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Title: Habitat type and altitude work in tandem to drive the community structure of dung beetles in Afromontane forest

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Abstract

Introduction

Dung beetles are a species group highly recognized for their sensitivity to anthropogenically induced change. There are few studies of the dung beetle communities found in Afromontane forests despite these forests forming part of a global hotspot of biodiversity.

Methods

We used comparisons of diversity to investigate the effect of habitat and altitude on the species composition of Scarabaeidae dung beetles in six Afromontane habitat types and identified indicator species associated with each forest type.

Results

A total of 8020 individuals from 34 species belonging to 16 genera were captured at twelve transect locations across a 1.5 km altitudinal gradient. All indices measuring diversity and dominance showed significant differences between forest types with little overlap in the species composition detected in each.

Altitude was negatively correlated with dung beetle abundance, species richness, and diversity (abundance: $R^2 = -0.392$, $P =<0.001$, richness: $R^2 = -0.779$, $P =<0.001$, diversity: $R^2 = -0.735$, $P =<0.001$), and there were also significant differences in abundance, species richness and diversity between altitude zones. Eight indicator species were identified for potential use in future conservation management or monitoring programs.

Discussion

This study found no significant relationship between species richness and forest type but an interaction between the two factors. Altitude in conjunction with forest type are the main factors in shaping dung beetle species composition in this Afromontane forest. Our results suggest the most important characteristic for determining community structure was mean canopy cover *per* forest type. Results from a previous short study conducted in 1974 indicate while there was significant overlap between dung beetle species caught 40 years ago and the present day there were also seven species which were absent. All seven of these species have climatic distributions centered around the wet highlands of East Africa and further work is urgently required to understand why these species are no longer detectable.

Implications for insect conservation

Our results have important conservation implications as they underscore the importance of preserving forest heterogeneity to maintain maximum dung beetle diversity within mountain ecosystems. The identified differences in dung beetle diversity between forest types and the high turnover of dung beetle species between altitude zones should heighten the importance for instigating future Scarabaeidae conservation initiatives in Afromontane regions.

Keywords: Afromontane forest, Altitude gradient, Beta diversity, Dung beetles, Indicator species

Declarations

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Conflicts of interest/Competing interests

The authors have declared that no competing interests exist.

Availability of data and material (data transparency)

The authors confirm that the data supporting the findings of this study are available within the article (and/or) its supplementary materials.

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Introduction

The high species richness and diversity found in tropical montane habitats are the result of three main factors: (1) the impact of climatic and geological history on biotic evolution; (2) species adaptations to environmental constraints; and (3) the continuous dispersal of fauna and flora over time. The alteration of very cold and wet and then warm and dry periods in the Pleistocene epoch encouraged the formation of refuges (Fjeldsa and Lovett 1997), which served as shelters for a rich diversity of species, and also sources for dispersion of biota to neighboring areas as warming of the climate allowed species ranges to expand. In East Africa these refuges are now mostly confined to the forest archipelago of mountains dotted from southern Tanzania to the Bale mountains in Ethiopia (Hedburg 1969). Altitudinal differences within mountain forests have also made for very varied climates and this wide diversity of climates combined with local differences owing to geomorphological, edaphic and plant cover have given rise to a range of microclimates which help generate a wide range of specific niches (Coe 1969).

The refugia hypothesis (Fjeldsa & Lovett, 1997) suggests that differences in species diversity and occurrence between isolated patches are the result of allopatric speciation. Changes in species distribution across environmental gradients may reflect habitat specialization by constituent species (Laurance et al. 2011) and limiters such as thermal tolerance and resource availability restrict niche space and determine the spatial extent of species distributions and successional patterns. One well-studied aspect of patterns in spatial biodiversity is the species turnover that occurs along altitudinal gradients, especially those which occur in tropical montane habitats (Escobar et al. 2005). These changes may arise over small spatial extents due to the close proximity of different habitats and, as a consequence, communities may differ dramatically in species composition over small distances, for example between valleys or mountain peaks (Jankowski et al. 2009).

Tropical montane forests constitute one of the biologically richest environments on earth (Aldrich et al. 1997) and often contain a large number of endemic species (Merckx et al. 2015). However, African montane (Afromontane) forests and their associated biota are poorly studied despite being important hotspots of terrestrial biodiversity (Mittermeier et al. 2011; CEPF 2012). In Kenya, Afromontane ecosystems are estimated to cover 7.4% (58 Mha) of the terrestrial area and montane forests represent 57% (740,000 ha) of forest cover (Paron et al. 2013). The majority of the studies that assess Afromontane biotic distributions in East Africa pertain to vertebrates (Martin et al. 2015; Rovero et al. 2016; Stanley and Kihaule 2016) and plants (Nyundo et al. 2006; Eisenring et al. 2016). Little is known about insect diversity of African forests or the factors which may explain their distribution. Invertebrates constitute the bulk of known biodiversity on Earth and dominate virtually every terrestrial ecosystem in terms of species richness, animal biomass, and the provision of essential ecosystem services (Samways 2015). Thus, understanding of the factors influencing invertebrate taxonomic richness and diversity at both local and regional scales is important for conserving biodiversity and for maintaining ecosystem services. Dung beetles are known to represent an important functional component of the animal fauna found in tropical forests (Krell-Westerwalbesloh et al. 2004; Banks et al. 2010) as they provide several key ecological functions such as seed dispersal, parasite suppression and dung removal (Nichols et al. 2008).

A recent global meta-analysis (Nichols et al. 2007) of 26 studies of dung beetle community responses to tropical forest modification and fragmentation showed that dung beetle species richness, abundance, and biomass undergo a gradual decline across a modification gradient from intact tropical forest to clear-cut areas, and as forest fragments became smaller and/or more isolated. Dung beetle communities are very sensitive to changes in abundance of food resources, microclimatic variables and soil characteristics (Hanski et al. 1979; Hanski and Cambefort 1991; Osberg et al. 1994; Pryke et al. 2013). Changes in community organization of dung beetles include alterations in species richness, composition, abundance and guild structure. The physical structure of habitats can be an important determining factor in the composition and distribution of dung beetle assemblages (Davis and Sutton 1998) with a complete species turnover observed across a natural ecotone spanning as little as 100m (Spector and Ayzama 2003). Consequently, dung beetles are a useful indicator group because they reflect structural differences between biotope types (Carpio et al., 2009; Nichols et al., 2013). From savannahs to tropical forests, dung beetles are highly habitat specific and there are distinct communities of beetles associated with forests, edges 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 2005).

A number of factors are thought to influence the spatial pattern of dung beetle species occurrence. Species may have their range restricted by lack of suitable habitat or the decline in quality of existing habitats (Raine and Slade 2019). To date there have been few published studies describing dung beetles in montane regions globally, and their ecology and response to biotic and abiotic factors in African montane forests has seldom been analyzed. The only previous studies assessing dung beetle species across an altitudinal gradient in African mountains are those by Davis et al. (1999) from the Drakensburg mountain range in South Africa and more recently from Mt. Kilimanjaro in Tanzania (Gebert et al. 2019). It is generally accepted that in most invertebrate taxa, species diversity and richness generally decline with increasing altitude (Wolda 1987). However, other studies have also reported mid-elevation peaks in dung beetle species richness (Escobar et al. 2006; Lobo et al. 2007; Herzog et al. 2013; Nunes et al. 2016). Both the African and the

Neotropical studies unravel specific and general patterns that help explain the mechanisms driving the distribution of dung beetles along elevation gradients and with significant implications for biogeographic analysis and conservation priorities. Understanding these patterns is important as there is growing evidence that the effects of climate change are amplified with elevation (Mayor et al. 2017).

In this study, we investigate the factors influencing the spatial pattern of dung beetle diversity in Afromontane vegetation. We sampled dung beetles associated with six different forest habitats which are characterized by differences in vegetation types and are located along an altitudinal gradient. We test the hypothesis that altitude and forest type underpin the variation of dung beetle diversity and species composition of dung beetles in Afromontane forests. Our objectives are: 1) to describe dung beetle alpha diversity (α) at the habitat scale; 2) to estimate beta diversity (β) between elevation zones; and 3) to estimate gamma diversity (γ) for the whole mountain range. We expected a decrease in species richness with increasing altitude but less species attenuation between forest types. Additionally, we hypothesize that different forest types will have distinct species assemblages from which indicator species can be described. We discuss the implications of these findings for future conservation planning and climate change monitoring within Afromontane forests.

Methods

Study area

The study was performed at six locations in the Aberdare National Park (ANP) which is located in the Aberdare mountain range in central Kenya (Figure 1). The mountain range belongs to the northern volcanic sub-region of the eastern Afromontane (EAM) biodiversity hotspot. The hotspot is well known for regional variation in vegetation, rainfall patterns, topography and high levels of endemism across its range (Taylor 2015). The ANP lies to the east of the Gregory Rift Valley and is about 80 km north of Nairobi and 17 km from Nyeri town (0.4167° S, 36.9500° E). It is an elongated massif, running approximately north south, parallel to the direction of the Rift Valley, 60 km to the west of Mt. Kenya. The Aberdare Forest Reserve, a protected area, surrounds the Park. The highest peaks are Oldonyo Lesatima (4000m) in the north and Il Kinangop (3906m) in the south. Between these peaks is an extensive moorland region distributed between 3300m and 3700m asl. Like many East African mountains, the Aberdare range was formed by volcanic activity during the Pleiocene and the elongate form of the range is a result of the lava spillage. As a result, the main peaks and ravines of the ANP run in almost straight lines linked by a series of ridges. Topographic and edaphic elements modify the distribution of the six main vegetation types (Bushland, *Juniperus* dominated forest, *Podocarpus* dominated forest, *Hagenia* dominated forest, Bamboo, and Ericaceous moorland) found within the park. The vegetation consists mainly of bamboo, high heath moorland with large areas of open and closed canopy forest. Bushland is prevalent at lower elevations occurring particularly in the Salient sector that extends eastwards from the main peaks.

Bushland Thicket

Bushlands are open stands of bushes (usually between 3 and 7 m tall) with a canopy cover of 40 percent or more. Thickets are closed stands of bushes (usually between 3 and 7 m tall) where the bushes are so densely interlaced that they are impenetrable except along tracks made by animals. Bushlands and thickets are taller than shrublands defined as open or closed stands of shrubs up to 2 m tall. Dominant vegetation includes *Hypoestes forskaolii* and *Ocimum suave*. The grass *Cynodon dactylon* is common along game-trails (Schmitt 1992).

Juniperus dominated forest

Afromontane single-dominant *Juniperus procera* forest mostly occurs on the drier slopes of mountains between 1800 and 2900 m, although it sometimes descends to 1000 m (Bussmann 2006). Dominant species include *Juniperus procera*, *Halleria lucida*, *Ilex mitis*, *Kiggelaria africana* and *Nuxia congesta.*

Podocarpus dominated forest

This forest type is very similar in structure to certain types of Guineo-Congolian rain forest (Kindt et al. 2014) but contains conifer species (*Podocarpus*) which are absent from this type of rain forest. These forests occur mainly between 1200 and 2500 m on the slopes of East African mountains.In the ANP this forest type is predominantly found in altitude zone Dominant species include *Podocarpus latifolia, Ocotea usambarensis*, and *Olea capensis*.

Afromontane Bamboo

In East Africa, *Sinarundinaria alpina* bamboo is mostly found between 2400 and 3000 m, although it ascends to 3500 m on Mt. Kenya and to 1630 m Uluguru Mts. (Tanzania). It grows most vigorously on deep volcanic soils and gently slopes where the annual rainfall exceeds 1250 mm. Afromontane bamboo covers almost 65000 ha in the Aberdare mountain Range (Kindt et al. 2014).

Hagenia dominated forest

Characteristically, *Hagenia abyssinica* forms almost pure stands of 9 to 15 m tall in a narrow and often interrupted zone between the montane Ericaceous belt and taller types of Afromontane rain forest. *Hagenia abyssinica* forest is a climax vegetation type where low night temperatures exclude other trees (Schmitt 1992).

Ericaceous grassland

Ericaceous vegetation includes well-developed cloud forest of *Erica excelsa*, and scrub with *E. trimera*, Stoebe *kilimanscharica* and *Cliffortia nitidula*. The altotropical grasslands are dominated by *Festuca pilgeri*, *Koeleria capensis*, the C4 grass *Andropogon lima* (White 1981).

Experimental design

Dung beetles (Coleoptera: Scarabaeidae and Aphodiidae) were collected with pitfall traps baited with elephant dung during three sampling periods; two periods during the wet season during June and August 2015, and one during the dry season in late February and early March 2016. Samples collected in both the wet and dry seasons were pooled for analyses. Two 1 km transects were established in each forest type (Figure 2). We used two transects *per* forest type as logistics and sampling time were limited by the availability of Kenya Wildlife Services security personnel. Eight pitfall traps were used per transect and were baited with 50g of elephant dung wrapped in fine gauge mesh netting and left open for four days at each site. Pitfall traps followed the design of Larsen (2005) and spaced 125 m apart. Traps were emptied and re-baited every 24 hours over a four-day period to provide a total sample of 64 samples *per* forest type and a total of 384 collections. Once collected, the dung beetles were transferred into a 70% ethanol solution for preservation and identification. Dung beetles were identified with the help of Darren Mann and Phillipe Moretto using the following keys: Ferreira (1972), Cambefort (1984), D'Orbigny (1911), Zídek & Pokorný (2004) and Cambefort & Nguyen-Phung, (1996).

Environmental variables

An elevation raster layer was created using the banding toolset in ArcMap 10.4. Digital elevation zones at 500m intervals were created for the land area within the ANP boundary (Figure 1). Supervised classification using Landsat7 data was then used to create a vegetation layer for the ANP (Figure 2). These layers were used to guide transect placement to ensure transects fell into each forest type and altitude zone. To collect data attributes at each pitfall trap location, a modified version of the Standard International Forestry Resources and Institutions method for vegetation sampling (Ostrom 2008) was used to collect the following data: tree species richness, abundance, herbaceous ground cover, and canopy cover surrounding each trap. Two concentric circles (1 m, and 10 m radius) were established around each trap to record these data. Tree seedlings and saplings (2.5–10 cm diameter) were counted in the 1 m radius circle, and mature trees (>10 cm diam.) in the 10 m radius circle. Tree diameter at breast height (dbh) was measured at 1.3 m height. Ground vegetation and canopy cover were determined in the 1 m radius circles. Estimates of percentage ground cover were taken for herbs when individuals were impractical to count. For each trap, the ground vegetation cover was visually scored on five scales as follows: (1) 0-5 percent of the total area of the 1 m radius circle; (2) 5–25 percent of the total area of the circle; (3) 26–50 percent of the total area of the circle; (4) 51–75 percent of the total area of the circle; and (5) >76 percent of the total area of the circle. Canopy cover was measured at three randomly selected points within the 1 m radius of every trap using a spherical densitometer.

Data Analyses

Species richness was estimated for each vegetation type using the non-parametric estimator 'Chao1' (Chao 1984). Chao1 gives an estimate of the absolute number of species in an assemblage based on the number of rare species (singletons and doubletons) in a sample. A Chao1 estimate of species richness is recommended for inventory completeness values, completeness being the ratio between observed and estimated richness (Cao and Epifanio 2010; Buddle et al. 2012). Alpha diversity (α-diversity) is the biodiversity within an area, community or ecosystem, and is usually expressed as the species richness of the area. This can be measured by counting the number of taxa (distinct groups of organisms) within the ecosystem (e.g., families, genera, and species). The Shannon Index (H') was used to measure diversity; the index is increased either by having additional unique species, or by having greater species evenness. Pielou's J' was used to estimate species evenness (based on the Shannon Index) that is the relative abundance or proportion of individuals among the species.

Comparison of species richness, diversity and evenness between habitat types

To test for differences in species richness, abundance and diversity between habitat types and altitude zones we used a Kruskal Wallis test with a post hoc Nemenyi test for multiple comparisons (Zar 2010). We used GLM with Poisson errors and the log link function with Habitat type and Altitude as factors. The χ^2 statistic was used to test for significant changes in deviance. We used a Mantel test to evaluate association patterns between distance matrices (Jankowski et al. 2009) using Bray-Curtis dissimilarities for dung beetle species composition, and Euclidean distance matrices for altitudinal distance, canopy cover and ground cover with 999 permutations.

The Beta.SOR function within the R package Betapart (Baselga 2013) was used to establish the percentage nestedness and turnover between altitude zones and between habitat types. Data were converted from relative abundance data into a presence/absence matrix for use with Sørensen's index. Data were further explored using the beta.core function within Betapart which evaluates the differences in shared species richness between samples.

The Bray-Curtis similarity coefficient was used to determine site similarities based on species abundances. Bray-Curtis cluster analysis (single link) was performed to identify the clustering of habitats into distinct groups. Hierarchical single link clustering takes the similarity matrix as the starting point and successively fuses the samples into groups and the groups into larger clusters, starting with the highest mutual similarities then gradually reducing the similarity level at which groups are formed resulting in a tree diagram or dendrogram plot. Where data conformed to parametric assumptions, such tests were used, otherwise GLMs with appropriate error structure were used. We used R version 3.3.1 (Development Core Team, 2017) to perform all statistical analyses. Mantel tests and calculations of Euclidean distances between altitude pairs were carried out using the 'vegan' (Oksanen 2015) and 'ecodist (Goslee and Urban 2007) packages.

CLAM analysis (Multinomial Species Classification Method (Chazdon et al. 2011) was used to determine which species are indicators of Afromontane habitat types in the Aberdare mountain range. CLAM is a multinomial model which uses relative abundance of species in two distinguishable habitats. One advantage of CLAM is that the procedure explicitly considers a threshold for rarity, meaning that species that are too rare cannot be classified, and distinguishes species that are generalists from those that demonstrate specificity to one habitat type (Chazdon et al., 2011). An important parameter of the multinomial model is K, which refers to the cut-off point for classifying species according to their habitat type. CLAM was used to classify generalists and specialists into open and closed vegetation types by setting a specialization threshold of $K = 0.667$, $P = <0.05$ (Bicknell et al. 2014). The model classifies species into one of four groups: (1) Generalist; (2) Habitat A specialist (specialist of open vegetation); (3) Habitat B specialist

(specialist of closed canopy vegetation); and (4) too rare to classify with confidence. Dung beetles were classified as an indicator of a particular habitat type if ≥66% of their occurrences were within that habitat during the sample period.

Habitat associations of individual species and functional guilds were ascertained using Pearson Chi-squared residuals and plotted using the hclust function in the Vegan package (Oksanen 2015) to visualize both positive and negative associations and also split dung beetle species into community groups. To see which species were indicative of the six forest types in the ANP, indicator species analysis in the form of association analysis was undertaken using these Pearson residuals. This analysis details which species have significant associations (either positive or negative) for each habitat type based on the co-occurrence of species and uses the probability that the observed frequency of co-occurrence is significantly large and greater than expected (positive association), significantly small and less than expected (negative association), or not significantly different and approximately equal to expected (random association) (Veech 2014).

Results

A total of 8020 individuals from 34 species belonging to 16 genera were captured at twelve transect locations across a 1.5 km altitudinal gradient that spanned from 1901 - 3972 m asl (Figure 1). Eleven species from a previous study conducted by (Davis and Dewhurst, 1993) were recorded plus a further 23 species, three of which were new records for Kenya; *Catharsius gibbicollis, Catharsius sesostris,* and *Hetronitis ragazzi*, plus one new species *Epidrepanus kenyensis* (Roggero et al. 2017). Tunnelling dung beetles constituted the majority of species collected with 82% of the total versus 15% for dwellers and just 3% of rollers. The non-parametric estimate of total species richness was 43 species, indicating that most of the species pool was collected (around 80%). The most abundant species across all habitats were, *Neocolobopterus kivuanus (*1362, 17%), *Onthophagus proteus (*935, 11.6%)*, Onthophagus sp 2*, *(*875, 10.9%), *Onthophagus spurcatus (*792, 9.8%)*, and Milichus picticollis (*587, 7.3%). These five species accounted for 57% of all individuals collected, demonstrating that habitats were dominated by a few abundant species. An overview of the dung beetle assemblages found in each habitat type is found in Appendix S1.

Variation of dung beetle assemblages in altitude between habitat types and altitude gradients

Each habitat type was described in terms of its diversity, evenness, and estimated richness (Table 1). Significant positive correlations were found between mean ground cover and dung beetle abundance (rho = 0.40, df = 95, <0.001) and species richness (rho = 0.42, df = 95, <0.001). Significant negative correlations were found between mean canopy cover and dung beetle abundance (rho = -0.24, df = 95, <0.01) and species richness (rho = -0.23, df = 95, 0.05). The overall abundance of individuals, species richness and diversity between habitats did not differ significantly when altitude was also accounted for (Table 2).

Altitude was negatively correlated with dung beetle abundance, species richness, and diversity (abundance: $R^2 = -0.392$, $P =<0.001$, richness: $R^2 = -0.779$, $P =<0.001$, diversity: $R^2 = -0.735$, $P =<0.001$), and there were also significant differences in abundance, species richness and diversity between altitude zones (Figure 3). However, dung beetle abundance, species richness, and diversity did not significantly differ among habitat types (Table 2).

Species composition and habitat specificity

Of the 34-species found in this study, eight (23%) were deemed indicator species by the Pearson residuals in Chi-squared tests of association - *Diastellopalpus johnsonii, Milichus picticollis, Neocolobopterus kivanus, Oniticellus planatus, Onitis anthracinus, Onitis meyeri, Onthophagus miricornis*, and *Onthophagus proteus*. Most habitats had more than one indicator species. The strongest positive associations for Bushland thicket were *Milichus picticollis,* followed by *Diastellopalpus johnsonii* and *Onitis meyeri* (Figure 4) all of which have also been indicated as either generalist or open vegetation specialists (Table 3). Bamboo habitat had four indicator species, with *Neocolobpterus kivunaus* belonging to the Aphodiine having the strongest positive association followed by *Oniticellus planatus, Onitis anthracinus,* and *Onthophagus miricornis. Onthophagus proteus* was positively associated with Ericaceous moorland along with *Neocolobpterus kivunaus*. Hagenia Forest had four indicator species but was most positively associated with *Onthophagus miricornis*. Two species were positively associated with Juniper forest; the large tunneller *Onitis anthracinus* and *Milichus picticollis*, while Podocarpus dominated forest had associated two species; *Oniticellus planatus* and *Onitis anthracinus.*

CLAM analysis (Chazdon et al., 2011) further identified which species could be considered forest and open vegetation specialists. Fourteen species (41%) were classified as open vegetation specialists, ten species (32%) were classified as forest specialists and five species (15%) were found in both open and closed vegetation. Five species (*Epidrepanus kenyensis*, *Catharsisus gibbicollis, Catharsisus setostris*, *Heteronitis ragazzii*, and *Heliocopris stroehli*) were categorised as too rare to classify as either a generalist or specialist.

Diversity Patterns

Overall beta diversity was high between all habitat types showing very little species overlap (Table 1). The dendrograms in Figure 5 illustrate the differences in community composition between habitats and altitude zones by measuring the degree of community overlap between habitat types. The axis height of the dendrogram signifies β values per habitat type or altitude band. The scale ranges between zero (no overlap) and one (perfect overlap). The Bray Curtis index grouped the species communities in *Juniperus* and *Podocarpus* lowland forest types together along with the mid altitude *Hagenia* dominated forest (Figure 5(B)) demonstrating that there are more shared species between these three sites in comparison to bushland thicket and bamboo habitat types. The upland Ericaceous moorland is the most dissimilar in terms of species composition between habitat types. The pattern is replicated with the analysis of dissimilarity between altitude zones with two branches separating zones above and below 2500m asl (Figure 5 A-C).

Analysis of β-diversity patterns revealed a significant positive correlation between dung beetle pairwise community dissimilarity (βSOR) and the Euclidean distance between transects (Mantel $r^2 = 0.65$, $P < 0.05$) demonstrating that variation in communities was strongly and significantly related to their spatial distance. β-diversity partitioning between altitude zones showed that effects were mostly due to species turnover, which accounted for 91% of total variation compared to 4% for nestedness. β-diversity partitioning between forest types showed that effects were split between species turnover, which accounted for 64% of total variation and 87% for species nestedness indicating that species replacement (turnover) occurs at a much higher rate between altitude zones than between forest types.

Discussion

This study addressed the effects of landscape heterogeneity and altitude on dung beetle communities by comparing community dissimilarity, species diversity and species abundance among sites that varied in forest type and altitude. This study found no significant relationship between species richness and forest type but an interaction between the two factors plus a significant negative relationship between species richness and altitude which demonstrates g that altitude in conjunction with forest type are the main factors in shaping dung beetle species composition in this Afromontane forest.

Variation in community structure between habitat types on an altitudinal gradient

Our results suggest the most important characteristic for determining community structure was mean canopy cover *per* forest type. A decrease in species richness was observed with increasing canopy cover but an increase in dung beetle abundance was detected in forest habitats with increased ground cover. The structure and complexity of forest canopies and understory vegetation can enact changes on local microclimatic conditions by causing changes in levels of radiant heat (Jay-Robert et al. 1997), light intensity and air and soil temperature. Many forest dung beetles are extremely sensitive to light intensity (Davis 2002) and as such may be restricted to either shaded or unshaded habitats. These differences may also be related to the temperature requirements of developing larvae. Halffter and Matthews (1966) suggested that the larvae of some species can only develop in shady forest habitats, whereas others will thrive in warm open pastures. Our results contrast those from previous studies conducted in the Neotropics (Pineda et al. 2005; Halffter et al. 2007; França et al. 2017). We found a greater number of species considered open vegetation specialists in comparison to forest specialists (Table 3).

Interestingly, comparisons may be drawn to the similarity in composition between temperate European dung beetle communities and those of the ANP. Both temperate and high-altitude dung beetle communities have a greater association with open vegetation and have demonstrated decreases in species richness as vegetation cover increases. The high proportion of tunnellers, the large number of individuals belonging to the genus *Neocolobopterus* in the Aphodiidae family, plus the paucity of roller species is more akin to a community found in a temperate ecosystem rather than an Afrotropical one. This undoubtedly is an altitudinal effect related to decreases in temperature and increases in rainfall found in high altitude montane areas (Byk and Piętka 2018). Similar findings in altitudinal replacement between the two main groups of dung beetles Aphodiini and Scarabaeinae (Lobo and Halffter 2000), have been reported from the mountainous areas of the Neotropics and the Afrotropics (Lobo and Davis 1999; Davis et al. 1999) and are similar to that which takes place along higher latitudes (Lobo, 2000). The cool-adapted species of Aphodiidae dominate the high altitude and species-poor temperate communities, while the warm-adapted Scarabaeinae species often dominate the low altitude and species-rich tropical communities (Escobar et al. 2005). We detected an almost complete absence of roller (telocoprid) species. This absence may be explained by telecoprid reproductive strategy, small body size (Hanski & Cambefort 1991) and inability to maneuver dung resources within densely forested habitats. A weak, but significant, correlation between beetle abundance and ground cover suggests that dung beetle distribution may be affected by another factor namely soil type (Osberg et al. 1994; Davis 1997), with the degree of vegetative cover being of lesser importance. However, as soil identification in each habitat type was not undertaken for this study, this cannot be verified.

Indicator species

Two species captured in open vegetation were not found in any of the *Juniperus, Hagenia* or *Podocarpus* dominated forests, (*Sisyphus sp1* and *Copris algol*), whilst one species, *Catharsius sesostris* was found to be unique to forested sites. These three beetle species were found in low abundance (<8 individuals) and were below the abundance threshold required by CLAM to conduct analyses. Of the 28 species used in CLAM, the majority of the dung beetles in the ANP are either restricted to closed canopy forest, or open vegetation that is located on the edges of forests and in glades, with few species inhabiting both (Table 3). Six of the eight species indicated as having strong associations with the habitat types studied are tunneling (paracoprid) dung beetles, with the remaining two, *Neocolopterus kivuanus* and *Oniticellus planatus* dweller (endocoprid). All eight species identified as indicators adhere to Caro's (2010) criteria for ecological disturbance indicator species in that their inventory, life history, and population forms a measurable temporal response to environmental change (Siddig et al. 2016). *Onthophagus proteus* and *O. miricornis* are considered regional endemics with a distribution likely centered around the Aberdare and Mount Kenya National Parks (D'Orbigny 1913). It is recommended that these species in particular be regarded as an ecological disturbance indicator and be used to monitor change in the health and distribution of habitats in the Aberdare National Park. However, very little is known about their dung preference (Stanbrook 2018) or the dispersal ability for these species and information on these traits would need to be collected to form part of a comprehensive future planning process.

Biogeographical drivers of Afromontane dung beetle community composition

Distinct differences in beetle abundance and species richness between open habitats and forested habitats have been found repeatedly throughout the Neotropics (Estrada and Coates-Estrada 2002; Vulinec 2002). Half of the dung beetle species which were found to be resident in forested habitats in the ANP belong to the genus *Onthophagus*. Onthophagine dung beetles are ubiquitous across all habitats in Afrotropical forests (Cambefort and Hanski 1991) and therefore their presence in large numbers in forested habitats in the ANP was expected. Onthophagines are generally smaller-bodied tunneller beetles that dig comparatively shallow nests and exist on a wide range of dung types (Davis et al. 2008). Over two thousand species of Onthophagines are currently described worldwide and the genus was determined to have diversified during the Oligocene, a diversification that coincided with the expansion of grasslands and the dispersal of mammals (Davis et al. 2002). Onthophagines were abundant in all habitats and across all elevation zones in the ANP up to 3800m asl. However, in South America this genus is mostly restricted to habitats below 2000m asl, with few species found at higher altitude on mountains (Zunino and Halffter 2007). The pattern of dung beetle species distribution clearly showed that the attenuation of dung beetle species richness at higher altitude zones is accompanied by species turnover, as species composition at low and high-altitude zones was largely different from that of mid-altitude zones. Numerous dung beetle species 'dropped out' with increasing elevation and were replaced by higher elevation specialists (e.g. *Onthophagus proteus* and species of the *Neocolobopterus* genera), resulting in little nestedness but high turnover. This type of high species compositional turnover along elevation gradients has been related to temperature and resource availability (Whittaker, 1956; MacArthur, 1972). High rates of turnover, as demonstrated here, have been documented for Central and South American (Alvarado et al. 2014) and African montane ecosystems (Gebert, Steffan-Dewenter, Moretto, & Peters, 2019). The rate at which species are replaced on an altitudinal gradient is related to a number of factors acting at landscape scales down to the availability of microhabitats along the gradient. The ANP forms part of the Aberdare range which when formed during the Miocene (23-11 mya) was an isolated uplift (Scoon 2018b) and was almost entirely covered by savannah grassland (Pound et al. 2012). Many geologically older mountain tops exhibit a filtered, less diverse set of species which are phylogenetically related to those inhabiting lower elevations (Lobo and Halffter, 2000) and this may account for the high degree of nestedness between forest types on older mountain tops where the species composition of species-poor sites is a subset of the species-rich sites.

Mountain peaks experience widely contrasting ecological conditions in comparison to their surrounding lowlands. In their comprehensive global study of altitudinal variation in dung beetle assemblages on different mountains, Lobo and Halffter (2000) proposed two separate biological processes to explain the conformation of montane biota, the patterns of species richness and variations in community composition. Firstly, vertical colonization defined as upland assemblages composed by species phylogenetically related with those inhabiting lowlands; and secondly, horizontal colonization defined as colonization of highland assemblages by lineages with a different evolutionary history and origin than those occupying lowlands. These processes as well as speciation are described as the drivers of mountain diversity (Lobo and Halffter, 2000b; Escobar et al., 2006; Arriaga-Jiménez et al., 2018).

Biogeography is important in terms of ascertaining how dung beetle colonization occurred in the ANP. When the Aberdare mountain range was formed it was an isolated uplift, with its nearest neighbor being Mount Elgon, also newly formed, 350 km away (Scoon 2018a). Mount Kenya, its current closest highland block was not formed until the Pliocene Epoch, two million years later (Scoon 2018b). This makes it unlikely that horizontal colonization occurred due to the source population of Mount Elgon being at a greater distance than dung beetle dispersal capabilities allow, meaning that it is likely dung beetle species originally colonized the Aberdare range vertically, from the lowlands upwards. Lobo and Halffter (2000) outline two criteria that govern vertical colonization of dung beetles from lowlands: (1) vertically colonized mountain tops exhibit a filtered, less diverse set of species which are phylogenetically related to those inhabiting lower elevations; and (2) species richness decreases with increasing altitude as consequence of the environmental restrictions imposed on the fauna from warmer altitudes, especially in tropical regions (Janzen 1983). The most recent published dung beetle survey in the lowlands of the Aberdare range occurred at Mpala Ranch approximately 75 km away in 2002 (Gordon and Barbero 2008). A comparison of the species found at Mpala and those in the ANP reveal a limited overlap with seven species present in both locations, accounting for 23.5% of the species present in the ANP. These common species have an East African or Central West African distribution and are widespread in savannah habitat. With this in mind, and by meeting the criteria described above, it is likely that vertical colonization of the Aberdare range occurred as there is a significant overlap between lowland species and those found in the ANP. Also, the ANP dung beetle fauna does exhibit a notable decrease in species richness with altitude dropping from 29 species found at ~2000m to just 18 residents at elevations greater 3500m asl (Appendix S2).

Conservation implications

Mountains are key environments for conservation of biodiversity during climatic change, providing refugia for species during postglacial cycles. Montane communities of dung beetles are important not only as historical and biographical reference points, and suppliers of values ecosystem services, but also as potential barometers of environmental change due to global warming. Global warming threatens montane dung beetle diversity by forcing species upslope, and reducing the space occupied by species specifically adapted to the cold or those that have limited thermal tolerance (Birkett et al. 2017). Any environmental change will cause local native populations to either adapt or migrate to avoid extirpation. Ectotherms are predicted to shift more rapidly in response to climate change than mammals (Paaijmans et al. 2013), due to having limited control of their body temperature compared to endothermic animals (Sheldon et al. 2011) and the unlinking of dung beetles and the food resources they depend upon may lead to declines and extinctions of Afromontane dung beetles in the future. Increased monitoring of dung beetle populations is urgently needed. Currently just 224 out of an estimated 7,500 species of sub-Saharan Scarabaeidae dung beetle have been assessed for inclusion in the Red List by the IUCN (www.iucn.org). We suggest those species whose distributions include montane ecosystems should take priority for future assessment for inclusion in future threatened species assessments. The increased conversion of available lowland habitats into commercial and agricultural small holdings and the upland shifting of these degraded habitats into montane lowland forest is expected. These impacts will effect montane species disproportionately as they become threatened with a loss of climate space and be pushed to the edge of their fundamental niche (Elsen and Tingley 2015).

Due to their biogeographical history and specialisms the dung beetles in Afromontane forest may be particularly negatively affected by temperature increases associated with global warming. Our results indicate that there is both intra- and interspecific variation in elevational placement and habitat preference of species and individuals. The upward shift in plant species, resulting in changes to habitat structure and even habitat loss is a well-documented occurrence in climate change literature (e.g. Thomas et al. 2004; Dirnböck et al. 2011); and will likely affect the dung beetle species in the ANP by pushing stenotypic species upwards into unsuitable habitat. Kohler and Maselli (2012) refer to mountains as early warning systems as they may provide an indication of the changes in species composition that lowland ecosystems can expect in the future due to climate change. Changes in the distribution of biota between lowlands and mountains in response to climate change are already widely documented (Gottfried et al. 2012; Menendez et al. 2014) and the use of dung beetles as indicators of environmental changes due to climate change is now growing (Menéndez and Gutiérrez 2004; Birkett et al. 2017). Results from a previous short study conducted in 1974 (Davis and Dewhurst, 1993) indicate while there was significant overlap between dung beetle species caught 40 years ago and the present day there were also seven species which were absent; *Euoniticellus inequalis, Euoniticellus triangulates*, *Copris nepos, Onitis vanderkellini*, two species in the genus *Caccobius* and *Liatongus spathulatus.* All of these species have climatic distributions centered around the wet highlands of East Africa (Davis and Dewhurst, 1993) and further work is urgently required to understand why these species are no longer detectable in the ANP.

The indicator species highlighted in this study should form a strong starting point for the instigation of a concerted management plan involving dung beetle distributional change in Afromontane ecosystems. Research exclusively focused on diversity patterns on tropical mountains at elevations higher than 2500m asl are rare (Mastretta-Yanes et al. 2015) and rarer still for African mountains. This study specifically concentrates on the dung beetle fauna found in Afromontane forests and the compositional changes which occur along an altitudinal gradient. Our results have important conservation implications as they underscore the importance of preserving forest heterogeneity to maintain dung beetle diversity within mountain ecosystems.

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Tables

Table 1 Alpha, Beta and Gamma diversity, Simpsons (H’); Simpsons (λ) and Evenness (J’) and Species Richness estimators for each habitat type in the Aberdare National Park, Kenya

Habitat type	Diversity			Indices			Richness estimator
	γ	β	α	H’	λ	J’	Chao1†
Bushland Thicket	32	1.63	21.43	2.94	0.922	0.828	36.87
Juniper dominated forest	31	1.95	17.37	2.86	0.923	0.811	34.15
Podocarpus dominated forest	32	2.05	15.56	2.85	0.925	0.823	32.11
Bamboo	26	2.53	10.25	2.36	0.837	0.727	31.62
Hagenia dominated forest	26	2.63	9.87	2.20	0.833	0.677	26.93
Ericaceous grassland	19	3.14	5.56	2.00	0.808	0.68	22.75

†(Chao,1984)

Table 2 Results of a generalized linear model assessing dung beetle community Richness(A); Abundance (B); and Shannon Index (C), for six habitats in the Aberdare National Park and five Altitude Zones (Z1-Z5)**.**

(A)Richness

Source	Sum of Squares	DF	Mean Squares	F	P
Habitat	2609.39	3	652.35	35.56	0.083
Altitude Zones	126.02	4	42.01	2.290	<0.001
Habitat*Altitude Zones	3314.06	88	22.156	16.14	<0.001

(B) Abundance

Source	Sum of Squares	DF	Mean Squares	F	P
Habitat	19793	3	6598	0.180	0.909
Altitude Zones	619846	4	154962	4.229	<0.05
Habitat*Altitude Zones	119546	88	95214	2.291	<0.01

(C) Shannon (H’)

Source	Sum of Squares	DF	Mean Squares	F	P
Habitat	0.9123	3	0.3041	2.1892	0.09
Altitude Zones	15.2140	4	3.8035	27.381	<0.001
Habitat*Altitude Zones	9.3184	88	1.9414	16.58	<0.001

Table 3 The results of CLAM analysis which assigned specialist or generalist status on the proportion of individuals found in each vegetation type.

Generalist species	Open Vegetation species	Forest Specialist Species
Copris atropolitus	*Catharsius setostris*	*Caccobius sp*
Helicopris neptunus	*Copris morphaeus*	*Copris algol*
Ixodina abyssinica	*Copris sp2*	*Euoniticellus intermedius*
Onitis meyeri	*Copris typhoeus*	*Neocolobterus kivuanus*
Onitis parvulus	*Diastellopalpus johnstonii*	*Onitis planatus*
	Helicopris hunteri	*Onthophagus nigriventris*
	Liatongus arrowi	*Onthophagus dochertyi*
	Milichus picticollis	*Onthophagus miricornis*
	Neocolobopterus maculicollis	*Onthophagus sp2*
	Onthophagus filicornis	*Onthophagus spurcatus*
	Onthophagus proteus	
	Onthophagus spp1	
	Proagoderus sexcornutus	
	Sisysphus sp1	

Figure legends

Fig 1 The location of the National Park in Kenya (a,b) and (c) the locations of vegetation transects and vegetation types within the Aberdare National Park. The altitude of each transect is indicated by red labels.

Fig 2 The study area showing boundary of the Aberdare National Park**,** Kenya and the distribution of the altitudinal zones found within the Aberdare NP. SRTM data was separated into 500m equidistant intervals to divide the Aberdare National Park into five elevation zones. Red dots represent transect locations. Yellow zone =Z1, Light Green zone = Z2, Dark Green zone =Z3, Blue zone = Z4, Purple zone =Z5.

Fig 3 Altitude as a predictor of dung beetle (a) abundance, (b) richness, and (c) diversity. The regression line is indicated in red, with the standard error of the mean plotted in grey.

Fig 4 Indicator species for each habitat using Pearson residuals derived from Chi Squared test of association. Positive residuals relate to positive associations, negative residuals relate to negative associations. Diasjohn: *Diastellopalpus johnstonii;* Milipict: *Milichus picticollis;* Neokivu: *Neocolobopterus kivuanus;* Onitplan: *Oniticellus planatus;* Onitanth: *Onitis anthracinus;* Onitmeyeri: *Onitis meyeri;* Onthmiri: *Onthophagus miricornis;* Onthprot: *Onthophagus proteus*.

Fig 5 Dendrograms showing the degree of dissimilarity in dung beetle beta diversity among (A) turnover (species replacement) in altitude zones B1 (1888-2000m asl), B2 (2001-2500m asl), B3 (2501-3000m asl), B4 (3001-3500m asl), and B5 (3501-4000m asl) and (B) habitats based on a cluster analyses using the Sørenson index. Nestedness (species subsets) between altitude bands is displayed in (C) and between habitat types in (D). The axis height of the dendrogram is β values per habitat type or altitude band.

Appendices

Appendix S1: The number of Dung beetle species recorded *per* forest type in Aberdare NP, Kenya.

Habitat **Species**	**Bushland thicket**	**Juniperus dominated Forest**	**Podocarpus dominated Forest**	**Hagenia dominated Forest**	**Bamboo**	**Ericaceous grassland**
Caccobius Spp1	30	173	67	15	1	0
Catharsius gibbicollis	1	2	0	1	0	0
Catharsius setosis gp	0	2	3	0	0	0
Copris algol	2	0	1	0	1	0
Copris atropolitus	21	30	25	22	0	0
Copris morphaeus	92	44	31	26	1	0
Copris Spp2	2	5	4	0	0	0
Copris typhoeus	22	19	21	13	0	0

Diastellopalpus johnstoni	7	4	2	0	0	0
Epidrepanus keniensis	1	4	0	0	0	0
Euoniticellus intermedius	54	116	45	77	11	0
Heliocopris hunteri	6	2	0	0	0	0
Heliocopris neptunus	3	1	0	0	0	0
Heliocopris stroehli	23	2	0	0	0	0
Hetronitis ragazzi	1	5	2	0	0	0
Ixodina abysinnicus	125	6	0	2	0	0
Liatongus arrowi	34	74	35	35	11	0
Milichus picticollis	52	444	89	0	0	2
Neocolobopterus kivuanus	232	287	259	379	173	32
Neocolobopterus macaucollis	20	103	46	11	5	0

Oniticellus planatus	63	105	39	3	8	0
Onitis anthracinus	15	30	37	0	1	0
Onitis meyeri	95	75	38	49	8	0
Onitis parvvulus	41	63	46	9	2	0
Onthophagis nigriventis	11	30	13	22	3	3
Onthophagus proteus	179	308	204	21	112	111
Onthophagus dochertyi	40	143	61	3	4	26
Onthophagus filicornis	67	46	0	51	51	29
Onthophagus fimetarius	4	22	8	0	9	1
Onthophagus miricornis	45	102	8	61	101	99
Onthophagus spp1	28	17	17	0	6	1
Onthophagus spp2	129	446	235	55	1	9

Onthophagus spurcatus	180	297	129	165	21	0
Proagoderus sexcornutus	40	3	9	3	0	0
Sisyphus sp1	5	0	0	0	0	0

Appendix S2: Dung beetle abundance, species richness and diversity recorded *per* Altitude zone in Aberdare NP, Kenya

Altitude Band	**Zone 1** **1888-2000m**	**Zone 2** **2001-2500m**	**Zone 3** **2501-3000m**	**Zone 4** **3001-3500m**	**Zone 5** **3500-4000m**
Species					
Caccobius n.sp	73	543	15	32	0
Catharsius gibbicollis	11	9	0	1	0
Catharsius setosis gp	5	7	0	0	0
Copris algol	6	152	6	8	13
Copris atropolitus	14	101	10	25	9
Copris morphaeus	19	189	10	33	1
Copris Spp2	18	99	13	50	1
Copris typhoeus	14	99	15	16	9
Diastellopalpus johnstoni	13	187	0	6	0
Epidrepanus keniensis n.sp	1	4	0	0	0
Euoniticellus intermedius	65	718	97	165	22
Heliocopris hunteri	31	24	0	0	0

Heliocopris neptunus	4	25	0	0	0
Heliocopris stroehli	9	31	0	0	0
Hetronitis ragazzi	0	5	0	0	0
Ixodina abysinnicus	16	66	2	3	0
Liatongus arrowi	38	185	13	10	0
Milichus picticollis	465	794	0	3	0
Neocolobopterus kivuanus	209	1450	51	1140	227
Neocolobopterus macaucollis	70	208	15	39	30
Oniticellus planatus	43	428	146	150	3
Onitis anthracinus	13	179	50	29	1
Onitis meyeri	28	77	28	8	0
Onitis parvvulus	33	213	6	20	4
Onthophagis nigriventis	9	92	8	19	5
Onthophagus proteus	72	422	77	40	2
Onthophagus dochertyi	22	235	50	154	86

Onthophagus filicornis	17	93	8	62	72
Onthophagus fimetarius	173	1096	193	703	43
Onthophagus miricornis	54	835	34	273	188
Onthophagus sp1	50	144	13	19	13
Onthophagus sp2	201	802	38	49	0
Onthophagus spurcatus	58	598	31	90	0
Proagoderus sexcornutus	23	43	0	3	0
Sisyphus sp1	4	1	0	0	0
Abundance	1881	10154	929	3150	727
Species Richness	33	34	24	26	18
Diversity (H’)	2.69	2.64	2.71	2.19	1.54