Chown 2001).

5.2.3.2. Functional guild composition

Tunneler guild dominated the edge assemblage as in other habitats of Western Ghats (Sabu 2011). As mentioned earlier superior competitive nature of tunnelers in utilizing the dung resource (Doube 1991; Krell-Westerwalbesloh *et al*. 2004) contributed to their success.

Rollers were the second dominant guild in the edge as in the forest habitat of Nelliampathi. Rollers were represented by only two species, the small rollers *Ochicanthon mussardi* and *Sisyphus araneolus*. Roller species sensitivity to habitat modification is seen in their overall reduced representation. Dweller guild was represented by only one species, *Tibiodrepanus setosus* that was rare. Superior competition from tunnelers and rollers which resulted in low availability of undisturbed dung pads could have led to the low representation of dwellers.

5.2.3.3. Temporal guild composition

Nocturnal guild dominated the assemblage similar to forest habitat. Higher dung resource availability in the night at the end of the feeding day (Gill 1991) could be the reason. Generalist was the second dominant guild. This is probably, because they could utilize the dung resource during the day and night. Diurnal species were the least dominant guild, possibly due to the low availability of dung resource during the day and the utilization of dung by the dominant nocturnal and generalist guild which leaves less amount of dung available to the diurnal species.

5.2.3.4. Seasonality

Dung beetle abundance showed seasonal differences with higher abundance during presummer and monsoon compared to summer. Similar results were observed in forest. High temperatures and dry climatic conditions are detrimental to dung beetle populations (Andresen 2005). High temperature and dry climatic conditions prevailing in summer in the open edge with no canopy could be the reason for their low abundance.

Nine species comprising eight tunnelers and one roller showed significant seasonality. Tunnelers such as *Onthophagus bronzeus, O. laevis, O. pacificus, O. turbatus* and *Paracopris davisoni* showed higher abundance in monsoon season. This suggests their ability to tolerate the heavy rains of the monsoon season. *Onthophagus amphicoma, O. insignicollis* and *Sisyphus araneolus* showed preference for the moderate weather conditions of presummer. Preference of *Onthophagus manipurensis* towards summer showed its capacity to tolerate the hot and dry summer conditions. Twelve species, 11 tunnelers and one roller was aseasonal. They did not show preference towards any particular season.

Nocturnal guild dominated presummer and monsoon season while diurnal guild dominated the summer season. Availability of trophic resource voided by mammals at the end of the day (Gill 1991) could be the reason for the dominance of nocturnal guild. The dominance of diurnal guild in summer may be the result of straying of domestic mammals from the agriculture habitat to edge providing dung during the day in the edge habitat.

5.2.4.1. Comparative study on dung beetle assemblages across a forest-agriculture habitat ecotone with reference to edge effects

Present effort is the first record on community structure of dung beetles across a forest- agriculture habitat ecotone from the moist South Western Ghats. Modern tribes which included Coprini, Gymnopleurini, Onitini, Oniticellini, Onthophagini and Sisyphini dominated the assemblage at Nelliampathi while old world tribe Canthonini was poorly represented in the region. Similar pattern was observed from Thekkady (unpublished) and Ranipuram (unpublished). Above mentioned tribes Coprini, Gymnopleurini, Onitini, Oniticellini, Onthophagini and Sisyphini prefer dung pads to pelleted dung which is the preferred diet of Canthonini (Davis *et al.* 2002; Sabu *et al.* 2011b). Abundance of dung pad preferring tribes at Nelliampathi points to higher abundance of large dung pad producing mammals (elephants and gaur) in the region when compared to pelleted dung producing mammals (Nilgiri Tahr, deer). *Onthophagus* was the most abundant and diverse genus in the three habitats. Similar abundance of *Onthophagus* was observed in Wayanad (Vinod 2009), Thekkady (unpublished) and Ranipuram (unpublished).The dominance of genus *Onthophagus* is the general trend in the Western Ghats region as *Onthophagus* is the most speciose genus with over 2400 extant species and is among the most speciose genera in the animal kingdom (Hanski & Krikken 1991; Emlen *et al.* 2007; Simmons & Ridsdill-Smith 2011).

Disturbed habitats generally have lower number of endemics (Hamer *et al.* 1997), but higher number of endemics was recorded in the open edge and modified agriculture habitat. Similar result was observed from the modified habitats like plantation forests of Borneo (Davis *et al.* 2000). Among the endemic species recorded from Nelliampathi, no forest interior specialist were present and the ones recorded which included *Caccobius gallinus, Liatongus indicus, Ochicanthon mussardi, Onthophagus amphicoma, O. andrewesi, O. bronzeus, O. vladimiri, Paracopris davisoni* and *Sisyphus araneolus* were species adapted to survive in the degraded and open forests of the region (Sabu

2011) and as the present study indicates they are able to tolerate and exist in exposed conditions of edge and man -made agriculture habitats.

Forest and ecotone recorded higher abundance compared to agriculture habitat. Meta-analysis done by Nichols *et al.* (2007) on studies conducted globally on dung beetle abundance in modified habitats also found similar results. Cultivated land often lacks the microhabitat diversity of natural habitats and there are fewer dung types available due to the disappearance of large wild mammals (Nielsen 2007). The main source of dung in agriculture habitat is from domestic cattle. Agriculture habitats in Nelliampathi are relatively small patches amidst vast stretches of plantations and forests and the number of domestic cattle it supports is also very low. This limits the availability of dung resources for the dung beetles which in turn would have affected their abundance.

Diversity of dung beetles in the Nelliampathi region did not vary significantly between habitats. This is in complete contrast to results recorded globally. Studies from Borneo (Davis *et al.* 2000), Neotropics (Avendaño-Mendoza *et al.* 2005), Southeast Asia (Shahabuddin *et al*. 2005), Africa (Nielsen 2007), Wayanad (Vinod 2009) all recorded lower species richness in modified habitats when compared to forests. 15 species were shared between forest, edge and agriculture habitats namely, *Catharsius molossus, Copris repertus, Onthophagus amphicoma, O. andrewesi, O. bronzeus O. ensifer, O. favrei, O furcillifer, O. insignicollis, O. laevis, O. manipurensis, O. pacificus, O. turbatus, Paracopris cribratus, Tibiodrepanus setosus.* Seven species namely, *Caccobius meridionalis, C. ultor, Liatongus indicus, Onitis subopacus, Onthophagus porcus, O. rectecornutus* and *Tibiodrepanus sinicus* were recorded only from the agriculture habitat. Three species namely, *Ochicanthon mussardi, Onthophagus deflexicollis* and *Paracopris signatus* were recorded only from edge. *Caccobius gallinus, Onthophagus fasciatus* and *Paracopris davisoni* were shared between agriculture and edge habitat.

Nelliampathi is a mosaic of forest fragments and agriculture habitats. Arrival of species from the forest that tolerate unshaded environmental conditions and presence of open habitat synanthropogenic species in the edge and agriculture habitat might have contributed to the species richness in the edge and agriculture habitats. The species namely, *Caccobius meridionalis, C. gallinus, C. ultor, Onthophagus fasciatus* and *Paracopris davisoni* which show low abundance in forests and high abundance in agriculture habitat with preference towards ruminant herbivore dung are considered as synanthropogenic species (Sabu 2011). Similar presence of synanthropogenic species were observed in Colombia (Escobar 2004), in guamil patches which are temporarily abandoned cropfields with secondary successions of Gautemala (Avendano-Mendoza *et al*. 2005) and in pastures of Central America (Horgan 2007). Presence of genus *Caccobius* which was well represented in agriculture habitat and not in the forest could be due to their preferential attraction towards herbivore dung (Hanski & Cambefort 1991c).

Caccobius meridionalis and *Onthophagus fasciatus* reported from edge and agriculture habitat of Nelliampathi are some of the prominent dung beetles in the agriculture belts in the Wayanad region. Also they are considered as heliophiles inhabiting open and dry forest habitat with preference towards ruminant herbivore dung (gaur, domestic cattle) (Sabu 2011).

Moreover studies on insects (Holloway *et al.* 1992; Hamer *et al.* 1997; Holloway 1998) and dung beetles (Davis *et al.* 2000; Horgan 2007) have shown that species occurring in disturbed habitats in high densities are species with wide spread geographic distribution and are able to tolerate disturbance. The distribution pattern of *Copris repertus, Onthophagus bronzeus, O. fasciatus, O. furcillifer, O. manipurensis* and *O. Pacificus* which are the major species occurring in agriculture habitat and edge in Nelliampathi showed that they have a widespread distribution in the Indian sub-continent and they are capable of surviving in different kinds of habitats and in different microclimatic conditions (Arrow 1931; Balthasar 1963a, b; Sabu *et al.* 2011a).

Dung beetle diversity in an area is also closely related to mammalian species richness. A large and diverse mammalian fauna is important for the maintenance of a large and diverse dung beetle fauna (Peck & Forsyth 1982; Klein 1989; Hanski & Cambefort 1991d). Although Nelliampathi forests forms a corridor for movement of long ranging species such as tiger, leopard, wild gaur and elephants, fragmentation and modifications drastically reduced the population of these mammals (Sukumar & Easa 2006; Latha & Unnikrishnan 2007; Prabhakaran 2011). Hence species richness of dung beetles was low in forest.

Forest habitat of Nelliampathi showed low evenness compared to agriculture habitat and ecotone. This is in contrast to results obtained from Wayanad where the forest assemblage showed high evenness followed by monoculture plantation and agroecosystem (Vinod 2009). High abundance of *Onthophagus pacificus* and *O. furcillifer* in forest and high number of rare species led to low evenness of forest assemblages in Nelliampathi region. Dominance of a few species is often a characteristic of biotic communities in habitats with higher levels of disturbance when compared to nearby sites with lower levels of disturbance (Feinsinger 2001), and studies with dung beetles have recorded this pattern for several tropical rainforests (Klein 1989; Davis *et al.*2001; Magurran 2004; Scheffler 2005).

Studies done by Didham *et al.* (1998) have shown that generalist species benefit while specialist species are negatively affected by fragmentation. Similar observation was made in Nelliampathi. Majority of species collected were generalists found in the three habitats. Only four species showed strong habitat association. *Onthophagus furcillifer* showed high abundance and strong association to forest habitat in the region. Earlier studies have also shown that it is a prominent dung beetle species in the forests of South Western Ghats (Sabu 2011). Majority of forest species do not move into open habitats because of strong preference for shade and may require shade for reproduction or during specific life-stages (Horgan 2007).

Caccobius meridionalis and *Onthophagus fasciatus* were the dominant species in the agriculture habitat with strong habitat association for the same.

Both the species were found in other forests of moist South Western Ghats (Vinod 2009) and are considered as open forest dwellers with preference for herbivore dung and could easily establish in the open agriculture habitats with bovine dung as the major dung resource (Sabu 2011). *Onthophagus dama* was the dominant species in the agriculture habitat of Wayanad (Vinod 2009) and *Caccobius vulcanus* and *Tiniocellus spinipes* were the dominant species in the semi- urban agriculture habitat in Wayanad (unpublished). Above results suggests that there are regional variations in the dominant species of the agriculture habitats of South Western Ghats region. *Onthophagus amphicoma* showed strong habitat association to edge. This could indicate its preference to open habitats.

Rank abundance plot in all the three habitats showed a steep slope as a result of dominance of two species and a long tail of several rare species. Uneven distribution of species is relatively common in unstable environments and point towards extreme disturbance (Magurran 2004). The rare species present in the present study may also be those that are at the edge of their ranges, are in habitats that are not entirely suitable for them or are transient (Brown *et al.* 1996). Moreover diffusive rarity is also relatively common in small-scale studies (Gaston 1994).

Small beetles dominated the assemblages in the three habitats. This is because large-bodied beetles tend to be more prone to land-use change from natural forest to human dominated land use type (Shahabuddin *et al.* 2005) and also habitat disturbances leading to local extinctions and abundance declines

(Jankielsohn *et al.* 2001; Feer 2008). Furthermore changes in the physiological tolerance to thermal stress, and alterations in the supply of dung resources affects dung beetle body size (Feer 2008). Also cooling rates in dung beetles are inversely related to body mass (Bartholomew & Heinrich 1978) and inability to dissipate excess heat in more open environments may incur severe physiological costs (Chown 2001) in open habitats. Additionally large dung beetles also use a disproportionately larger share of resources (Doube 1990) and therefore may be negatively affected by reductions in resource availability as in disturbed habitats. Small size also has the advantage because it permits the utilization of a greater range of microhabitats and food resources (Feer 2008).

Highest taxonomic diversity and evenness was recorded from agriculture habitat. Dung beetle assemblage in agriculture habitat was represented by four tribes, eight genera and 25 species which were evenly distributed when compared to edge with five tribes, eight genera and 25 species and forest with six tribes, seven genera and 21 species. Overrepresentation of genus *Onthophagus* represented by 15 species (71% of species), underrepresentation of genera *Paracopris* and *Tibiodrepanus* represented by one species each (4.8% of species) and absence of genus *Caccobius* led to low taxonomic evenness and hence distinctness value in forest compared to agriculture habitat with 14 *Onthophagus* species (56% of species), three *Caccobius* species (12% of species) and two species of *Paracopris* and *Tibiodrepanus* (8% of species). Overrepresentation of genus *Onthophagus* decreases the taxonomic distinctness and evenness of the forest assemblage. In agriculture habitat abundance of heliophilic species that prefer cow dung are high which are lower in forests (Sabu 2011). The agriculture habitats of Nelliampathi and the South Western Ghats in general were natural forests earlier and the heliophilic species belonging to *Caccobius* and *Paracopris* genera were present even before the habitat modification. After habitat modifications they became more abundant and dominant in the new open and dry agriculture habitats (Sabu 2011) which led to the increased taxonomic distinctness and evenness values in agriculture habitat.

High specificity and fidelity of *Onthophagus furcillifer* and *O. pacificus* to forest; *O. furcillifer* to edge and *O. fasciatus* to agriculture habitat makes them ideal indicators of respective habitats. Habitat change in forested ecosystems is typically measured in terms of change in the aerial extent of native forest and human land-uses. Such studies do not give information on the consequences of forest land-use change into changes in actual species and populations, without which our understanding of the conservation value of degraded lands will remain grossly inadequate (Gardner *et al.* 2007). So indicator taxa are now used far more frequently to demonstrate the effects of environmental change (such as habitat alteration and fragmentation and climate change) on biotic systems (Gardner *et al.* 2007). Since ecological indicator is a characteristic taxon or assemblage that is sensitive to identified environmental stress factors, demonstrates the effect of these stress factors on biota, and whose response is representative of the response of at least a subset of other taxa present in the habitat (McGeoch 1998) identification of indicator taxa in the habitats of Nelliampathi will help in monitoring the region for subsequent changes and in devising suitable sustainable management practices (Spector & Forsyth 1998). The detector species for the forests were *Copris repertus* and *Paracopris cribratus*; for edge were *Onthophagus bronzeus, O. pacificus* and *Copris repertus* and for agriculture habitat were *Caccobius meridionalis* and *Onthophagus furcillifer*. Monitoring the status of detector species will help in monitoring the direction of change in habitats (McGeogh *et al.* 2002) such as Nelliampathi where leased estates are encroaching into forest lands and modifications of the land for tourism and other unsustainable practices are continually taking place.

High similarity in species composition and abundance pattern existed between forest and ecotone when compared to ecotone and agriculture habitat and forest and agriculture habitat. This suggests that species living in these forests are heliophiles capable of living in the open edge and the encroachment of wild animals into the edge provides abundant and diverse amount of dung resource to the dung beetles living in the edge. *Onthophagus pacificus* contributed to highest dissimilarity between forest and ecotone, *Caccobius meridionalis* contributed to dissimilarity between edge and agriculture habitat and *Onthophagus fasciatus* contributed to highest dissimilarity between forest and agriculture habitat. The above mentioned species were the dominant species in the respective habitats such as *O. pacificus* in forest, *C. meridionalis* in agriculture habitat and *O. fasciatus* in agriculture habitat. Reasons for their dominance in the respective habitat were already discussed. Rarefaction curves for the agriculture habitat and edge reached an asymptote, indicating sampling was satisfactory for these two habitats whereas the curve for the forest indicates further sampling required and more species could be found for the habitat.

Tunnelers dominated the assemblages in all the three habitats. High abundance of tunnelers is typical of dung beetle assemblages in Western Ghats (Sabu *et al*. 2006, 2007; Vinod & Sabu 2007, Vinod 2009) and across the globe (Mittal & Vadhera 1998; Cambefort & Walter 1991; Andresen 2005), and their dominance is attributed to their superior competitive nature (Doube 1991; Krell-Westerwalbesloh *et al*. 2004). Rollers were the second dominant guild in forest and edge. They were absent from agriculture habitat. Rollers are sensitive to land use and many rollers of the forested patches disappear from the open areas (Escobar 1997). Moreover rollers prefer omnivore dung (Hanski & Cambefort 1991d) which is less abundant in agriculture habitat. Low abundance of dwellers in the three habitats compared to the forest and agriculture habitats of Wayanad region of South Western Ghats (Vinod 2009) is due to the low availability of undisturbed dung pats which are essential for their feeding and breeding (Hanski & Cambefort 1991c; Krell *et al*. 2003; Krell-Westerwalbesloh *et al*. 2004). Higher abundance of dwellers in the agriculture habitat of Nelliampathi when compared to forest and edge is linked to the reduced competition they face due to the absence of rollers and lower abundance of tunnelers.

Nocturnal guild dominated the assemblage in forest and edge which could be due to the higher availability of the trophic resource at night. In forests, megaherbivores like elephants, gaur produce dung after the feeding peak and as the largest amount of dung is voided at the end of the feeding period (Tribe 1975) it seems probable that more fresh dung becomes available to nocturnal species than to diurnal species. Agriculture habitat of the Nelliampathi region showed the dominance of diurnal species. Studies in agriculture habitat of the South Western Ghats region also showed dominance of diurnal guild (Sabu 2011). This is related to availability of dung predominantly from grazing domestic mammals during the day and their confinement in sheds at night.

Edge effect

This is the first such study on edge effects on dung beetle assemblages across a forest- agriculture habitat ecotone in the South Western Ghats. Forest and edge showed high overall abundance compared to agriculture habitat. But contrasting results were obtained in studies done on dung beetles across a forest-savanna ecotone of Bolivia (Spector & Ayzama 2003), across forest-cerrado ecotone in Brazil (Duraes *et al.* 2005), across bushland and agriculture habitat in Tanzania (Nielsen 2007), across forest-savanna edge and forest-roadside edge (Feer 2008) and across forest-pasture edges (Diaz *et al.* 2010) where higher abundance was observed in forest and significant decrease in abundance was observed towards edge.

Availability of trophic resource is one the main factor that determines abundance of dung beetles in a habitat. Forest mammals (elephant, gaur, monkey and deer) are constantly infringing into edge in Nelliampathi and providing enough dung resource to sustain the dung beetle assemblage in the edge habitat. This led to the absence of any significant difference in abundance between edge and forest habitat. Microclimate is another factor that affects dung beetle abundance. In the edge it is warmer and drier due to absence of canopy. Such shaded and unshaded conditions of habitats are found to affect dung beetle species as observed by Davis *et al.* (2002, 2003). But dung beetle species of Nelliampathi are heliophiles able to survive in the open degraded forest of the region and able to tolerate the unshaded conditions of the edge. This is another reason for the absence of any difference in abundance in the edge.

Dung beetle diversity did not vary between habitats. Three aspects of mammalian species richness affects dung beetle diversity namely, general abundance of mammals, kinds of mammals present and size of the mammals present in a habitat (Hanski & Cambefort 1991d). Frequent incursions of forest mammals into forest edge must have made all the different sources of dung available in the forest to the edge species and domestic mammals from agriculture habitat may also stray into the edge.

Habitat structure is another factor that can affect dung beetle diversity. It affects local microclimates such as light intensity, temperature and humidity (Botes *et al.* 2006) and may also provide physical barriers to flight (Nealis

1977; Steenkamp & Chown 1996; Davis 2002). But the differences in habitat did not seem to affect dung beetle assemblage in Nelliampathi. Studies have shown that species adapted to exposed forest-gap microsites fared better in disturbed forest and open habitats than stenotopic species confined to closed canopy habitat. This could be due to the very different environmental conditions found in gaps compared to closed forest (Spitzer e*t al.* 1997). The dung beetle species in the forests of South Western Ghats could be classified as shade tolerant umbrophiles and sun loving heliophiles (Sabu 2011). The Nelliampathi region is inhabited by heliophiles tolerant to open forests of the region degraded due to logging and other anthropogenic pressures (Sukumar and Easa 2006; Latha & Unnikrishnan 2007; Prabhakaran 2011). And such heliophilic species are able to survive in the open edge and agriculture habitat. This leads to the nearly similar species richness in the three habitats. Similar observations were made by Davis *et al.* (2002, 2003) in Africa and Horgan (2007) in Central America.

Presence of generalist species in the region as opposed to stenotopic species with narrow habitat preference also lead to the absence of any significant difference in diversity between the forest, edge and agriculture habitat. Similar higher proportion of ubiquitous dung beetle species was found in disturbed forests of Central America (Horgan 2007).

Edge effect is also remnant size-related (Laurance *et al.* 2002). The size of forest fragments determines the presence of forest interior species. The forests in Nelliampathi are forest patches interspersed by plantations and they lack true interior species. They are also open and highly disturbed so no great movement of heliophilic species was noticed into the edge (Davis *et al*. 2000) to cause any serious edge effect as they were present in forest patch and also in the agriculture habitat. Hence no edge effect was observed in the region.

CONCLUSION

Latha Mathews "Systematics and ecology of dung beetles (coleoptra: scarabaeidae: scarabaeinae) in the Nelliampathi region of South Western Ghats" Thesis. Department of Zoology, St. Joseph's College Devagiri , University of Calicut, 2013

Chapter 6

CONCLUSION

Three first reports namely, *Onthophagus deflexicollis, O. manipurensis* and *Tibiodrepanus sinicus* recorded for the South Indian region reveal that similar studies in other high elevation regions in the Western Ghats might disclose new additions to the species lists for the South Indian region. Presence of nine endemics in the Nelliampathi region highlights the importance of this region as a centre of endemism and a region of conservation priority. Low record of old world tribe Canthonini in the present study compared to earlier collections suggests that habitat modification and degeneration in the Nelliampathi region had affected the dung beetle assemblage composition. Checklist prepared provides baseline information on the composition of dung beetle fauna of the Nelliampathi region and will be useful for comparison of dung beetle faunal lists from other regions of the Western Ghats. Pictorial key provided will make identification of dung beetles accurate and easy.

First ecological study on dung beetles across a forest-agriculture habitat ecotone in the South Western Ghats studied the effects of habitat fragmentation and effect of edges on diversity, guild structure, diel periodicity and seasonality of dung beetles across the habitats. High abundance of dung beetles in the forest and ecotone indicate the presence of higher abundance of dung resources. This proves that natural habitats supports higher population of dung beetles when compared to anthropogenic habitats like agriculture field by affecting the abundance of trophic resource.

Tunnelers were the dominant guild in all the habitats at all seasons owing to their superior competitive nature in using the dung resources.

Dominance of diurnal guild in agriculture habitat as opposed to nocturnal guild in ecotone and forest is associated with the availability of dung resource from domesticated mammals during the day in agriculture habitat in contrast to availability of dung from wild mammals in the night in ecotone and forest. Thus habitat modification affected diel periodicity in dung beetles in modified habitats by affecting the time of availability of dung resource.

Dung beetle abundance in forest and edge showed higher abundance in presummer and monsoon seasons while in agriculture habitat higher abundance was observed during summer and monsoon seasons. This is a direct consequence of agricultural practices in the region which affected the seasonal availability of dung resource.

No specific edge effects in abundance or diversity were observed. Severe habitat degradation in the Nelliampathi forests had led to the establishment of synanthropogenic and heliophilic species capable of surviving in modified habitats like agriculture habitat, open edge and degraded forest in the region. Hence no preferred movement of dung beetles towards the open edge from agriculture habitat or forest was observed which led to the absence of any edge effects and decline in habitat specialist in the region.

Higher similarity between the dung beetle assemblages of forest and ecotone was the direct result of heliophilic species colonizing the region and the absence of forest interior specialist. The heliophilic species can survive well in the open and degraded forest and unshaded edge of the region. Uneven distribution of dung beetle species with dominance of few species and presence of several rare species was characteristic of the dung beetle assemblage in the three habitats and this is indicative of the high level of disturbance in the region. Identification of indicator and detector species in the region will help in monitoring the effects of habitat modification in future and in planning sustainable management practices for the region.

Chapter 7

REFERENCES

Abraham S.K., Easa P.S. & Sivaram M. 2006. Status and distribution of Nilgiri Tahr *Hemitragus hylocrius* in Kerala part of Western Ghats. *Zoo's print journal,* 21(9):2379–2385.

Aguilar-Amuchastegui N. & Henebry GM. 2007. Assessing sustainability indicators for tropical forests: Spatio-temporal heterogeneity, logging intensity, and dung beetle communities. *Forest Ecology and Management*, 253(1–3): 56–67.

Ali S. 1999. *Birds of Kerala,* 3rd edition. Kerala Forests and Wildlife Department.

Amézquita S.J., Forsyth A., Lopera A. & Camacho A. 1999. Comparación de la composición y riqueza de especies de escarabajos coprófagos (Coleoptera: Scarabaeidae) en remanentes de bosque de la Orinoquía Colombiana. *Acta Zoológica Mexicana (n.s.)*, 76: 113–126.

Anderson A.B. 1990. Deforestation in Amazonia: dynamics, causes, and alternatives. In: Anderson A.B, editor. *Alternatives to deforestation: steps toward sustainable use of the Amazon rain forest*, 3–23. Columbia University Press.

Andresen E. 2000. *The Role of Dung Beetles in the Regeneration of Rain Forests Plants in Central Amazonia*. Ph.D. Thesis, University of Florida.

Andresen E. 2001. Effect of dung presence, dung amount, and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in Central Amazonia. *Journal of Tropical Ecology,* 17: 61–78.

Andresen E. 2002. Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecological Entomology,* 27: 257–270.

Andresen E. 2003. Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. *Ecography,* 26: 87–97.

Andresen E. 2005. Effects of season and vegetation type on community organization of dung beetles in a tropical dry forest. *Biotropica,* 37: 291–300.

Andresen E. 2007. Dung beetle assemblages in primary forest and disturbed habitats in a tropical dry forest landscape in western Mexico. *Journal of Insect Conservation*, 1–2. Online: DOI 10.1007/s10841-007-9100-y.

Andresen E. & Laurance S. 2007. Possible indirect effects of mammal hunting on dung beetle assemblages in Panama. *Biotropica*, 39: 141–146.

Anduaga S. 2004. Impact of the activity of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) inhabiting pasture land in Durang, Mexico. *Environmental Entomology*, 33: 1306–1312.

Anu A. 2006. *Entomofaunal Dynamics and Biochemistry of Litter Decomposition in an Evergreen Forest with Special Reference to Systematics of Dung Beetles (Coleoptera: Scarabaeinae).* Ph.D. Thesis, University of Calicut.

Arellano L. & Halffter G. 2003. Gamma diversity: derived from and a determinant of alpha diversity and beta diversity. An analysis of three tropical landscapes. *Acta Zoologica Mexicana*, 90: 27–76.

Arellano L., Favila M.E. & Huerta C. 2005. Diversity of dung and carrion beetles in a disturbed Mexican tropical montane cloud forest and on shade coffee plantations. *Biodiversity conservation*, 14: 601–615.

Arellano L., Leon-Cortes J.L. & Halffter G. 2008. Response of dung beetle assemblages to landscape structure in remnant natural and modified habitats in southern Mexico. *Insect Conservation and Diversity*, 1(4): 253–262.

Arrow G.J. 1931. *The Fauna of British India including Ceylon and Burma, Coleoptera: Lamellicornia (Coprinae).* Taylor and Francis. London. 3: pp. i-xii+428.

Avendano-Mendoza C., Moron-Rios A., Cano E.B. & Leon-Cortes J. 2005. Dung beetle community (Coleoptera: Scarabaeidae: Scarabaeinae) in a tropical landscape at the Lachua Region, Guatemala. *Biodiversity conservation*, 14: 801–822.

Baker J., French K. & Whelan R.J. 2002. The edge effect and ecotonal species: Bird communities across a natural edge in southeastern Australia. *Ecology*, 83: 3048–3059.

Balthasar V. 1955. Scarabaeidae der Afghanistan- Expedition (1952-53). J. Klapperichs. *Acta Entomologica Musei Nationalis Pragae*, 30: 409–439.

Balthasar V. 1959. Beitrag zur Kenntnis der Gattung *Onthophagus* Latreille. *Acta Entomologica Musei Nationalis Pragae*, 33: 461–471.

Balthasar V. 1963a. *Monographic der Scarabaeidae und Aphodiidae der Palaearktischen und Orientalischen Region (Coleoptera: Lamellicornia).* Volume 1, Verlag der Tschechoslowakischen Akademie der Wissenschaften. Prag, 391 pp, PI. XXIV

Balthasar V. 1963b. *Monographic der Scarabaeidae und Aphodiidae der Palaearktischen und Orientalischen Region (Coleoptera: Lamellicornia).* Volume 2. Verlag der Tschechoslowakischen Akademie der Wissenschaften. Prag, 627 pp, PI. XVI.

Baraud J. 1992. *Coleopteres Scarabaeoidea: Fauna De France 78*. Publication de la Fèdèration Franáaise des Sociètès de Sciences Naturelles, et de la Societe Linnvenne, 856 pp.

Barragán F., Moreno C.E., Escobar F., Halffter G. & Navarrete D. 2011. Negative Impacts of Human Land Use on Dung Beetle Functional Diversity. *PLoS ONE*, 6(3): e17976.

Bartholomew G.A. & Heinrich B. 1978. Endothermy in African dung beetles during flight, ball making, and ball rolling. *Journal of Experimental Biology*, 73: 65–83.

Bawa K.S., Das A., Krishnaswamy J., Karanth K.U., Kumar N.S. & Rao M. 2007. *Ecosystem profile, Western Ghats and Sri Lanka biodiversity hot spot, Western Ghats region*. Critical Ecosystem Partnership Fund, 95 pp.

Begon M., Harper J.L. & Townsend C.R. 1996. *Ecology, Individuals, Populations and Communities*, 3rd edition. Oxford: Blackwell Science.

Bertone M., Green J., Washburn S., Poore M., Sorenson C. & Watson D.W. 2005. Seasonal activity and species composition of dung beetles (Coleoptera: Scarabaeidae and Geotrupidae) inhabiting cattle pastures in North Carolina. *Annals of Entomological Society of America*. 98(3): 309–321.

Berytenbach W. & Berytenbach G.J. 1986. Seasonal patterns in the dung feeding Scarabaeidae in the southern Cape. *Journal of the Entomological Society of Southern Africa*, 49: 359–366.

Biswas S. 1978a. Studies on Scarab beetles (Coleoptera: Scarabaeidae) of North-East India: A new species and notes on other Indian species of subgenus Strandius, genus *Onthophagus*. *Journal of Bombay Natural History Society*, 75(3): 911–913.

Biswas S. 1978b. Studies on Scarab beetles (Coleoptera: Scarabaeidae) of North- East India Part II: Three new species and two new records from India. *Journal of Bombay Natural History Society*, 76: 339–344.

Biswas S. & Chatterjee S.K. 1985. Insecta: Coleoptera: Scarabaeidae: Coprinae. Fauna of Namdapha Wildlife Sanctuary. *Records of the Zoological Survey of India*, 82(1-4): 147–177.

Biswas S. & Chatterjee S.K. 1986. Scarabaeidae (Coleoptera) of Silent Valley, Kerala, India, with description of three new species. Silent Valley special issue. *Records of the Zoological Survey of India,* 84(1-4): 79–96.

Biswas S. & Mulay S.V. 2001. Insecta: Scarabid (Coleoptera), Fauna of Nilgiri Biosphere Reserve: Fauna of Conservation Area. *Zoological Survey of India*, 11: 129–142.

Biswas S., Mukhopadhyaya P., Saha S.K., Basu C.R., Chatterjee S.K., Chakraborty S.K., Biswas D.N., Halder S.K., Ghosh S.K. & Chakraborty P. 1997. *Coleoptera State Fauna Series, Fauna of Delhi*. Zoological Survey of India, 6: 325–353.

Blackwelder R.E. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies & South America. *Bulletin of the United States National Museum*, 185(2): 189–341.

Bossuyt F., Meegaskumbura M., Beenaerts N., Gower J.D., Pethiyagoda R., Roelants K., Mannaert A., Wilkinson M., Bahir M.M., Arachchi M.K., Peter K.L.N., Schneider J.C., Oommen V.O. & Milinkovitch C.M. 2004. Local endemism within the Western Ghats, Sri Lanka biodiversity hotspot. *Science*, 306: 479–481.

Botes A., McGeoch M.A. & van Rensburg B.J. 2006. Elephant and human-induced changes to dung beetle (Coleoptera: Scarabaeidae) assemblages in the Maputaland Centre of Endemism. *Biological Conservation*, 130: 573–583.

Boucomont A. 1914. Les Coprophages de l'Archipel Malais. *Annales de la Société Entomologique de France*, 83: 238–350.

Bray J.R. & Curtis J.T. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs*, 27: 325–349.

Brown J.M., Abrahamson W.G. & Way P.A. 1996. Mitochondrial DNA phylogeography of host races of the goldenrod ball gallmaker, *Eurosta solidaginis* (Diptera: Tephritidae). *Evolution*, 50: 777–786.

Browne D.J. & Scholtz C.H. 1995. Phylogeny of the families of Scarabaeoidea (Coleoptera) based on characters of the hindwing articulation, hindwing base and wing venation. *Systematic Entomology*, 20: 145–173.

Browne D.J. & Scholtz C.H. 1998. Evolution of the scarab hindwing articulation and wing base: A contribution toward the phylogeny of the Scarabaeidae (Scarabaeoidea: Coleoptera). *Systematic Entomology*, 23: 307–326.

Bustamante-Sánchez M.A., Grez A.A. & Simonetti J.A. 2004. Dung decomposition and associated beetles in a fragmented temperate forest. *Revista Chilena de Historia Natural*, 77: 107–120.

Cambefort Y. 1984. Etude écologique des coléoptères Scarabaeidae de Côte d'Ivoire. *Travaux des Chercheurs de la Station de Lamto*, 3: 1–294.

Cambefort Y. 1985. Les especes orientales du genre *Cleptocaccobius* (Coleoptera: Scarabaeidae). *Revue Française d'Entomologie (N.S.)*, 7(3): 125–130.

Cambefort Y. 1991. Dung beetles in Tropical Savannas. In: Hanski I. & Cambefort Y., editors. *Dung beetle ecology*, 156–178. Princeton University Press.

Cambefort Y. & Hanski I. 1991. Dung beetle population biology. In: Hanski I. & Cambefort Y., editors. *Dung beetle ecology*, 36–50. Princeton University Press.

Cambefort Y. & Walter P. 1991. Dung beetles in Tropical forests in Africa. In: Hanski I. & Cambefort Y., editors. *Dung beetle ecology*, 198–210. Princeton University Press.

Cardillo M., Mace G.M., Jones K.E., Bielby J., Bininda-Emonds O.R.P., Sechrest W., Orme C.D.L. & Purvis A. 2005. Multiple causes of high extinction risk in large mammal species. *Science*, 309: 1239–1241.

Carne P.B. 1956. An ecological study of the pasture scarab *Aphodius howitti* Hope, *Australian Journal of Zoology*, 4: 259–318.

Caveney S., Scholtz C.H. & McIntyre P. 1995. Patterns of daily flight activity in onitine dung beetles (Scarabaeinae: Onitini). *Oecologia*, 103: 444–452.

Champion H.G. & Seth S.K. 1968. *A Revised Survey of the Forest Types of India*. Manager of Publications, 404 pp.

Chandra K. 2000. Inventory of Scarabaeid beetles (Coleoptera) from Madhya Pradesh, India. *Zoo's Print Journal*, 15(11): 359–362.

Chandra K. 2005. Insecta: Coleoptera: Scarabaeidae. Fauna of Western Himalaya. *Zoological Survey of India*, 2: 141–155.

Chandra K. & Ahirwar S.C. 2005. Scarabaeid beetles (Coleoptera) of Kanha Tiger Reserve, Madhya Pradesh. *Zoological Survey of India*, 105(1-2): 147–155.

Chandra K. & Ahirwar S.C. 2007. Insecta: Coleptera: Scarabaeidae. Fauna of Madhya Pradesh (including Chhattisgarh), State Fauna Series. *Zoological Survey of India*, 15(1): 273–300.

Chandra K. & Rajan P.T. 2004. Faunal Diversity of Mount Harriett National Park (South Andaman): Conservation Area series. *Zoological Survey of India*, 17: 142 pp.

Chandra K. & Singh R.K. 2004. On a collection of Scarabaeid beetles (Coleoptera) from Pachmarchi Biosphere Reserve, Madhya Pradesh. *Records of the Zoological Survey of India,* 102(3-4): 43–46.

Chatterjee S.K. & Biswas S. 2000. Insecta: Coleoptera: Scarabaeidae. State Fauna Series 7: Fauna of Tripura. *Zoological Survey of India*, 3: 87–98.

Cheng W. 1999. Rhizosphere feedbacks in elevated CO_2. *Tree Physiology***,** 19: 313–320.

Chown S.L. 2001. Physiological variation in insects: hierarchical levels and implications. *Journal of Insect Physiology*, 47: 649–660.

Chown S.L., Scholtz C.H., Klok C.J., Joubert, F.J. & Coles K.S. 1995. Ecophysiology, range contraction and survival of a geographically restricted African dung beetle (Coleoptera: Scarabaeidae). *Functional Ecology*, 9(1): 30–39.

Clarke K.R. & Gorley R.N. 2001. Primer v5. User manual/tutorial, PRIMER-E, Plymouth UK.

Clarke K.R. & Warwick R.M. 1994. Similarity-based testing for community pattern: the 2-way layout with no replication. *Marine Biology*, 118: 167–176.

Clarke K.R. & Warwick R.M. 1998. A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology*, 35: 523–531.

Clarke K.R. & Warwick R.M. 1999. The taxonomic distinctness measures of biodiversity: weighing of step lengths between hierarchical levels. *Marine Ecology Progress Series*, 184: 21–29.

Clarke K.R. & Warwick R.M. 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine Ecology Progress Series*, 216: 265–278.

Clements F.E. 1916. *Plant succession; an analysis of the development of vegetation*. Carnegie Institution of Washington, Washinton, DC.

Clifford H.T. & Stephenson W. 1975. *An Introduction to Numerical Classification*. Academic Press, 229 pp.

Colwell R.K. & Gotelli N.J. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4: 379–391.

Creutzer C. 1799. *Entomologische Versuche*. Schaumourg, Wien.

Davis A.J. 1999. Species packing in tropical forests: diel flight activity of rainforest dung-feeding beetles (Coleoptera: Aphodidae, Scarabaeidae, Hybosoridae) in Borneo. *Raffles Bulletin of Zoology*, 47: 473–486.

Davis A.J. 2000a. Does reduced- impact logging help to preserve biodiversity in tropical rainforests? A case study from Borneo using dung beetles as indicators. *Environmental Entomology*, 29(3): 467–475.

Davis A.J. 2000b. Species richness of dung-feeding beetles (Coleoptera: Aphodiidae, Scarabaeidae, Hybosoridae) in tropical rainforest at Danum Valley, Sabah, Malaysia. *Coleopterist's Bulletin*, 54: 221–231.

Davis A.J. & Sutton S.L. 1998. The effect of rainforest canopy loss on arboreal dung beetles in Borneo: implications for the measurement of biodiversity in derived tropical ecosystems. *Diversity and Distributions*, 4: 167–173.

Davis A.J., Holloway J.D., Huijbregts H., Kirk-Spriggs A.H. & Sutton S.L. 2001. Dung beetles as indicators of change in the forests of northern Borneo. *Journal of Applied Ecology,* 38: 593–616.

Davis A.J., Huijbregts J., Kirk-Spriggs A.H., Krikken J. & Sutton S.L. 1997. The ecology and behaviour of arboreal dung beetles in Borneo. In: Stork N.E., Adis J. & Didham R., editors. *Canopy Arthropods*, 417–432. Chapman and Hall.

Davis A.J., Huijbregts J. & Krikken J. 2000. The role of local and regional processes in shaping dung beetle communities in tropical forest plantations in Borneo. *Global Ecology and Biogeography*, 9: 281–292.

Davis A.L.V. 1987. Geographical distribution of dung beetles (Coleoptera: Scarabaeidae) and their seasonal activity in south-western Cape

Province. *Journal of the Entomological Society of Southern Africa*, 50: 275–285.

Davis A.L.V. 1996. Habitat associations in a South African, summer rainfall, dung beetle community (Coleoptera: Scarabaeidae, Aphodiidae, Staphylinidae, Histeridae, Hydrophilidae). *Pedobiologia*, 40: 260–280.

Davis A.L.V. 2002. Dung beetle diversity in South Africa: influential factors, conservation status, data inadequacies, and survey design. *African Entomology*, 10: 53–65.

Davis A.L.V. & Philips T.K. 2005. Effect of Deforestation on a Southwest Ghana Dung beetle assemblage (Coleoptera: Scarabaeidae) at the Periphery of Ankasa Conservation Area. *Environmental Entomology*, 34(5): 1081–1088.

Davis A.L.V. & Scholtz C.H. 2001. Historical vs. ecological factors influencing global patterns of scarabaeine dung beetle diversity. *Diversity and Distributions*, 7: 161–174.

Davis A.L.V., Scholtz C.H. & Philips T.K. 2002. Historical biogeography of scarabaeine dung beetles. *Journal of Biogeography*, 29: 1217–1256.

Davis A.L.V., Scholtz C.H., Dooley P.W., Bham N. & Kryger U. 2004. Scarabaeinae dung beetles as indicators of biodiversity, habitat transformation and pest control chemical in agro-ecosystems. *South African Journal of Science*, 100: 415–424.

Davis A.L.V., Van Aarde R.J., Scholtz C.H. & Delport J.H. 2003. Convergence between dung beetle assemblages of a post-mining vegetational chronosequence and unmined dune forest. *Restoration Ecology*, 11(1): 29–42.

Deloya C., Parra-Tabla V. & Delfin-Gonzalez H. 2007. Fauna of Scarabaeidae-Laparosticti and Trogidae (Coleoptera: Scarabaeoidea) associated with Cloud Forest, shaded coffee plantations and transformed communities in Central Veracruz, Mexico. *Neotropical Entomology*, 36(1): 5–21.

Díaz A., Galante E. & Favila M.E. 2010. The effect of the landscape matrix on the distribution of dung and carrion beetles in a fragmented tropical rain forest. *Journal of Insect Science*, 10: 1–81.

Didham R.K. 1997. The influence of edge effects and forest fragmentation on leaf litter invertebrates in Central Amazonia. In: Laurance W.F. & Bierregaard R.O.Jr., editors. *Tropical forest remnants. Ecology, Management and Conservation of fragmented communities*, 55–70. The University Chicago Press.

Didham R.K., Lawton J.H., Hammond P.M. & Eggleton P. 1998. Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. Philosophical Transactions of the Royal Society, London. *Biological Sciences*, 353: 437–451.

Doube B.M. 1983. The habitat preference of some bovine dung beetles (Coleoptera: Scarabaeidae) in Hluhluwe Game Reserve, South Africa. *Bulletin of Entomological Research*, 73: 357–371.

Doube B.M. 1987. Spatial and temporal organization in communities associated with dung pads and carcasses. In: Gee J.H.R. & Giller P.S., editors. *Organization of Communities. Past and Present*, 255–280. Blackwell.

Doube B.M. 1990. A functional classification analysis of the structure of dung beetle assemblages. *Ecolological Entomology*, 15: 371–383.

Doube B.M. 1991. Dung beetles of South Africa. In: Hanski I. & Cambefort Y., editors. *Dung Beetle Ecology*, 133–155. Princeton University Press.

Doube B.M., Macqueen A., Ridsdill-Smith T.J. & Weir T.A. 1991. Native and introduced dung beetles in Australia. In: Hanski I. & Cambefort Y., editors. *Dung Beetle Ecology,* 255–278. Princeton University Press.

Dufrêne M. & Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67: 345–366.

Durães R., Martins W.P. & Vaz-De-Mello F.Z. 2005. Dung Beetle (Coleoptera: Scarabaeidae) Assemblages across a Natural Forest-Cerrado Ecotone in Minas Gerais, Brazil. *Neotropical Entomology*, 34(5): 721–731.

Edwards P.B. 1991. Seasonal activity in the dung of African grazing mammals, and its consequences for coprophagous insects. *Functional Ecology*, 5: 617–628.

Emlen D.J., Lavine L.C. & Ewen-Campen B. 2007. On the origin and evolutionary diversification of beetle horns. *Proceedings of National Academy of Sciences of the United States of America*, 104(1): 8661–8668.

Errouissi F., Jay-Robert P., Lumaret J.P. & Piau O. 2004. Composition and structure of dung beetle (Coleoptera: Aphodiidae, Geotrupidae, Scarabaeidae) assemblages in mountain grasslands of the Southern Alps. *Annals of Entomological Society of America*, 97: 701–709.

Escobar F. 1997. Estudio de la comunidad de coleópteros coprófagos (Scarabaeidae) en un remanente de bosque seco al norte del Tolima, Colombia. *Caldasia*, 19: 419–430.

Escobar F. 2000. Diversidad de colepteros coprofagos (Scarabaeidae: Scarabaeinae) en un mosaico de habitats en la reserva natural Nukak, Guiviare, Colombia. *Acta Zoolologica Mexicana*, 79: 103–121.

Escobar F. 2004. Diversity and composition of dung beetle (Scarabaeinae) assemblages in a heterogeneous Andean landscape. *Tropical Zoology*, 17: 123–136.

Escobar F. & Chacon de Ulloa P. 2000. Distribución especialy temporal en un gradient de sucesión de la fauna de coleopteros coprófagos (Scarabaeinae, Aphodinae) en un bosque tropical montano, Narino-Colombia. *Revista Biología Tropical*, 48(4): 961–975.

Estrada A. & Coates-Estrada R. 1991. Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas, Veracruz, Mexico. *Journal of Tropical Ecology*, 7: 459–474.

Estrada A. & Coates-Estrada R. 2002. Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. *Biodiversity conservation*, 11: 1903–1918.

Estrada A., Anzures A. & Coates-Estrada R. 1999. Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*), and dung beetles at Los Tuxtlas, Mexico. *American Journal of Primatology*, 48: 253–262.

Estrada A., Coates-Estrada R., Anzures A. & Cammarano P. 1998. Dung and carrion beetles in tropical rainy forest fragments and agricultural habitats at Los Tuxtlas, Mexico. *Journal of Tropical Ecology*, 14: 577–593.

Fabricius J.C. 1798. *Supplementurn Entomologiae Systematicae*. Hafniae, 572 pp.

Favila M.E. & Hallfter G. 1997. The use of indicator groups for measuring biodiversity as related to community structure and function. *Acta Zoologica Mexicana*, 72: 1–25.

Feer F. 1999. Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rainforest. *Journal of Tropical Ecology*, 15: 129–142.

Feer F. 2000. Les Coléoptères Coprophages Et Nécrophages (Scarabaeidae S. Str. Et Aphodiidae) De La Forêt De Guyane Française: Composition Spécifique Et Structure Des Peuplements. *Annales de la Société Entomologique de France (Nouvelle série)*, 36: 29–43.

Feer F. 2008. Responses of dung beetle assemblages to characteristics of rain forest edges. *Ecotropica*, 14: 49–62.

Feer F. & Pincebourde S. 2005. Diel flight activity and ecological segregation with in an assemblage of tropical forest dung and carrion beetles. *Journal of Tropical Ecology*, 21: 21–30.

Feinsinger T. 2001. *Designing Field Studies for Biodiversity Conservation.* Island Press, 212 pp.

Fincher G.T., Blume R.R., Hunter J.S. & Beerwinkle K.R. 1986. Seasonal distribution and diel flight activity of dung-feeding scarabs in open and wooded pasture in east-central Texas. *Southwestern Entomological Supplement*, 10: 1–35.

Fincher G.T., Davis R. & Stewart T.B. 1971. Flight activity of coprophagous beetles on a swine pasture. *Annals of Entomological Society of America*, 64: 855–860.

Floate K.D. & Gill B.D. 1998. Seasonal activity of dung beetles (Coleoptera: Scarabaeidae) associated with cattle dung in southern Alberta and their geographic distribution in Canada. *Canadian Entomologist*, 130: 131–151.

Foggo A., Ozanne C.M.P., Speight M.R. & Hambler C. 2001. Edge effects and tropical forest canopy invertebrates. In: Linsenmair K.E., Davis A.J., Fiala B. & Speight M.R., editors. *Tropical Forest Canopies: Ecology & Management,* 347–359. Kluwer Academic Publishers.

Fourcroy A.F.de. 1785. Entomologia parisiensis, sive catalogus insectorum quae in agro parisiensi reperiuntur. Pars secunda, Via et Aedibus Serpentineis, (1): 233–544.

Galante E., Garcı´a-Roma´n M., Barrera I. & Galindo P. 1991. Comparison of spatial distribution patterns of dung-feeding scarabs (Coleoptera: Scarabaeidae, Geotrupidae) in wooded and open pastureland in the Mediterranean "dehesa" area of the Iberian Peninsula. *Environmental Entomology*, 20: 90–97.

Gardner T.A., Barlow J., Parry L.T.W. & Peres C.A., 2007. Predicting the uncertain future of tropical forest species in a data vacuum. *Biotropica*, 39, 25–30.

Gardner T.A., Hernández M.I.M., Barlow J. & Peres C.A. 2008. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *Journal of Applied Ecology,* 45: 883–893.

Gascon C. & Lovejoy T.E. 1998. Ecological impacts of forest fragmentation in central Amazonia. *Zoology*, 101 (4): 273–280.

Gaston K.J. 1994. *Rarity*. London: Chapman & Hall.Gaston K.J., Blackburn T.M., Hammond P.M. and Stork N.E. 1993. Relationships between abundance and body size: where do tourists fit? *Ecological Entomology*, 18: 310–314.

Gill B.D. 1991. Dung beetles in Tropical American Forests. In: Hanski I. & Cambefort Y., editors. *Dung Beetle Ecology,* 211–229. Princeton University Press.

Gillet J.J.E. 1908. Coprides d' Afrique tropical. *Memoires de la Société entomologique de Belgique*, 16: 63–81.

Gillet J.J.E. 1911. Coprophaga Africana. *Annales de la Société entomologique de Belgique*, 55: 308–312.

Gillet J.J.E. 1924. Scarabaeides coprophages de Sumatra. *Annales de la Société entomologique de Belgique*, 64: 102–104.

Gillet J.J.E. 1935. Schwedisch-chinesische wissensch. Expedition nach den nordwestl. Provinzen Chinas. Scarabaeidae. *Arkiv For Zoology*, 27 (3): 1–12.

González-Maya J.F. & Mata-Lorenzen J. 2008. Dung-beetles (Coleoptera: Scarabeidae) from the Zona Protectora Las Tablas, Talamanca, Costa Rica. *Check List*, 4(4): 458–463.

Grange W.B. 1949. *The Way to Game Abundance: with an Explanation of Game Cycles*. Charles Scribner's Sons, 365 pp.

Halffter G. 1991. Historical and ecological factors determining the geographical distribution of beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Folia Entomologica Mexicana*, 82: 195–238.

Halffter G. & Arellano L. 2002. Response of dung beetle diversity to human-induced changes in a tropical landscape. *Biotropica*, 34: 144–154.

Halffter G. & Favila M.E. 1993. The Scarabaeinae (Insecta: Coleoptera) an animal group for analysing, inventorying and monitoring biodiversity in tropical rainforest and modified ecosystems. *Biology International*, 27: 15–21.

Halffter G. & Mathews E.G. 1966. The natural history of dung beetles of the sub family Scarabaeinae (Coleoptera, Scarabaeidae). *Folia Entomologica Mexicana*, 12-14: 1–132.

Halffter G., Favila M.E. & Halffter V. 1992. A comparative study of the structure of the scarab guild in Mexican tropical rain forest and derived ecosystems. *Folia Entomologica Mexicana*, 84: 131–156.

Halffter G., Pineda E., Arellano L. & Escobar F. 2007. The instability of copronecrophagous beetles assemblages (Coleoptera: Scarabaeinae) in a mountainous tropical Landscape of Mexico. *Environmental Entomology*, 36: 1397–1407.

Hamer K.C., Hill J.K., Lace L.A. & Langhan A.M. 1997. Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba, Indonesia. *Journal of Biogeography*, 24: 67–75.

Hanski I. 1983. Distributional ecology and abundance of dung and carrion-feeding beetles (Scarabaeidae) in tropical rain forests in Sarawak, Borneo. *Acta Zoologica Fennica*, 167: 1–45.

Hanski I. 1986. Individual behaviour, population dynamics and community structure of *Aphodius* (Scarabaeidae) in Europe, *Acta Oecologica Oecologia Generalis*, 7: 171–187.

Hanski I. 1989. Dung beetles. In: Lieth H. & Werger M.J.A., editors. *Tropical Rain Forest Ecosystems. Biogeographical and Ecological Studies*, 489–511. Ecosystems of the World 14B.

Hanski I. 1990. Density dependence, regulation and variability in animal populations. *Philosophical Transactions of the Royal Society of London*, B 330: 141–150.

Hanski I. 1991. The dung insect community. In: Hanski I. & Cambefort Y., editors. *Dung Beetle Ecology*, 5–21. Princeton University Press.

Hanski I. & Cambefort Y. 1991a. *Dung beetle ecology*, Princeton University Press, Princeton, xiii: 481 pp.

Hanski I. & Cambefort Y. 1991b. Competition in dung beetles. In: Hanski I. & Cambefort Y., editors. *Dung Beetle Ecology*, 305–329. Princeton University Press.

Hanski I. & Cambefort Y. 1991c. Resource partitioning. In: Hanski I. and Cambefort Y., editors. *Dung Beetle Ecology*, 330–349. Princeton University Press.

Hanski I. & Cambefort Y. 1991d. Species richness. In: Hanski I. and Cambefort Y., editors. *Dung Beetle Ecology*, 350–365. Princeton University Press.

Hanski I. & Krikken J. 1991. Dung beetles in Tropical Forests in South-East Asia. In: Hanski I. & Cambefort Y., editors. *Dung Beetle Ecology*, 179–197. Princeton University Press.

Harris R.J. & Burns B. 2000. Beetle assemblages of kahikatea forest fragments in a pasture-dominated landscape. *New Zealand Journal of Ecology*, 24: 57–68.

Harvey C., Gonzalez J. & Somarriba E. 2006. Dung beetle and terrestrial mammal diversity in forests, indigenous agroforestry systems and plantain monocultures in Talamanca, Costa Rica. *Biodiversity and Conservation*, 15: 555−585.

Heliöla J., Koivula M. & Niemelä J. 2001. Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest-clearcut ecotone. *Conservation Biology*, 15: 370−377.

Hill C.J. 1993. The species composition and seasonality of an assemblage of tropical Australian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Australian Entomologist*, 20: 121−126.

Hill C.J. 1995. Linear strips of rain forest vegetation as potential dispersal corridors for rain forest insects. *Conservation Biology*, 9: 1559–1566.

Hill C.J. 1996. Habitat specificity and food preferences of an assemblage of tropical Australian dung beetles. *Journal of Tropical Ecology*, 12: 449–460.

Hingston R.W.G. 1923. *A Naturalist in Hindustan*. H.F. and G. Witharby, London, 292 pp.

Holloway J.D. 1998. The impact of traditional and modern cultivation practices, including forestry, on Lepidoptera diversity in Malaysia and Indonesia. In: Newbery D.M., Prins H.H.T. & Brown N.D., editors. *Dynamics of Tropical Communities*, 567–597. Blackwell Science.

Holloway J.D., Kirk-Spriggs A.H. & Chey Vun Khen.1992. The response of some rain forest insect groups to logging and conversion to plantation. *Philosophical Transactions of the Royal Society*, B 335: 425–436.

Hope F.W. 1837. *The Coleopterist's Manual*, *Containing the Lamellicorn Insects of Linneus and Fabricius*. Bohn, 125 pp.

Horgan F.G. 2001. Burial of bovine dung by coprophagous beetles (Coleoptera: Scarabaeidae) from horse and cow grazing sites in El Salvador. *European Journal of Soil Biology*, 37: 103–111.

Horgan F.G. 2002. Shady field boundaries and the colonization of dung by coprophagous beetles in Central American pastures. *Agriculture, Ecosystems and Environment*, 92: 25–39.

Horgan F.G. 2007. Dung beetles in pasture landscapes of Central America: proliferation of synanthropogenic species and decline of forest specialists. *Biodiversity and Conservation*, 16: 2149–2165.

Houston W.W.K. & McIntyre P. 1985. The daily onset of flight in the crepuscular dung beetle *Onitis alexis*. *Entomologia Experimentalis et Applicata*, 39: 223–232.

Howden H.F. & Gill B.D. 1987. New species and new records of Panamian and Costa Rican Scarabaeinae (Coleoptera: Scarabaeidae). *Coleopterist's Bulletin*, 41(3): 201–224.

Howden H.F. & Nealis V.G. 1975. Effects of clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). *Biotropica*, 7: 77–83.

Howden H.F. & Young O.P. 1981. Panamerican Scarabaeinae: taxonomy, distribution, and habits (Coleoptera, Scarabaeidae). *Contributions American Entomological Institute*, 18: 1–204.

Howden H.F., Howden A.T. & Storey R.I. 1991. Nocturnal perching of Scarabaeidae dung beetles (Coleoptera, Scarabaeidae) in an Australian tropical rain forest. *Biotropica*, 23: 51–57.

Hurlbert S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, 52: 577–586.

Huston M.A. 1994. *Biological diversity- the coexistence of species on changing landscape*. Cambridge University Press, Cambridge, xix: 681pp.

Hutton S.A. & Giller P.S. 2003. The effects of the intensification of agriculture on northern temperate dung beetle communities. *Journal of Appied Ecology*, 40: 994-1007.

Illiger J.C.W. 1803. Verzeichniss der in Portugall einheimischen Kafer. Erste Lieferung. *Magazine fur Insektenkunde*, 2: 186–258.

Jameson M.L. 1989**.** Diversity of coprophagous Scarabaeidae (Coleoptera) in grazed versus ungrazed sandhills prairie in Western Nebraska. *Transactions of the Nebraska Academy of Sciences*, 17: 29–35.

Jankielsohn A., Scholtz C.H. & Louw S.V. 2001. Effect of Habitat Transformation on Dung Beetle Assemblages: A Comparison between South African Nature Reserve and Neighboring Farms. *Environmental Entomology*, 30(3): 474–483.

Janssens A. 1949. Contribution a l' etude des Coleopteres Lamellicornes. Table synoptique et essai de classification practique des Coleopteres Scarabaeidae. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Entomologie*, 25: 1–30.

Janzen D.H. 1983. Seasonal change in abundance of large nocturnal dung beetles (Scarabaeidae) in a Costa Rican deciduous forest and adjacent horse pasture. *Oikos*, 41: 274–283.

Johnson R.A. & Wichern D.W. 1992. *Applied multivariate statistical analysis*, 3rd edition. Prentice Hall.

Joseph K.J. 1991. SEM study of the stridulatory organs in the giant elephant dung beetle, *Heliocopris dominus* Bates (Scarabaeidae) with observations on the significance of the sound production. *Entomon*, 16: 319–322.

Joseph K.J. 1994. Sexual dimorphism and intra-sex variations in the elephant dung beetle, *Heliocopris dominus* (Coprinae: Scarabaeidae). *Entomon*, 19: 165–168.

Joseph K.J. 1998. Biology and breeding behaviour of the elephant dung beetle, *Heliocopris dominus* Bates (Coprinae: Scarabaeidae). *Entomon*, 23: 325–329.

Joseph K.J. 2003. The life cycle, ecological role and biology of immature stages of *Heliocopris dominus* Bates (Coleoptera: Scarabaeidae: Coprinae). *Entomon*, 28(3): 247–251.

Joy M.S. 1991. *Keralathile Vanyajeevisankethangal (Wild Life Reserves in Kerala)*. State Institute of Languages, Kerala.

Kerala Forests and Wildlife Department, Government of Kerala. 2004. Accessed on March 30, 2009. http://www.keralaforest.gov.in/html/flora/index.htm.

Kingston T.J. 1977. *Natural Manuring by Elephants in the Tsavo Natural Park, Kenya*. Ph.D. Thesis. University of Oxford.

Kirby W. 1828. A description of some coleopterous insects in the collection of the Rev. F.W. Hope, F.L.S. *Journal of Zoology*, 3: 520–525.

Klein B.C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology*, 70: 1715–1725.

Kohlmann B. 1991. Dung beetles in Subtropical North America. In: Hanski I. & Cambefort Y., editors. *Dung Beetle Ecology*, 116–132. Princeton University Press.

Kotze D.J. & Samways M.J. 2001. No general edge effects for invertebrates at Afromontane forest/grassland ecotones. *Biodiversity Conservation*, 10: 443–466.

Krajcik M. 2006. *Checklist of Scarabaeoidea of the World*. 1. Scarabaeinae Animma. X, Supplement, 3: 1–189.

Krell F.T., Krell-Westerwalbesloh S., Weiß I., Eggleton P. & Linsenmair K.E. 2003. Spatial separation of Afrotropical dung beetle guilds: a trade-off between competitive superiority and energetic constraints (Coleoptera: Scarabaeidae). *Ecography*, 26: 210–222.

Krell-Westerwalbesloh S., Krell F.T. & Kelinsenmair E. 2004. Diel separation of Afrotropical dung beetle guilds-avoiding competition and neglecting resources (Coleoptera: Scarabaeoidea). *Journal of Natural History*, 38: 2225–2249.

Krikken J. 2009. Drepanocerine dung beetles: a group overview, with description of new taxa (Coleoptera: Scarabaeidae: Scarabaeinae). *Haroldius*, 4: 3–30.

Larsen T.H. & Forsyth A. 2005. Trap spacing and transect design for dung beetle biodiversity studies. *Biotropica*, 37(2): 322–325.

Latha A. & Unnikrishnan S. 2007. *RBO driven campaign to preserve downstream ecological flows of a Western Ghats river*. Accessed on March 10, 2010. www.riversymposium.com.

Latha M., Cuccodoro G., Sabu T.K. & Vinod K.V. 2011. Taxonomy of the dung beetle genus *Ochicanthon* Vaz-de-Mello (Coleoptera: Scarabaeidae: Scarabaeinae) of the Indian subcontinent, with notes on distribution patterns and flightlessness. *Zootaxa*, 2745: 1–29.

Latreille P.A. 1802. *Histoire naturelle generale et particuliere des crustacees et des insectes*. F. Dufart, Paris, 3: 467 pp.

Latreille P.A. 1807. *Genera Crustaceorum et Insectorum Secundum Ordinem Naturalem in Familias Disposita, Iconibus Exemplisque Plurimis Explicata*. Tome Tertius, 280 pp.

Laurance W.F. 1999. Gaia's lungs: are rainforests inhaling Earth's excess Carbon dioxide? *Natural History*, 96.

Laurance W.F. 2000. Mega-development trends in the Amazon: implications for global change. *Environmental Monitoring and Assessment*, 61: 113–122.

Laurance W.F. & Bierregaard R.O.Jr. 1997. *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, 632 pp.

Laurance W.F. & Yensen E. 1991. Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation*, 55: 77–92.

Laurance W.F., Williamson G.B., Delamonica P., Olivera A., Gascon C., Lovejoy T.E. & Pohl L. 2002. Effects of a severe drought on Amazonian forest fragments and edges. *Journal of Tropical Ecology*, 17: 771–785.

Lawrence J.F. & Newton A.F. 1995. Families and subfamilies of Coleoptera (with selective genera, notes, reference and data on family-group names). In: Pakaluk A.F.J. & Lipiski S.A., editors. *Biology, Phylogeny and Classification of Coleoptera*, 779–1006. Muzeum i Instytut Zoologii PAN.

Leopold A. 1933. *Game Management*. Charles Scribner's Sons, New York, 481 pp.

Linnaeus K. 1758. *Systema naturae per regna tria naturae :secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio X.

Löbl I. & Smetana A. 2006. Catalogue of Palaearctic Coleoptera. *Apollo Books Stenstrup*, 3: 1–690.

Lobo J.M. 2000. Species diversity and composition of dung beetle (Coleoptera: Scarabaeoidea) assemblages in North America. *Canadian Entomologist*, 132: 307–321.

Lobo J.M. 2001. Decline of roller dung beetle (Scarabaeinae) populations in the Iberian Peninsula during the 20th century. *Biological Conservation*, 97: 43–50.

Lobo J.M., Martin P.F. & Veiga C.M. 1988. Las trampas pitfall con cebo, sus posibilidades en el estudio de Scarabaeoidea (Col.). I. Caracteristicas determinantes de su capacidad de captura. *Revue D' Ecologie Et De Biologie Du Sol*, 25: 77–100.

Lobo J.M., Hortal J. & Cabrero-Sañudo F.J. 2006. Regional and local influence of grazing activity on the diversity of a semi-arid dung beetle community. *Diversity Distribution*, 12: 111–123.

Loozada J.N.C. & Lopez F.S. 1997. The dung beetle community from an Atlantic forest fragmentation. *The Revista Brasileira de Entomologia*, 41: 117–121.

Lopera A. 1996. Distribución y diversidad de escarabajos coprófagos (Scarabaeidae: Coleoptera) en tres relictos de bosque altoandino (Cordillera Oriental, Vertiente Occidental, Colombia). *Trabajo de Grado*. Pontificia Universidad Javeriana. Santafé de Bogotá.

Lumaret J.P. 1983. Structure des peuplements de coprophages Scarabaeidae en region mediterraneenne franc aise: Relations entre lesconditions ecologiques et quelques parametres biologiques des especes. *Bulletin de la Societe Entomologique de France*, 88: 481–495.

Lumaret J.P. & Iborra O. 1996. Separation of trophic niches by dung beetles (Coleoptera, Scarabaeoidea) in overlapping habitats. *Pedobiologia*, 40: 392–404.

Lumaret J.P. & Kim J.I. 1989. Les larves du genre *Onthophagus* Latreille, 1802. Les sous genres *Onthophagus*, *Gibbonthophagus*, *Furconthophagus*, *Phanaeomorphus*, et *Parentius* (Coleoptera, Scarabaeidae). *Annales de la Société Entomologique de France (Nouvelle série)*, 25: 235–241.

Lumaret J.P. & Kirk A.A. 1991. South temperate dung beetles. In: Hanski I. & Cambefort Y., editors. *Dung Beetle Ecology*, 97–115. Princeton University Press.

Lumaret J.P. & Stiernet N. 1991. Montane dung beetles. In: Hanski I. & Cambefort Y., editors. *Dung Beetle Ecology*, 242–254. Princeton University Press.

Lumaret J.P., Kadiri N. & Bertrand M. 1992. Changes in resources: consequences for the dynamics of dung beetle communities. *Journal of Applied Ecology*, 29: 349–356.

Magurran A.E. 2004. *Measuring Biological Diversity*. Blackwell Publishing Ltd., 256 pp.

Manilal K.S. 1997. National Parks and Conservation: A case study of Silent Valley. In: Pushpangadan P., Ravi K. & Santhosh V., editors.

Conservation and Economic Evaluation of Biodiversity, 1: 97–101, Oxford & IBH Publishing Co. Pvt. Ltd.

Margules C.R., Pressey R.L. & Williams P.H. 2002. Representing biodiversity: data and procedures for identifying priority areas for conservation. *Journal of Bioscience*, 27(2): 309–326.

Martin-Piera F. 1986. The palearctic species of the subgenus *Parentius* Zunino, 1979 (Coleoptera, Scarabaeidae, Onthophagini). *Bulletin of the Museo Regionale di Scienze Naturali Bollettino (Torino)*, 4: 77–122.

Martin-Piera F. 2000. Familia Scarabaeidae. In: Ramos M.A., *et al.*, editors. *Coleoptera, Scarabaeoidea*, *Fauna Iberica*, 215–446. Museo Nacional de Ciencias Naturales.

Martin-Piera F. & Zunino M. 1983. *Amphionthophagus*, nuovo sotogener e di *Onthophagus* Latr. (Coleoptera, Scarabaeidae). *Bulletin of the Museo Regionale di Scienze Naturali Bollettino (Torino)*, 1: 59–76.

Martin-Piera F. & Zunino M. 1986. Analisi systematica, filogenetica e biogeografica di un gruppo di specie del sottogener e Palaeonthophagus Zunino, 1979 (Coleoptera, Scarabaeidae, genere Onthophagus): II gruppo ovatus. *Bulletin of the Museo Regionale di Scienze Naturali Bollettino (Torino)*, 4: 413–467.

Mathew G. 2004. *Biodiversity Documentation for Kerala*. Part.7: Insects. Kerala Forest Research Iinstitute Handbook No. 17, 281 pp.

Mathew G., Rugmini P. & Sudheendrakumar V.V. 1998. *Insect Biodiversity in Disturbed and Undisturbed Forests in the Kerala Parts of Western Ghats*. Kerala Forest Research Iinstitute research report No. 135, 113 pp.

McAleece N., Lambshead P.J.D. & Paterson P.L.J. 1997. *BiodiversityPro* (Version 2). The Natural History Museum, London.

McGeoch M.A. 1998. The selection, testing & application of terrestrial insects as bioindicators. *Biological Reviews*, 73: 181–201.

McGeoch M.A. & Chown S.L. 1998. Scaling up the value of bioindicators. *Trends in Ecology and Evolution*, 13: 46–47.

McGeoch M.A., van Rensburg B.J. & Botes A. 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. *Journal of Applied Ecology*, 39: 661–672.

Mittal I.C. 1981. Distributional patterns in Scarabaeidae (Coleoptera): A study on north-west India. *Entomologische Blatter*, 77 (1-2): 75–85.

Mittal I.C. 1986. Dung beetles attracted to human faeces. *Entomologische Blatter*, 82(1-2): 55–64.

Mittal I.C. 1993. Natural manuring and soil conditioning by dung beetles. *Tropical Ecology*, 34(2): 150– 159.

Mittal I.C. 2005. Diversity and conservation status of dung beetles (Laparosticti: Scarabaeidae: Coleoptera) in north India. In: Gupta S.R., Matta N.K., Aggarwal A., Kohli R.K. & Chawla A.K., editors. *Ecology and Environmental Management: Issues and Research Needs*, 43–51. National Institute of Ecology.

Mittal I.C. & Bhati R. 1998. Food preferences of some dung beetles (Coleoptera: Scarabaeidae). *Journal of Entomological Research Society*, 22(2): 107–115.

Mittal I.C. & Kakkar N. 2005. Community dynamics of dung beetles (Scarabaeidae) in a semi-arid region at Kurukshetra in northern India. In: Gupta S.R., Matta N.K., Aggarwal A., Kohli R.K. & Chawla A.K., editors. *Ecology and environmental management: issues and research needs*, 15: 53–59. National Institute of Ecology.

Mittal I.C. & Vadhera S. 1998. Succession and community structure in dung beetles (Coleopera: Scarabaeidae) in ageing cattle dung. *Journal of Entomological Research Society*, 22(3): 253–264.

Mittermeier R.A., Robles-Gil P., Hoffmann M., Pilgrim J.D., Brooks T.M., Mittermeier C.G., Lamoreux J.L. & Fonseca G. 2004. *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions.* CEMEX, Mexico City.

Montes de Oca E.T. & Halffter G. 1995. Daily and seasonal activities of a guild of coprophagous, burrowing beetles (Coleoptera: Scarabaeidae: Scarabaeinae) in tropical grasslands. *Tropical Zoology*, 9: 159–180.

Montreuil O. 1998. Analyse phylogenetique et paraphylie des Coprini et Dichotomiini (Coleoptera: Scarabaeidae). Scenario biogeographique. *Annales de la Société Entomologique de France (Nouvelle série)*, 34: 135–148.

Morelli E., Gonzalez-Vainer P. & Baz A. 2002. Coprophagous Beetles (Coleoptera: Scarabaeoidea) in Uruguayan Prairies: Abundance, Diversity and Seasonal Occurrence. *Studies on Neotropical Fauna and Environment*, 37(1): 53–57.

Murcia C. 1995. Edge effects in fragmented forests: Implications for conservation. *Tree*, 10: 58–62.

Myers N. 2003. Biodiversity hotspots revisited. *Bioscience*, 53: 916–917.

Nair S.C. 1991. *The Southern Western Ghats- a biodiversity conservation plan.* Indian National Trust for Art and Cultural Heritage, New Delhi, 92 pp.

Nair V.G. 2006. *Impact of Western Ghats Orography on the weather and climate over southern peninsular India- A mesoscale modeling study*. Ph.D. Thesis, Cochin University of Science and Technology.

Nakane T. & Shirahata K. 1957. A list of coprophagous Lamellicornia collected from Shansi, North China. *Scientific reports of the Saikyo University*, 2: 229–232.

Nakane T. & Tsukamoto K. 1956. On the Scarabaeidae of Japan III. (Subfamily Scaraabeinae). *Entomological Review of Japan*, 7(1): 23–27.

Navarrete D. & Halffter G. 2008. Dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) diversity in continuous forest, forest fragments and cattle pastures in a landscape of Chiapas, Mexico: the effects of anthropogenic changes. *Biodiversity Conservation*, 17: 2869–2898.

Nealis V.G. 1977. Habitat associations and community analysis of South Texas dung beetles (Coleoptera: Scarabaeinae). *Canadian Journal of Zoology*, 55: 138–147.

Newton P.N. & Malcolm J.C. 1985. Dung and dung beetles in Kanha Tiger Reserve, Central Indian highlands. *Journal of the Bombay Natural History Society*, 85: 218–220.

Nichols E., Larsen T., Spector S., Davis A.L. & Escobar F. 2007. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. *Biological Conservation*, 137: 1–19.

Nielsen S.T. 2007. Deforestation and biodiversity: effects of bushland cultivation on dung beeles in semi-arid Tanzania. *Biodiversity and Conservation*, 16: 2753–2768.

Noss R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, 4: 355–364.

Novotny V. & Basset Y. 2000. Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos*, 89: 564–572.

Nummelin M. & Hanski I. 1989. Dung beetles of the Kibale forest, Uganda: a comparison between virgin and managed forests. *Journal of Tropical Ecology*, 5: 349–352.

Nyeko P. 2009. Dung beetle assemblages and seasonality in primary forest and forest fragments on agricultural landscapes in Budongo, Uganda. *Biotropica*, 41(4): 476–484.

Odum E.P. 1971. *Fundamentals in ecology*, 3rd edition. Saunders.

Oppenheiner J.R. 1977. Ecology of dung beetles (Scarabaeidae: Coprinae) in two villages of West Bengal. *Records of the Zoological Survey of India*, 72: 389–398.

Orris J.B. 2005. Megastat version 10.0. Butler University, College of Business Administration, 4600 Sunset Ave, Indianapolis. Distributed by McGraw-Hill. Available online: http://www.mhhe.com/support.

Osberg D.C., Doube B.M. & Hanrahani S.A. 1994. Habitat specificity in African dung beetles: the effect of soil type on the survival of dung beetle immatures (Coleoptera Scarabaeidae). *Tropical Zoology*, 7: 1–10.

Owen-Smith, R.N. 1988. *Megaherbivores-The Influence of Very Large Body Size on Ecology*. Cambridge University Press, 369 pp.

Paarmann W. & Stork N.E. 1987. Seasonality of ground beetles (Coleoptera: carabidae) in the rain forests of N. Sulawesi. (Indonesia). *Insect Science and its Applications*, 8: 483–487.

Palestrini C. 1985. Note sistematiche e zoogeografiche su lun sotogener e indoafricano di Onthophagus (Coleoptera, Scaraboidea: Onthophagini). *Bollettino del Museo Regionale di Scienze Naturali - Torino*, 3: 29–52.

Pascal J.P. 1991. Floristic composition and distribution of evergreen forests in the Western Ghats, India. *Palaeobotanist*, 39(1): 110–126.

Paschalidis K.M. 1974. *The genus Sisyphus Latr. (Coleoptera, Scarabaeidae) in Southern Africa*. M.Sc. Dissertation, Rhodes University.

Paulian R. 1938. Expedition to south west Arabia (1937-1338). Coleoptera: Scarabaeidae: Troginae, Geotrupinae, Dynamopinae, Hybosorinae, Coprinae, Aphodiinae. *British Museum*, 1(12): 141–155.

Paulian R. 1945. Coléoptères Scarabéides de l'Indochine. *Faune de l'Empire Français*, 3: 1–225.

Paulian R. 1980. Coléoptères Scarabaeidae canthoninae d'Inde du sud revue suisse de zoologie. *Geneve*, 87(1): 57–66.

Paulian R. 1983. Sur quelques coléoptères Scarabaeoidea de la region Orientale. *Revue Suisse de Zoologie*, 90: 615–622.

Pearson D.L. & Cassola F. 1992. World-wide species richness patterns of Tiger beetles (Coleoptera: Cicindelidae): Indicator taxon for biodiversity and conservation studies. *Conservation Biology*, 6: 376–391.

Pearson D.L. & Ghorpade K. 1989. Geographical distribution and ecological history of tiger beetles (Coleoptera: Cicindelidae) of the Indian subcontinent. *Journal of Biogeography*, 16: 333–344.

Peck S.B. & Forsyth A. 1982. Composition, structure, and competitive behaviour in a guild of Ecuadorian rain forest dung beetles (Coleoptera, Scarabaeidae). *Canadian Journal of Zoology*, 60: 1624–1634.

Peringuey L. 1900. Descriptive catalogue of the Coleoptera of the South Africa (Lucanidae and Scarabaeidae). *Transactions of the South African Philosophical Society*, 12: 1–563.

Philips K., Pretorius E. & Scholtz C.H. 2004. A phylogenetic analysis of dung beetles (Scarabaeinae: Scarabaeidae): unrolling an evolutionary history. *Invertebrate Systematics*, 18: 53–88.

Pineda E. & Halffter G. 2004. Species diversity and habitat fragmentation: frogs in a tropical landscape in Mexico. *Biological Conservation*, 117: 499–508.

Pineda E., Moreno C., Escobar F. & Halffter G. 2005. Frog, Bat and Dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. *Conservation Biology*, 19 (2): 400–410.

Prabhakaran G. 2011. 27 Nelliampathi estates broke rules, says report. *The Hindu*, July 15.

Quintero I. & Halffter G. 2009. Temporal changes in a community of dung beetles (Insecta: Coleoptera: Scarabaeinae) resulting from the modification and fragmentation of tropical rain forest. *Acta Zoológica Mexicana (nueva serie)*, 25: 625–649.

Quintero I. & Roslin T. 2005. Rapid recovery of dung beetle communities following habitat fragmentation in central Amazonia. *Ecology*, 86(12): 3303–3311.

Rajan P.D. 2006. Insecta: Coleoptera: Scarabaeoidea: Scarabaeidae (Dung beetles), fauna of Biligiri Rangaswamy temple wildlife sanctuary, conservation area. *Zoological Survey of India*, 27: 91–135.

Ratcliffe B.C. 1991. The scarab beetles of Nebraska. *Bulletin of the University of Nebraska State Museum*, 12: 1–333.

Reitter E. 1892. Bestimmungs-tabelle der Lucaniden und coprophagen Lamellicornien des palaearctischen Faunengebietes. *Verhandlungen des naturforschenden Vereines in Brünn*, 30: 141–262.

Ridsdill-Smith T.J. & Hall G.P. 1984a. Beetles and mites attracted to fresh cattle dung in south-western Australian pastures. *CSIRO Australia Division of Entomology Report*, 34: 1–29.

Ridsdill Smith T.J. & Hall G.P. 1984b. Seasonal patterns of adult dung beetle activity in south-western Australia. *Proceedings of the 4th International Conference on Mediterranean Ecosystems*, 139–140. The Botany Department, University of Western Australia.

Risser P.G. 1995. The status of the science examining ecotones. *Bio Science*, 45: 318–325.

Rosenstock S.S. 1998. Influence of Gambel Oak on breeding birds in ponderosa pine forests of northern Arizona. *Condor*, 100: 485–492.

Rosenzweig M.L. 1995. *Species Diversity in Space and Time*. Cambridge University Press, 460 pp.

Roslin T. & Koivunen A. 2001. Distribution and abundance of dung beetles in fragmented landscapes. *Oecologia*, 127: 69–77.

Rougon D. & Rougon C. 1991. Dung beetles of the Sahel region. In: Hanski I. & Cambefort Y., editors. *Dung Beetle Ecology*, 230–241. Princeton University Press.

Sabu T.K. 2011. *Guild structure, taxonomic diversity and biosystematics of dung beetles (Coleoptera: Scarabaeinae) in the agriculture and forest* *habitats of south Western Ghats*. Project report submitted to University Grant Commission, India.

Sabu T.K. & Vinod K.V. 2005. Comparative assessment of the guild structure and taxonomic diversity of two beetle (Coleoptera: Scarabaeinae) assemblages in the Wayanad region of Western Ghats. In: Mary R., editor. *Proceedings of the National Conference safe environment for the future generations*, 47–52. Dept. of Zoology, Auxilium College.

Sabu T.K., Vinod K.V. & Vineesh P.J. 2006. Guild structure, diversity and succession of dung beetles associated with Indian elephant dung in South Western Ghats forests. *Journal of Insect Science*, 6: 17.

Sabu T.K., Vinod K.V. & Vineesh P.J. 2007. Succession of dung beetles (Scarabaeinae: Coleoptera) in the dung pats of gaur, *Bos gaurus* H. Smith (Artiodactyla: Bovidae), from the moist deciduous forests of southern Western Ghats. *Biosystematica*, 1(1): 59–69.

Sabu T.K., Nithya S. & Vinod K.V. 2011a. Faunal survey, endemism and possible species loss of Scarabaeinae (Coleoptera: Scarabaeidae) in the western slopes of the moist South Western Ghats, South India. *Zootaxa*, 2830: 29–38.

Sabu T.K., Vinod K.V., Latha M., Nithya S. & Boby J. 2011b. Cloud forest dung beetles (Coleoptera: Scarabaeinae) in the Western Ghats, a global biodiversity hotspot in southwestern India. *Tropical Conservation Science*, 4(1): 12–24.

Sachs L. 1992. *Angewandte Statistik*. Springer, Berlin, Heidelberg.

Saunders D.A., Hobbs R.J. & Margules C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, 5:18–32.

Scheffler P.Y. 2002. *Dung Beetle (Coleoptera: Scarabaeidae) Ecology in the Intact and Modified Landscape of Eastern Amazonia.* Ph.D. Thesis. Pennsylvania State University.

Scheffler P.Y. 2005. Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. *Journal of Tropical Ecology*, 21: 9–19.

Schelhas J. & Greenberg R.S. 1996. *Forest patches in tropical landscapes.* Island Press, 463 pp.

Schoener T.W. 1974. Resource partitioning in ecological communities. *Science*, 185: 27–38.

Schoolmeesters P. 2011. *World Scarabaeidae database, species 2000 & it is Catalogue of Life: 2012 Annual Checklist.* Accessed on 1, December 2012. www.datascaraebaeoidea.net/Index.html.

Schoolmeesters P. & Thomas S.K. 2006. A new *Onthophagus* species from Kerala, India. *Phegea*, 34(2): 73–75.

Serville J.G.A. 1825. In encyclopedie methodique. *Entomologie*, 10: 1–344.

Sewak R. 1985. Male genitalia of some species of *Catharsius* Hope (Coleoptera: Scarabaeidae) and its taxonomic importance. *Journal of Animal Morphology and Physiology*, 32(1–2): 269–271.

Sewak R. 1986. Male genitalia of Indian *Onthophagus* Latr. (Coleoptera: Scarabaeidae) and its taxonomic importance. *Journal of Animal Morphology and Physiology*, 33(1-2): 135–140.

Sewak R. 1988. Male genitalia of Indian *Oniticellus serville* (Coleoptera: Scarabaeidae) and its taxonomic importance. *Journal of Animal Morphology and Physiology*, 35(2): 165–168.

Sewak R. 2004. Insecta: Coleoptera: Scarabeidae: Coprinae (dung beetles). Fauna of Gujarat, state fauna series. *Zoological Survey of India*, 8: 105–125.

Sewak R. 2006. Insecta: Coleoptera: Scarabaeidae: Coprinae (dung beetles). Fauna of Arunal Pradesh, state fauna series. *Zoological Survey of India*, 13(2): 191–224.

Sewak R. & Yadva V.K. 1991. Dung beetles (Coleoptera: Scarabaeidae: Coprinae) from five districts of western Uttar Pradesh. *Oikoassay*, 8: 1–2.

Shahabuddin. 2010. Diversity and community structure of dung beetles (Coleoptera: Scarabaeidae) across a habitat disturbance gradient in Lore Lindu National Park, Central Sulawesi. *Biodiversitas*, 11(1): 29–33.

Shahabuddin. 2011. Effect of land use change on ecosystem function of dung beetles: Experimental evidence from Wallacea Region in Sulawesi, Indonesia. *Biodiversitas*, 12(3): 177–181.

Shahabuddin, Schulze C.H. & Tscharntke T. 2005. Changes of dung beetle communities from rainforests towards agroforestry systems and annual cultures in Sulawesi (Indonesia). *Biodiversity conservation*, 14: 863–877.

Shannon C.E. & Weaver W. 1949. *The Mathematical Theory of Communication*. University of Illinois Press, 117 pp.

Simmons L.W. & Ridsdill-Smith T.J. 2011. *Reproductive competition and its impact on the Evolution and Ecology of dung beetles*. Blackwell Publishing Ltd., 347 pp.

Simpson E.H. 1949. Measurement of diversity. *Nature*, 163:688.

Skole D. & Tucker C.J. 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science*, 260: 1905–1910.

Smith A.B.T. 2003. Checklist of the Scarabaeoidea of the Nearctic Realm. *Papers in Entomology*, *Paper3*. University of Nebraska, 74 pp.

Smith D. 2004. Dung beetles- Controlling parasites of cattle. Accessed on 08 May, 2010, http://www.dpi.qld.gov.au/beef/13127.html.

Sowig P. & Wassmer T. 1994. Resource partitioning in coprophagous beetles from sheep dung: phenology and microhabitat preferences. *Zoologische Jahrbuecher Systematik,* 121: 171–192.

Spector S. & Ayzama S. 2003. Rapid turnover and edge effects in dung beetle assemblages (Scarabaeidae) at a Bolivian Neotropical forest–Savanna Ecotone. *Biotropica*, 35(3): 394–404.

Spector S. & Forsyth A.B. 1998. Indicator taxa for biodiversity assessment in the vanishing tropics. In: Mace G., Balmford A. & Ginsberg R., editors.

Conservation in a Changing World, 181–209. Cambridge University Press.

Spitzer K., Jaros J., Havelka J. & Leps J. 1997. Effect of small-scale disturbance on butterfly communities of an indochinese montane rainforest. *Biological Conservation*, 80: 9–15.

Steenkamp H.E. & Chown S.L. 1996. Influence of dense stands of an exotic tree, *Prosopis glandulosa* Benson, on a savanna dung beetle (Coleoptera: Scarabaeinae) assemblage in southern Africa. *Biological Conservation*, 78: 305–311.

Sukumar R. & Easa P.S. 2006. Elephant conservation in south India: issues and recommendations. *Gajah*, 25: 71–86.

Tarasov I.S. 2010. Seven new synonyms within the genus *Onthophagus* (Coleoptera: Scarabaeidae) from the Oriental Region. *Zootaxa*, 2566: 45–48.

Thomson C.G. 1863. *Skandinaviens Coleoptera. Synoptisk bearbetade*, Vol. 5. Tryckt uti Berlingska Boktryckeriet, Lund, 340 pp.

Tribe G.D. 1975. Pheromone release by dung beetles (Coleoptera: Scarabaeidae). *South African Journal of Science*, 71: 277–278.

Tyndale-Biscoe M. 1994. Dung burial by native and introduced dung beetles (Scarabaeidae). *Australian Journal of Agricultural Research*, 45: 1799–1808.

Valencia G., Alonso A., Dallmeier F. & Campbell P. 2001. Diversity and trophic relationships of dung beetles of the lower Urubamba region, Peru. *Urubamba: The Biodiversity of a Peruvian Rainforest*, 7: 121–128.

van Rensburg B.J., McGeoch M.A., Chown S.L. & van Jaarsveld A.S. 1999. Conservation of heterogeneity among dung beetles in the Maputaland centre of endemism, South Africa. *Biological Conservation*, 7: 945–965.

Vane-Wright R.I. 1996. Identifying priorities for the conservation of Biodiversity: systematic biological criteria within a socio-political framework. In Gaston K.J., editor. *Biodiversity: a Biology of Numbers and Difference*, 309–344. Blackwell.

Vane-Wright R.I., Humphries C.J. & Williams P.H. 1991. What to protect? Systematics and the agony of choice. *Biological Conservation*, 55: 235–254.

Vaz-de-Mello F.Z. 2003. *Ochicanthon*, a new name for *Phacosoma* Boucomont (Coleoptera, Scarabaeidae), preoccupied with *Phacosoma* Jukes-Browne (Mollusca). *Coleopterist's Bulletin*, 57: 25–26.

Veenakumari K. & Veeresh G.K. 1996a. Dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) fauna of Banglore, Karnataka. *Journal of the Bombay Natural History Society*, 94: 171–173.

Veenakumari K. & Veeresh G.K. 1996b. Notes on the feeding and breeding behaviour of *Gymnopleurus gemmatus* Harold and *Gymnopleurus miliaris* (Fabricius) (Coleoptera: Scarabaeidae). *Journal of the Bombay Natural History Society*, 93: 13–19.

Veenakumari K. & Veeresh G.K. 1996c. Some aspects of the reproductive biology of *Onthophagus gazella* (F.) and *Onthophagus rectecornutus* Lansb. (Coleoptera: Scarabaeidae). *Journal of the Bombay Natural History Society*, 93: 250–256.

Veenakumari K. & Veeresh G.K. 1997. Subsociality in dung beetles of *Copris repertus* Walker and *Copris indicus* Gill (Coleoptera: Scarabaeidae). *Journal of the Bombay Natural History Society*, 94: 530–535.

Veiga C.M., Lobo J.M. & Martin-Piera F. 1989. Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades de Scarabaeoidea (Col.). II. Analisis de efectividad. *Revue D' Ecologie Et De Biologie Du Sol*, 26: 91–109.

Vernes K., Pope L.C., Hill C.J. & Barlocher F. 2005. Seasonality, dung specificity and competition in dung beetle assemblages in the Australian Wet Tropics, north-eastern Australia. *Journal of Tropical Ecology*, 21: 1–8.

Vinod K.V. 2009. *Studies on the Systematics and Distribution of Dung Beetles (Scarabaeinae: Coleoptera) in the Forests and Agricultural Fields of Wayanad*. Ph.D. Thesis, Forest Research Institute University.

Vinod K.V. & Sabu T.K. 2007. Species composition and community structure of dung beetles attracted to dung of gaur and elephant in the moist forests of South Western Ghats. *Journal of Insect Science*, 7: 1–56.

Vitousek P.M. 1994. Beyond global warming: ecology and global change. *Ecology*, 75: 1861–1876.

Vulinec K. 2000. Dung beetles (Coleoptera: Scarabeiadae), monkeys and conservation in Amazonia. *Florida Entomologist*, 83: 229–241.

Vulinec K., Lambert J. & Mellow D.J. 2006. Primate and dung beetle communities in secondary growth rainforests: Implications for conservation of seed dispersal systems. *International Journal of Primatology*, 27: 855–879.

Waage J.K. & Best R.C. 1985. Arthropod associates of Sloths. In: Montgomery G.G., editor. *The Evolution and Ecology of Armadillos, Sloths and Vermi linguas*, 319–322. Smithsonian Institution.

Walter P. 1978. *Recherches Ecologiques et Biologiques sur les Scarabéides Coprophages d'une Savane du Zaïre*. Thèse Docteur d'État, Université des Sciences et Techniques du Languedoc.

Walter P. 1985. Diurnal and nocturnal flight activity of Scarabaeine coprophages in tropical Africa. *Revue internationale de géologie, de géographie et d'écologie tropicales*, 9: 67–87.

Warwick R.M. & Clarke K.R. 2001. Practical measures of marine biodiversity based on related of species. *Oceanography and marine biology- An Annual Review*, 39: 207–231.

Warwick R.M., Ashman C.M., Brown A.R., Clarke K.R., Dowell B., Hart B., Lewis R.E., Shillabeer N., Somerfield P.J. & Tapp J.F. 2002. Inter-annual changes in the biodiversity and community structure of the macrobenthos in Tees bay and Tees estuary, UK, associated with local and regional environmental events. *Marine ecology progress series*, 234: 1–13.

Webb N.R. 1989. Studies on the invertebrate fauna of fragmented heathland in Dorset, UK, and the implications for conservation. *Biological Conservation*, 47: 153–165.

Webb N.R., Clarke R.T. & Nicholas J.T. 1984. Invertebrate diversity on fragmented Calluna-heathland: effects of surrounding vegetation. *Journal of Biogeography*, 11: 41–46.

Weber F. 1801. *Observationes Entomologicae*, *Continentes Novorum Quae Condidit Generum Characteres*, *et Nuper Detectarum Specierum Descriptiones*. Impensis Bibliopolii Academici Novi, 116 pp.

Whitmore T.C. 1990. *An Introduction to Tropical Rain Forest*. Clarendon Press, 12: 226 pp.

Whittaker R.H. 1965. Dominance and diversity in land plant communities. *Science*, 147: 250–260.

Wiens J.A. 1997. *Metapopulation dynamics and landscape ecology*. Hanski I.A. & Gilpin M.E., editors, 43–62. Academic Press, San Diego, CA.

Wilcove D.S., McLellan C.H. & Dobson A.P. 1986. Habitat fragmentation in the temperate zone. In: Soulé M., editor. *Conservation Biology: the Science of Scarcity and Diversity*, 237–256. Sinauer.

Williams P.H. 1996. Biodiversity value and taxonomic relatedness. In: Hochberg M.E., Clobert J. & Barbault R., editors. *Aspects of the Genesis* *and Maintenance of Biological Diversity*, 261–277. Oxford University Press.

Woodruff R.E. 1973. The scarab beetles of Florida (Coleoptera: Scarabaeidae). Part 1. The Laparosticti (subfamilies Scarabaeinae, Aphodiinae, Hybosorinae, Ochodaeinae, Geotrupinae, Acanthocerinae). Arthropods of Florida and Neighboring Land Areas. *Florida Department* of *Agriculture and Consumer Services*, 8: 1–22.

Wright K.L. 1997. *An Examination of the Commensal Interaction between the Australian Native Bung Beetle, Onthophagus peramelinus and the Rufous Bettong, Aepyprymnus rufescens*. B.Sc. Dissertation. James Cook University.

WWF 2008. South Western Ghats Landscape. Accessed on May7, 2009. http://www.wwfindia.org/about_wwf/what_we_do/forests/western_ghats/.

Zunino M. 1979. Gruppi artificiali e gruppi naturali negli *Onthophagus* (Coleoptera, Scaraboidea). *Bollettino del Museo Regionale di Scienze Naturali - Torino*, 1: 1–18.

Zunino M. 1981. Insects of Saudi Arabia. Coleoptera: Family Scarabaeidae, Tribe Onthophagini. *Fauna of Saudi Arabia*, 3: 408–416.

Zunino M. 1983. Essai pre´liminaire sur l'e´volution des armatures genitales des Scarabaeinae, par rapport a` la taxonomie du groupe et a` l'e´volution du comportement de nidification (Col. Scarabaeidae). *Bulletin de la Societe Entomologique de France*, 88: 531–542.

Zunino M. 1984. Analisi sistematica e zoogeografica della sottofamiglia Taurocerastinae Germain (Coleoptera, Scarabaeoidea: Geotrupidae). *Bollettino del Museo Regionale di Scienze Naturali- Torino*, 2: 445–464.

LIST OF PLATES

Plate 1: Map showing (A) The Western Ghats and (B) Study region of Nelliampathi.

Plate 2: Study sites at Nelliampathi (A) Forest habitat (B) Ecotone and (C) Agriculture habitat.

Plate 3: Dung Beetle species- First report from South India (A) *Onthophagus deflexicollis* (B) *O. manipurensis* and (C) *Tibiodrepanus sinicus*. Endemics to the Western Ghats (A) *Caccobius gallinus* (B) *Liatongus indicus* (C) *Ochicanthon mussardi.*

Plate 4: Dung Beetle species-Endemics to the Western Ghats (contd.) (G) *Onthophagus amphicoma,* (H) *O. andrewesi,* (I) *O. bronzeus,* (J) *O. vladimiri,* (K) *Paracopris davisoni* and (L) *Sisyphus araneolus.*

Plate 5: Dominant dung beetle species associated with Forest and Ecotone (A) *Onthophagus pacificus,* (B) *O. furcillifer*; Agriculture habitat (C) *Caccobius meridionalis,* (D) *Onthophagus fasciatus*.

Plate 6: Indicator species associated with Forest (A) *Onthophagus pacificus*; Forest and Ecotone (B) *Onthophagus furcillifer* and Agriculture habitat(C) *Onthophagus fasciatus.*

LIST OF FIGURES

Figure 1: Overall rank abundance plot of dung beetles in a semi-evergreen forest habitat at Nelliampathi during 2007-08 study period.

Figure 2: Rank abundance plot of dung beetles in a semi-evergreen forest habitat at Nelliampathi during 2007-08 study period (A- Presummer, B- Summer, C- Monsoon).

Figure 3: Functional guild composition and abundance of dung beetles in a semi-evergreen forest habitat at Nelliampathi during 2007-08 study period (A- Overall, B- Presummer, C- Summer, D- Monsoon)

Figure 4: Temporal guild composition and abundance of dung beetles in a semi-evergreen forest habitat at Nelliampathi during 2007-08 study period (A- Overall, B- Presummer, C- Summer, D- Monsoon).

Figure 5: Seasonal abundance of dung beetles in a semi-evergreen forest habitat at Nelliampathi during 2007-2008 study period.

Figure 6: Overall rank abundance plot of dung beetles in an agriculture habitat at Nelliampathi during 2007-08 study period.

Figure 7: Rank abundance plot of dung beetles in an agriculture habitat at Nelliampathi during 2007-08 study period (A- Presummer, B- Summer, C- Monsoon).

Figure 8: Functional guild composition and abundance of dung beetles in an agriculture habitat at Nelliampathi during 2007-08 study period (A- Overall, B- Presummer, C- Summer, D- Monsoon).

Figure 9: Temporal guild composition and abundance of dung beetles in an agriculture habitat at Nelliampathi during 2007-08 study period (A- Overall, B- Presummer, C- Summer, D- Monsoon).

Figure 10: Seasonal abundance of dung beetles in an agriculture habitat at Nelliampathi during the 2007-2008 study period.

Figure 11: Overall rank abundance plot of dung beetles in an ecotone between a semi-evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period.

Figure 12: Rank abundance plot of dung beetles in an ecotone between a semi-evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period (A- Presummer, B- Summer, C- Monsoon).

Figure 13: Functional guild composition and abundance of dung beetles in an ecotone between a semi-evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period (A- Overall, B- Presummer, C- Summer, D- Monsoon).

Figure 14: Temporal guild composition and abundance of dung beetles in an ecotone between a semi-evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period (A- Overall, B- Presummer, C- Summer, D- Monsoon).

Figure 15: Seasonal abundance of dung beetles in an ecotone between a semi-evergreen forest and an agriculture habitat during 2007-2008 study period.

Figure 16: Diversity of dung beetles between a semi-evergreen forest, ecotone and agriculture habitat at Nelliampathi during 2007-08 study period.

Figure 17: Dendrogram based on hierarchical clustering (group-average linking) of dung beetles in a semi- evergreen forest, ecotone and agriculture habitat at Nelliampathi during 2007-08 study period.

Figure 18: Rarefaction curves (expected species accumulation curve) showing the expected number of dung beetle species $ES_{(n)}$ plotted on Y axis as a function of the accumulated number of the individuals (n) of agriculture habitat, ecotone and semi-evergreen forest at Nelliampati during 2007-08 study period.

LSIT OF TABLES

Table 1: Abundance (mean ± SD and percentage), temporal and functional guild composition and seasonality of dung beetle assemblage associated with a semi- evergreen forest at Nelliampathi during 2007-08 study period.

Table 2: Abundance of small and large dung beetle species associated with a semi- evergreen forest at Nelliampathi during 2007-08 study period.

Table 3: Functional guild composition of dung beetles associated with a semi-evergreen forest at Nelliampathi during 2007-08 study period.

Table 4: Statistical analysis of functional and temporal guild composition of dung beetle species in a semi- evergreen forest at Nelliampathi during 2007-08 study period.

Table 5: Seasonal abundance (mean ± SD) of dung beetle species associated with a semi- evergreen forest at Nelliampathi during 2007-08 study period.

Table 6: Statistical analysis of seasonal variation in overall abundance and abundance of functional and temporal guild of dung beetle species in a semi-evergreen forest at Nelliampathi during 2007-08 study period.

Table 7: Abundance (mean ± SD and percentage), temporal and functional guild composition and seasonality of dung beetle assemblage associated with an agriculture habitat at Nelliampathi during 2007-08 study period.

Table 8: Abundance of small and large dung beetle species associated with an agriculture habitat at Nelliampathi during 2007-08 study period.

Table 9: Functional guild composition of dung beetle species associated with an agriculture habitat at Nelliampathi during 2007-2008 study period.

Table 10: Statistical analysis of functional and temporal guild composition of dung beetles in an agriculture habitat at Nelliampathi during 2007-08 study period.

Table 11: Seasonal abundance (mean ± SD) of dung beetle species associated with an agriculture habitat at Nelliampathi during 2007-2008 study period.

Table 12: Statistical analysis of seasonal variation in overall abundance and abundance of functional and temporal guild of dung beetle species in an agriculture habitat at Nelliampathi during 2007-08 study period.

Table 13: Abundance (mean ± SD and percentage), temporal and functional guild composition and seasonality of dung beetle assemblage associated with an ecotone between a semi- evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period.

Table 14: Abundance of large and small dung beetle species associated with an ecotone between a semi- evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period.

Table 15: Functional guild composition of dung beetle species associated with an ecotone between a semi- evergreen forest and an agriculture habitat at Nelliampathi during 2007-2008 study period.

Table 16: Statistical analysis of functional and temporal guild composition of dung beetle species associated with an ecotone between a semi- evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period.

Table 17: Seasonal abundance (mean ± SD) of dung beetle species associated with an ecotone between a semi- evergreen forest and an agriculture habitat at Nelliampathi during 2007-08 study period.

Table 18: Statistical analysis of seasonal variation in overall abundance, functional guild and temporal guild of dung beetle species in an ecotone between a semi- evergreen forest and an agriculture habitat at Nelliampathi during 2007-2008 study period.

Table 19: Statistical analysis of variation in overall abundance, diversity, functional guild and temporal guild of dung beetle species across a semi-evergreen forest, agriculture habitat and ecotone at Nelliampathi during 2007-2008 study period.

Table 20: Analysis of the similarity of dung beetle assemblage across a Semi-evergreen forest, agriculture habitat and ecotone at Nelliampathi during 2007-2008 study period.

Table 21: Percentage contribution of species towards dissimilarity between a semi- evergreen forest, agriculture habitat and ecotone at Nelliampathi during 2007-08 study period.

Table 22: Indicator value of species collected from a semi- evergreen forest, ecotone and agriculture habitat at Nelliampathi during 2007-08 study period.

LIST OF SYMBOLS AND ABBREVIATIONS

‘@’= endemic to the Western Ghats

‘$’= rare in the region

‘*’= no significant variation /statistical interpretation not possible

Di= diurnal

N= nocturnal

G= generalist

Dw= dweller

R= roller

T= tunneler

SE= seasonal

AS= aseasonal

S= small beetles

L= large beetles

PS= presummer

SU= summer

M= monsoon

SEG= semi- evergreen forest

ECO= ecotone

AGR= agriculture habitat