Research Article

Cloud forest dung beetles (Coleoptera: Scarabaeinae) in the Western Ghats, a global biodiversity hotspot in southwestern India

T. K. Sabu*, K.V. Vinod, M. Latha, S. Nithya and J. Boby
Litter Entomology Research Unit, Post Graduate & Research Department of Zoology,
St. Joseph's College, Devagiri, Calicut, Kerala, India, 673008.
E-mail: sabukthomas@gmail.com

Abstract
First-time 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 is provided. High level of endemism, predominance of two montane endemic species of which one is a flightless local endemic, greater proportional abundance of roller guild, and the total absence of dweller guild, make the cloud forest dung beetle community different from the communities in the low-altitude montane forests. Distribution of major proportion of montane species in the low altitude supports the hypothesis for the origin of montane fauna through vertical colonization of the high altitudes by low-altitude species. Abundance of rollers is attributed to the availability of dung pellets of local endemic mountain goat, Nilgiri Tahr (*Nilgiritragus hylocrius*) and Sambar deer (*Cervus unicolor*) throughout the year and absence of dweller guild to the seasonal availability of fresh dung pads of Asian elephant (*Elephas maximus)* and gaur (*Bos gaurus*). Dominance by the flightless local endemic dung beetle *Ochicanthon devagiriensis*, belonging to the old-world tribe Canthonini with Gondwanaland distribution, indicates the stability, refugial isolation, and archaic nature of the dung beetle assemblage in the studied montane region. Since flightless species show a high level of fidelity to their preferred habitat and are efficient indicators of historical changes in their habitats, dominance and local endemism of flightless species *Oc. devagiriensis* makes it an ideal indicator species and effective forecaster of habitat modifications of the unique cloud forest study region in the Western Ghats.

Key words: montane forests, shola, flightless dung beetles, Canthonini, endemism.

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Introduction

Patches of tropical montane cloud forests (TMCF) occur in Central and South America, tropical Africa and tropical Asia, where humid mountains are frequently covered by trade wind-derived orographic clouds and fog in combination with convectional rainfall [1–3]. Many features of these forests, from vegetation morphology and nutrient budgets to solar insolation, are directly or indirectly related to cloud formation. A direct impact of frequent cloud cover is the deposition of cloud droplets through contact with vegetation (cloud stripping), fog drip to the forest floor (fog precipitation), and presence of moss cover on the stem of trees [4–7]. TMCFs often occur either on mountain tops or along ridge lines between 1,000 and 3,500 m asl. Under exceptional conditions they also occur at lower altitudes such as 300–500 m asl [3, 8]. TMCFs are among the most endangered of all tropical forest types and usually harbor a high proportion of many endemic plant and animal taxa specifically adapted to cool temperatures and moist-humid conditions. Although the TMCFs are less diverse than the lowland forests, when their exceptionally high levels of regional endemism are considered their collective species diversity would probably exceed any other forest type [2, 8, 9].

A majority of the studies in Asian TMCFs refer to vertebrates [10–13] and plants [14–17] and little is known of the ground-dwelling arthropod diversity in such habitats. Search for data on the dung beetle assemblage in Asian TMCFs revealed that no data exists except that of Hanski [18] from Southeast Asia. Data from Southeast Asian TMCFs revealed low tribal, generic, and species richness, but high abundance of two species, with one being an endemic wingless species, and absence of dwellers. Moreover, no data on diel periodicity, seasonality, and functional guild composition of dung beetles is available. In such a context, we analyzed the diel periodicity (diurnal, nocturnal), seasonality (southwest and northeast monsoon, pre-summer, and summer seasons) and functional guild composition (dwellers, rollers, tunnelers) of dung beetle assemblage in a TMCF in the Western Ghats, a global diversity hotspot in southwestern India. Based on the data on dung beetles from TMCFs in Southeast Asia, we hypothesized that TMCF in the region may also have low tribal, generic, and species richness and a high abundance of endemic flightless species. In addition, we explain the rationale for the uniqueness of cloud forest dung beetle assemblage in this region with regard to their isolation, composition of major dung-producing mammals, and dung diversity.

Methods

Study area

The study site was at Eravikulam National Park [ENP (77º0’30”–77º10’E; 10º10’– 10º 20’N; 1400-2694 m asl, 97 km^2; Idukki District, Kerala State) (Fig.1)] on the western slopes of the South Western Ghats Montane Rain Forests Ecoregion [19]. Patches of stunted montane evergreen forests surrounded by vast montane grasslands (also referred to as “shola forests” and “shola grasslands”) [20, 21] occur in the high altitudes at ENP (Fig.2)]. These forests occurring in the midst of montane wet grasslands, at altitudes above 1,500-1,800 m asl in the Western Ghats in southwestern India, are referred to as tropical upper montane rain forests and montane temperate forests [22, 23]. Following the recent classification of montane forests [3, 6], shola forests are categorized as tropical montane cloud forests (cloud forests). The landscape of the shola forests can be best described as “islands” of cloud forests within vast tracts of grasslands. As in other regions in the Western Ghats, as of now only small patches of these unique ecosystems remain in the ENP, because of human-induced modifications to the landscapes (e.g., plantations and settlements). Modification of the shola forests in the ENP started around the 14th century with the entry of native tribes from the eastern slopes of the Western Ghats and the slash-and-burn cultivation techniques they practiced. This was followed by the intense transformation of high-altitude shola forests into tea plantations and game belts in the later part of the 19th century with the arrival of the British [19, 24].

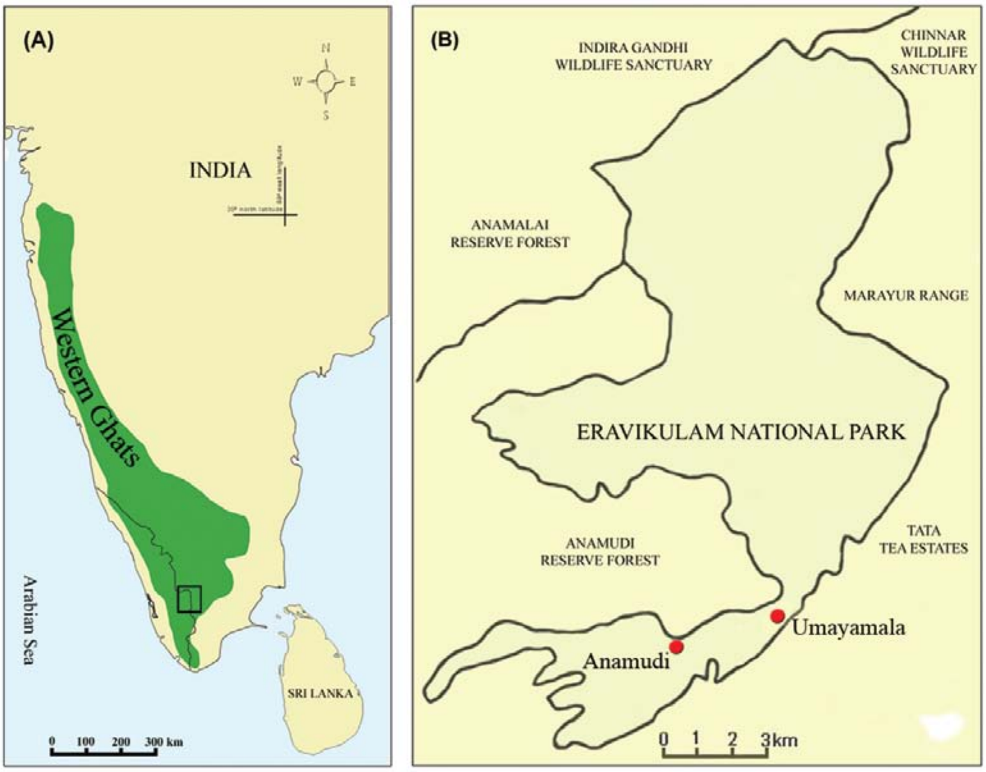

Fig. 1. (A) Map of southwestern India showing the location of the Western Ghats; (B) Study sites in the Eravikulam National Park.

Key herbivorous mammals in ENP are the Nilgiri Tahr [*Nilgiritragus hylocrius* (Ropiquet and Hassanin, 2005)], Asian elephant (*Elephas maximus* Linnaeus, 1758), Sambar deer (*Cervus unicolor* Kerr, 1792), gaur (*Bos gaurus* Hamilton Smith, 1827), barking deer [*Muntiacus muntjak* (Zimmermann, 1780)] and mouse deer (*Moschiola indica,* Gray, 1852). Intensely undulating terrain, the climate, and the altitude of ENP make this region hostile for any mammal other than the resident endemic, the Nilgiri Tahr. ENP does not hold any resident population of Asian elephant and gaur, but serves as a corridor linking the wet western and dry eastern slopes [19, 25].

Annual climate features include temperature ranging from 17 to 20°C; relative humidity 40–90%; mean annual rainfall 1,300 mm; mean rainfall during southwest monsoon time (June–August) 260 mm, northeast monsoon time (September–November) 105 mm, pre-summer (December–February) 20 mm; and summer (March–May) 50 mm [26].

Sampling

Dung beetles were sampled using baited pitfall traps on a seasonal basis (northeast monsoon: September 2006, pre-summer: January 2007, summer: May 2007) for 24-hour periods from September 2006–May 2007. No sampling was done during the southwest monsoon time (June-August), as the heavy rain leaves the forest floor soggy and access to the site extremely difficult. Each trap consisted of a plastic tub (210 mm diameter, 150 mm deep), buried to its rim in soil, and holding a mixture of water and propylene glycol. Each trap was covered with a circular plastic tray supported on iron rods to restrict desiccation on warm days and flooding on rainy days. Two hundred grams of fresh cow dung was placed on a wire grid between the basin and the tray. Twenty such traps were placed in three shola forest patches [ten traps along a linear transect in a large forest patch at Umayamala (2,250 m asl) and four and six traps in two small patches at Anamudi (2,200 m asl)) with an intertrap distance of 50 m to minimize trap interference [27]. Beetles were collected at 0800 h and 1800 h each day. Both diurnal and nocturnal collections were made separately.

Fig. 2. Tropical Montane Cloud Forest patch amidst grass land in Eravikulam National Park of the Western Ghats with local flightless endemic *Oc. devagiriensis* (inset; adopted from Latha *et al* 2011).

Beetles were determined to species using Arrow [28] and Balthasar [29] and confirmed by comparing with the verified specimens. Voucher specimens are temporarily deposited in the insect collections of St. Joseph's College, Devagiri, Calicut, and will be transferred to the National Insect Collections at the Zoological Survey of India (ZSI), Calicut, and the Indian Agricultural Research Institute (IARI), New Delhi. The determined species were sorted into three functional guilds: dwellers (endocoprids), rollers (telecoprids), and tunnelers (paracoprids), following Cambefort and Hanski [30], and three temporal guilds: nocturnal, diurnal, and generalist beetles based on the significance level of variation in the abundance in nocturnal and diurnal traps.

Evaluation of the sampling effort was done with the Mao-Tau sample-based rarefaction curve in the EstimateS program 8 [31]. The changes in community structure during different seasons were compared based on the number of individuals per species with dominance-diversity (rank abundance) curves [32, 33].

Significant levels of variation in the overall and species-wise abundance during seasons were tested with Kruskal-Wallis tests and species-wise abundance in nocturnal and diurnal traps with one-way analysis of variance (ANOVA). When significant differences occurred, the Mann-Whitney U-test was applied to determine which pairs of seasons differed significantly [34]. Seasonal variations in functional-guild composition based on abundance were analyzed with a Chi-square test. All statistical analyses were done using MegaStat Version 10.0 [35].

Results

Dung beetles belonging to five species, three tribes, and three genera were collected (Table 1). *Onthophagus refulgens* (57.96%), followed by the flightless *Ochicanthon devagiriensis* (24.92%) were the dominant species (Table 1). No seasonal variation in overall abundance was evident (H=1.44, df=2, p>0.05). Populations of *Oc. devagiriensis* peaked during the monsoon season (H=21.19, df=2, p<0.05) and those of *On. refulgens* in pre-summer (H=21.25, df=2, p<0.05). *Ochicanthon devagiriensis* was recorded throughout the study period, whereas *Panelus keralai* was recorded only during summer (H=10.73, df=2, p<0.05) and *On. quaestus* only in pre-summer (H=18.04, df=2, p<0.05). Seasonality of *On. castetsi* could not be determined due to low abundance. No *Onthophagus* species was recorded during summer and only *On. refulgens* and *Oc. devagiriensis* were recorded during the monsoon period. *Onthophagus refulgens* and *Oc. devagiriensis* did not display diel periodicity. *Onthophagus quaestus* (N) was nocturnal and *On. castetsi* (D) and *P. keralai* (D) were diurnal (Table 1). The assemblage of dung beetles consisted of tunnelers (three species) and rollers (two species). Tunnelers represented 60.0% of total species richness and were the most abundant functional guild (72.67 % of total abundance). Functional guild (tunnelers and rollers) composition based on abundance varied significantly among seasons (χ^2=167.59, df=2, p<0.05), whereas richness-based composition of functional guilds did not (χ^2=3.00, df=2, p>0.05). Tunnelers were the dominant functional guild in pre-summer and were absent in summer. Rollers dominated the assemblage in both summer and the monsoon period.

Table 1. Seasonal abundance, species richness, diversity, diel periodicity, and functional guild composition of dung beetles in the tropical montane cloud forests of Eravikulam National Park in the Western Ghats. G-generalist, D-diurnal and N-nocturnal.

Species/Guild/Diversity/ Diel periodicity	Annual data		Presummer period		Summer period		Monsoon period	
	mean±SD	Total	mean±SD	Total	mean±SD	Total	mean±SD	Total
Onthophagus refulgens Arrow, 1931 (G)	1.93±4.24	116	5.55±5.91	111	0	0	0.25±0.55	5
Onthophagus quaestus Sharp, 1875 (N)	0.43±1.53	26	1.3±2.47	26	0	0	0.00	0
Onthophagus castetsi Lansberge, 1887 (D)	0.05±0.22	3	0.15±0.37	3	0	0	0.00	0
Panelus keralai Paulian, 1980 (D)	0.08±0.28	5	0.00	0	0.25±0.44	5	0.00	0
Ochicanthon devagiriensis Sabu & Latha, 2010 (G)	0.83±2.3	50	0.1±0.31	2	0.2±0.52	4	2.2±3.62	44
Abundance	200		142		9		49	
Species richness	5		4		2		2	
Nesting guilds								
Rollers	27.63		1.41		100		89.8	
Tunnelers	72.67		98.59		0		10.2	

Species accumulation curves for all seasons reached a perfect level-off, denoting that sampling was adequate with less likelihood of finding more species (Fig. 3).

Dissimilar shapes and slopes of the rank-abundance curves showed differences in patterns of species diversity between the seasons. Species richness was highest during pre-summer and lowest and equal during summer and monsoon periods (Fig. 4). Dominance patterns were dissimilar among the seasons with *On. refulgens* dominating in pre-summer, *P. keralai* and *Oc. devagiriensis* in summer, and *Oc. devagiriensis* during the monsoon period.

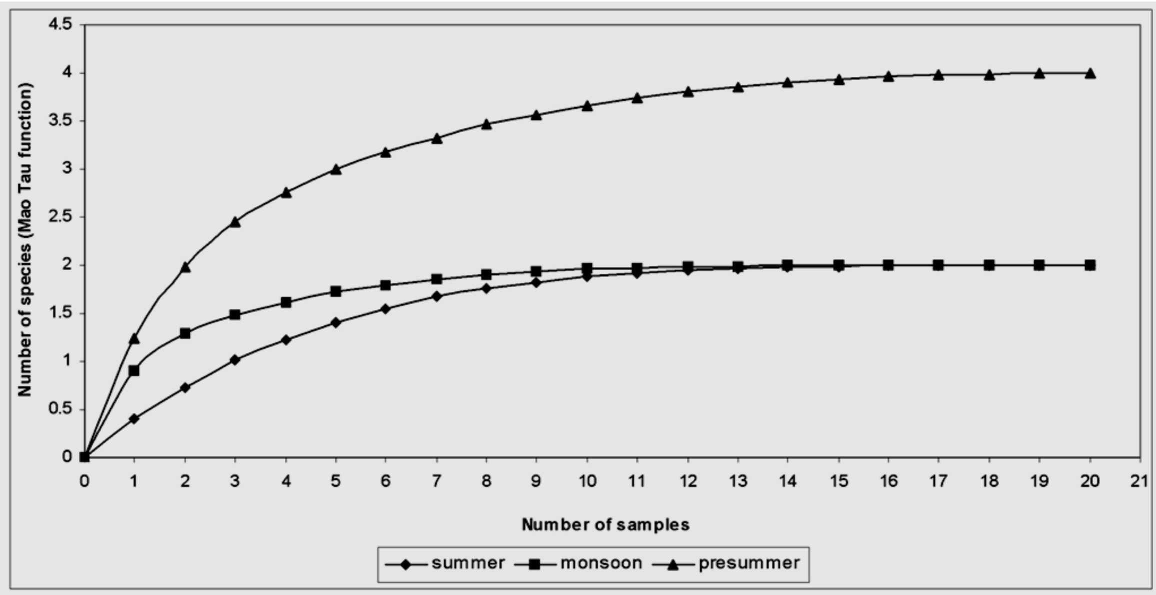

Fig. 3. Expected species accumulation curves based on the Mao-Tau function for all seasons.

Discussion

The cloud forest dung beetle assemblage of ENP in southwestern India is similar to that from Southeast Asia and Neotropics in showing low species richness, diversity, and abundance [18, 36]. Community structure and species composition of the assemblage vary from those of the Neotropical region, but resemble those of Southeast Asia. Comparison of dung beetle faunal composition between the TMCFs in montane regions of Southeast Asia (Borneo) and the present study region in South Asia reveals notable similarities and dissimilarities. Similarity in the composition of dung beetle fauna represented by Canthonini and Onthophagini, incidence of flightless local endemics *Ochicanthon hanski* in southeast Asia and, *Oc. devagiriensis* in the Western Ghats in south Asia [18, 39, 40] and presence of low altitude montane species in the TMCFs in Borneo and the Western Ghats is obvious. These three features make it an archetypical instance of parallel evolution of related groups, but isolated spatially. However, three major differences namely, (1) higher species richness of *Onthophagus*, (2) presence of a non-endemic *On. quaestus and*, (3) presence of *Panelus* in the TMCFs in the Western Ghats in contrast to the low species richness of *Onthophagus*, total absence of non-endemics and non-record of *Panelus* in the peaks of south-east Asian TMCFs (18) are striking. Occurrence of *Panelus* in the present study site and TMCFs of Sri Lanka and North-eastern India [28, 29, 41, 42] indicate that *Panelus* is a widespread member of the TMCF dung beetle assemblage of South Asia and its non-record in Southeast Asia [18] may be due to the inefficiency of the fish-baited traps used.

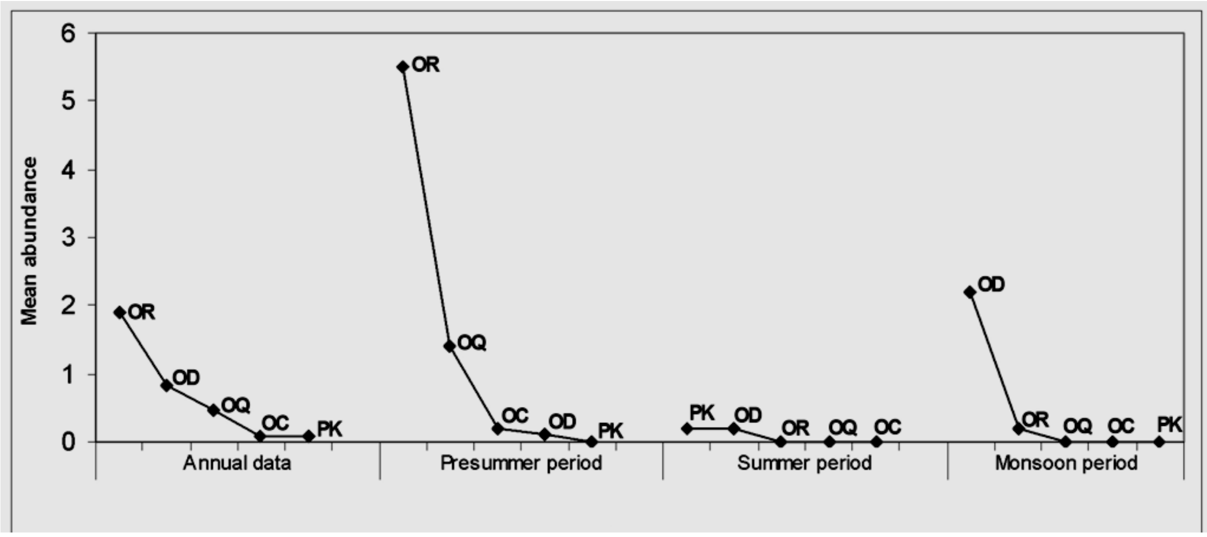

Fig. 4. Dominance diversity curves based on the number of individuals (mean abundance) per species of overall and seasonal data. OR- *On. refulgens*, OQ- *On. quaestus*, OC- *On. castetsi*, OD- *Oc. devagiriensis*, PK- *P. keralai.*

Distribution of TMCF species in low-altitude montane forests indicates that vertical colonization by low-altitude montane species with greater dispersal abilities and adaptations to exist in cold habitats [43-45] lead to the movement of dung beetles to the TMCF region. However, since the Scarabaeinae are predominantly a warm-climate species [46], the relatively cooler climate of the TMCFs would have made the vertical colonization difficult for most warm-climate-adapted dung beetle species of lower altitudes [43, 47]. Among the vast list of warm-climate dung beetle species belonging to six tribes present at low-altitude montane forests [48, 28], only selected species belonging to Canthonini and Onthophagini could colonize the TMCF. These selected species might have more general dispersal abilities, ability to use both large and small dung types available (56), and special physiological adjustments for thermoregulation to withstand the low temperatures [49, 50, 51] that allow them to become established in the TMCFs. Although flightlessness is a common feature in high- altitude montane habitats with environmental stability, isolation, and limitation of habitat area [52, 53, 54], such flightlessness is unusual among dung beetles, who depend on flight capacity to reach dung resources that are often spatially and temporarily limited [55, 44]. This raises the question why only the ball-rolling and dung-pellet-preferring *Oc.devagiriensis* species lost flight in the region and not dung beetle species of the genera *Onthophagus* or *Panelus*. Literature on the evolutionary history and biogeographic distribution of dung beetles and dung-contributing herbivorous mammals [56-58]; pellet dung feeding habits of *Ochicanthon* and *Panelus* belonging to the Old World Canthonini and their ancient Gondwanaland distribution; basal position of Canthonini in the cladistic analysis of dung-beetle phylogeny [57-59]; and occurrence of dung pellet-producing Nilgiri Tahr as key resident mammalian herbivores in the TMCFs of the Western Ghats [19, 24] lead to several propositions. One is that *Ochicanthon* and *Panelus* belonging to the Old World Canthonini represent the archaic dung beetle species that reached the TMCF region before the mid-Cenozoic arrival of dung-pad producing mega herbivores (Asian elephant and gaur) and the dung-pad preferring modern tribe, Onthophagini. Among the two Canthonine taxa, *Ochicanthon*, whose possible dung resource is dung pellets of small mammals [59], lost flying capacity in response to the steady dung-pellet resource availability from Nilgiri Tahr, lack of competition for dung resources from other dung beetle species, and habitat persistence, environmental stability, and isolation [53, 54] in the TMCF. Presence of wings in *Panelus* may be due to its dependence on flight capacity to reach the generally scarce insect and rat dung pellets [59]. Subsequent arrival of the dung-pad-producing mega herbivores, Asian elephant and gaur, across Afro-Asian region in the mid- to late-Cenozoic period [56, 57, 60] might have led to the colonization and population build-up of tunnelers (*Onthophagus*) belonging to the dung-pad-preferring younger modern tribe, Onthophagini.

Functional guild composition of the assemblage differed from the assemblages in the low-altitude montane forests of the Western Ghats (37, 38, 48) in the total absence of dwellers and in the comparatively high proportion of rollers belonging to the rare Old World tribe Canthonini. Dwellers are well represented in regions where undisturbed large droppings are common [57, 38], and relatively high proportions of ball-rolling taxa occur in regions with low diversity in dung types, comprising mainly pellets and small droppings of omnivores and carnivores [56]. Hence, the non-record of dwellers in the TMCF study region is attributed to the seasonally limited availability of mega herbivore dung pads (personal observations) and abundance of rollers to the ready availability of mammalian dung pellets.

The abundance of tunnelers (*Onthophagus*) peaks during the pre-summer period that coincides with the seasonal arrival of dung-pad-producing mega herbivores (elephant and gaur) [19], and the low abundance of tunnelers during other periods leads to the suggestion that the life cycle of tunnelers in the region is synchronized with the arrival of mega herbivores and the availability of their dung pads. The chance of tunnelers (*Onthophagus*) moving along with the seasonal mega herbivores (elephant and gaur) is ruled out, as *On.refulgens* and *On.castetsi* are montane endemics and *On.quaestus* is not recorded from the surrounding low-altitude moist forests (48). Similarly, the high abundance of *Ochicanthon* during the wet season, which coincides with the movement of mega herbivores to dry deciduous forests in the eastern slopes of the study region, is likely to be linked to the dung pellet resource availability from the major resident mammal, Nilgiri Tahr, and of sambar deer taking shelter within TMCFs [19, 25] to escape the incessant rains and wind in the surrounding grasslands. Reasons for the rare occurrence of *P. keralai* during summer may be their rarity and the seasonal availability of preferred pellet dung resources of insects and rats [59].

Absence of diel periodicity by the two dominant and seasonal montane endemic species (*On. refulgens* and *Oc. devagiriensis*) may be adaptations to exploit the seasonally abundant dung resources. The nocturnal and diurnal activity in *Oc. devagiriensis*, along with its abundance during the wet season, indicates that a generalization saying ball rollers are diurnal and thermophilic (since warm conditions make dung-ball making easier [61]) is not applicable for *Ochicanthon*. Warm conditions may be a prerequisite for dung-ball making in the modern rollers (Sisyphini and Gymnopleurini), associated with the more moist, wet dung pads of larger herbivores in the low altitude montane forests of the Western Ghats [37, 38], but this is not the case for the Old World Canthonine roller, *Ochicanthon*. Lack of data on the life biology characteristics and low abundance of *On. castetsi, On. quaestus, and P.keralai* makes interpretations on diel periodicity and seasonality difficult. It highlights the need to study the habits of endemic dung beetle species in the TMCFs in the Western Ghats in order to obtain a better understanding of their habitat requirements and endemism as a study that would also help preserve the TMCFs, with their long history of geographical isolation, from further habitat modifications.

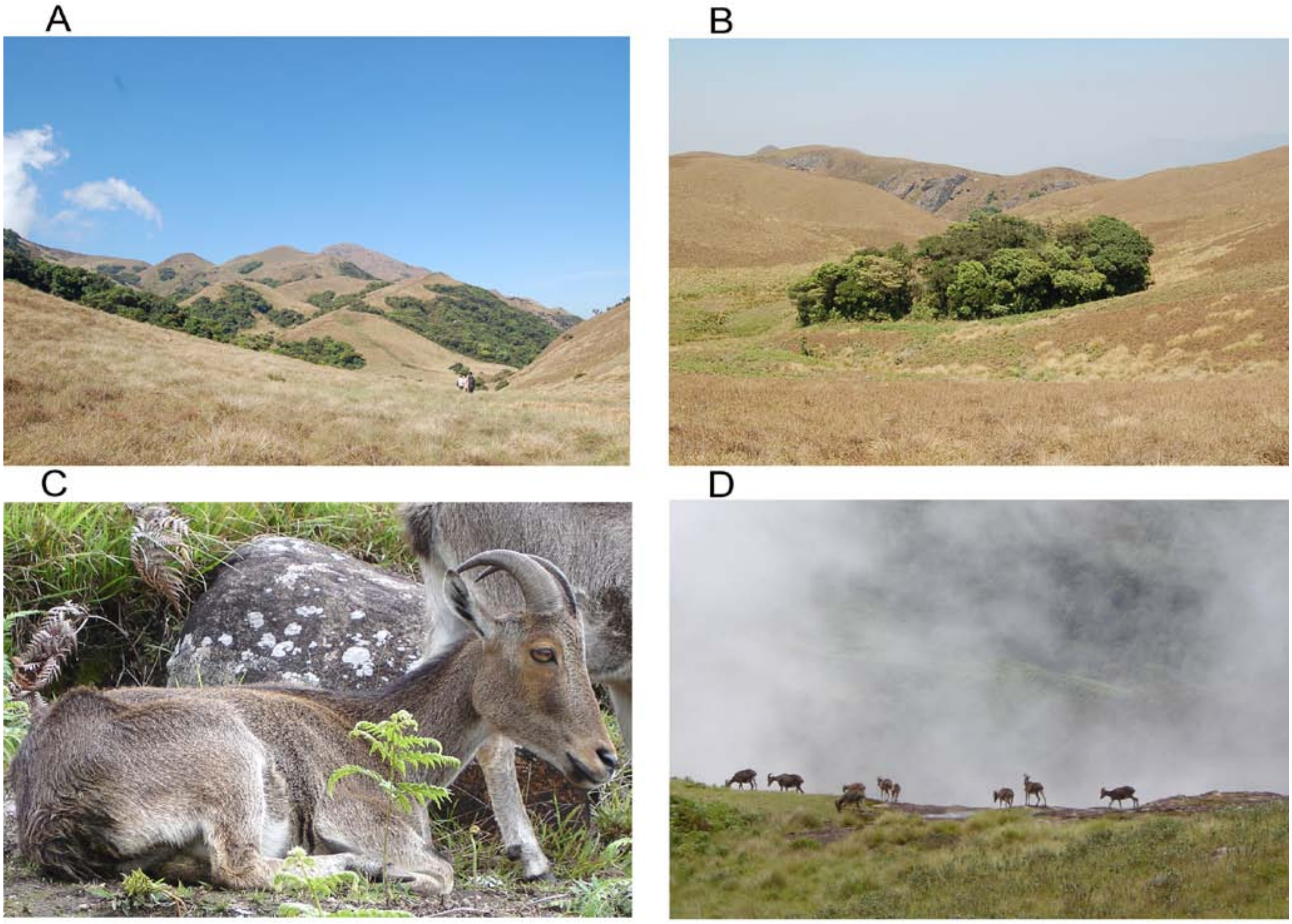

Fig.5. Habitat of flightless local endemic dung beetle species, *Oc. devagiriensis,* at Eravikulam National Park of the South Western Ghats (A); "islands" of tropical montane cloud (shola) forest within a vast tract of grassland in the peak area of the Western Ghats (B); major resident mammal and local endemic mountain goat (*Nilgiritragus hylocrius*) (C); a herd of mountain goats along the cliff edge (D). Photos A and B by Sabu K Thomas; C and D by Joe Jesudurai.

Implications for conservation

1. Dominance by a flightless local endemic species, belonging to the Old World tribe that occupies a basal position in dung-beetle phylogeny and with ancient Gondwanaland distribution, is indicative of the archaic nature of the dung-beetle assemblage in the TMCF region and its long history of geographical isolation. Since flightless species show high fidelity to their preferred habitat and are efficient indicators of historical changes in their habitats [62], abundance and local endemism of *Oc. devagiriensis* makes it an effective indicator of conservation priority and future habitat modifications of the unique TMCF ecosystem in the Western Ghats (Fig. 5).

2. The record of the flightless local endemic *Ochicanthon* species in other TMCFs in the Western Ghats, the northeast of the Indian subcontinent [40], and the Southeast Asian region [18, 39] indicates that TMCFs of the Asian region are centers of differentiation and refuge for Old World dung beetles. This highlights the need to treat TMCFs as high-priority zones from a conservation viewpoint.

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