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ORIGINAL RESEARCH ARTICLE

Dung Beetle (Coleoptera: Scarabaeidae, Scarabaeinae) diversity of the highest elevation in West Africa: the Nimba Mountain Range

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Abstract
The Nimba Mountain Range located in the West African countries of Guinea, Cote d'Ivoire, and Liberia is part of the Upper Guinean Forest ecosystem, a critical biodiversity hotspot highly threatened by human activities. Dung beetle sampling on the Mount Nimba Strict Nature Preserve and in the nearby Bossou Forest or Hills Reserve in Guinea was done to document the dung beetle species diversity of the area in both different habitats and elevations ranging from about 600 to 1600 m and to assess, via this surrogate fauna, the biotic integrity of this World Heritage Site. As expected, evidence revealed a trend of lower diversity and abundances at the highest elevations but sometimes high variability even between similar habitats and at similar elevations. While a total of 50 species and 955 individuals were collected from all sites, the highest diversity and abundances were found in a high elevation forested savanna at ~1200 m where a total of 24 species and 402 individuals were collected. At the highest elevation sampled at ~1600 m, a total of only eight species and 20 individuals were collected and all of these taxa were also found at lower elevations. Forests sampled at moderate elevations had similar faunas in some but not in all cases and always a unique pattern of species abundances. A high elevation savannah had the highest species diversity and abundance and may still have a relatively intact dung beetle fauna. Comparatively lower diversity and abundances than what was expected at some sites may reflect a declining ecosystem due to low mammal populations brought on either by small habitat size in Bossou or bush meat hunting in the Nimba Range. Preservation of this truly unique West African ecosystem will require continued protection from or careful regulation of human activities.

Keywords Guinea · Ivory Coast · Liberia · Biodiversity · Upper guinean forest

Introduction

The Nimba Mountain Range includes Mount Richard-Molard and at 1,752 m in height, is the highest elevation in the western block of the Upper Guinean Forests of West Africa (UNEP-WCMC 2008). At its northern end, this range is situated along the border between eastern Guinea and west-central Cote d'Ivoire and extends south into Liberia. Due to the range of elevation from less than 600 to over 1,700 m, the area offers a variety of habitats including lowland, montane, and cloud forests, as well as savanna. Montane forests are present between 550 and 1,000 m. Cloud forest predominates above 900 m, and montane grasslands can be dominant ~1,100 m and higher with gallery forests located within ravines. Disturbed habitats are found on the lower elevations typically between 500 and 600 m but up to 800 m in some locations.

The Upper Guinean Forest of West Africa that include the Nimba Range is considered a critical biodiversity hotspot as it has both a high concentration of endemic species and is highly threatened (Myers et al. 2000; Mittermeier et al. 2004; Fauna and Flora International 2009; Conservation International 2021a). While these forests retain only 10% of their primary vegetation, they contain 2,250 endemic vascular plant species (Conservation International 2021b; Myers et al. 2000). More specifically, the Nimba Mountain Range and vicinity also holds notable and threatened animal

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species including the Bossou population of chimpanzees, the endemic Nimba otter-shrew, a wealth of bat diversity, several range-restricted bird species, and the endemic viviparous Nimba toad (Monadjem et al. 2016, 2019; Bryson-Morrison et al. 2017; Sandberger-Loua et al. 2017; Birdlife International 2021). Moreover, the range has acted as an important forest refuge during glacial periods, further increasing its biodiversity conservation value (Cotillon and Tappan 2016).

The Nimba Mountain Range region is highly threatened by human activities that both alter and fragment habitats and likely modify species distributions as well, including those of dung beetles. The assaults include agriculture, hunting, mining, logging, encroachment by grazing cattle, and bush fires (Lebbie 2001). Further issues for this World Heritage site are inadequate management, funding, and staff, and lack of transboundary cooperation (International Union for Conservation of Nature and UN Environment World Conservation Monitoring Centre 2017).

Studies focusing on the effects of deforestation on dung beetle assemblages in West Africa suggest that deforestation and habitat fragmentation caused by agriculture and industry alter assemblage structure, negatively affecting forest dung beetle species while favoring savanna species (Davis and Philips 2005, 2009). Bush meat hunting and trade, provoked by economic hardship brought on by conflict and political instability (Fauna and Flora International 2009), has also been suggested as a cause for dung beetle decline as it reduces the abundance of larger mammals in this region (e.g. Lebbie 2001).

Research on the effect of elevation on species diversity on mountains can be more convenient and potentially more appropriate for gaining insight into causes of spatial variation of diversity than studying latitudinal gradients (Sanders and Rahbek 2012). Mountains and ranges can act as replicates for study, variables can be manipulated on the ascent of mountains, and it is often easier to collect data across gradients due to the relatively smaller two-dimensional extent of mountains, i.e., less distance needs to be traveled to observe a variety of habitat conditions. Also, the potential causes of spatial variation of diversity on mountains do not covary along latitudinal gradients. It has been suggested that studying the abiotic and biotic elevational gradients on mountains will grant insight into species diversity and produce information valuable to conservation (McCain and Grytnes 2010; Sanders and Rahbek 2012). The most influential factors that cause variability across elevational gradients are thought to be climatic that affect various taxa differently (McCain and Grytnes 2010). Considering this, montane communities will change as the climatic factors affecting diversity are altered via the ongoing effects of the climate crisis.

Dung beetle (Scarabaeidae: Scarabaeinae) surveys were conducted in 2010 and 2011. The primary goals of the research were to document the dung beetle species diversity and trends of the Nimba Mountain Range in various habitats and elevations in particular, but also to possibly discover unique high elevation species. Dung beetles were chosen as the focal taxon for their easy and standard sampling methods, taxonomic accessibility, response to environmental change, ecological importance through nutrient cycling and tightly linked relationships with habitat, dung type, and importantly, mammal abundance and diversity (Cambefort 1982; Cambefort and Walter 1991; Cambefort and Walter 1991; Halffter and Favila 1993; Davis 1994, 1996; McGeoch et al. 2002; Spector 2006). Further, they are ideal for extrapolation of the health of other taxa and hence can be used as a surrogate for the biotic integrity of the area. Lastly, the acquisition of baseline data can be used to track and monitor future changes in this biologically valuable Nimba ecosystem.

Fig. 1 Map of the Nimba Mountain Range study area and the locations of the study sites (from Google Maps)

Methods and materials

Study sites

Data were collected on the Nimba Mountain Range and Bossou forest located in the Nzéré Koré region, southeast Guinea, West Africa (Fig. 1). The Bossou, Made Camp, and Kalazeyeila Plateau sites were sampled in July, 2010 and the Seringbara, SMFG (Société des Mines de Fer de Guinée), Protea, and Richard-Molard sites through May-June, 2011. These sites were chosen for their different elevations as well as their various habitats to maximize the collection of different species on the Nimba range. Habitat types sampled (Fig. 2; Table 1) included low and high elevation moist forests, a high elevation grassland-forest mosaic (the Kalazeyeila Plateau where half the traps were placed in the

Fig. 2 Representative habitats that were sampled during this study. **A** The SMFG (Société des Mines de fer du Guinea) site is near the primary Nimba mine camp, and represents low elevation (875 m asl) moist forest. Similar forest occurs in the Bossou, Made Camp, and Seringbara sites. **B** The high elevation (1165 m) Kalazeyeila Plateau site is comprised of a grassland-forest mosaic habitat. **C** The Protea site is a high elevation site (1185 m asl) with some *Protea* sp. plants and several other unidentified tree species. **D** The Richard-Molard site is a high elevation (1615 m asl) grassland site with a few scattered trees and is habitat for the endemic viviparous Nimba toad

Table 1 Site elevation, coordinates, and number of traps set with each dung type

Site	Elevation (~m)	Habitat Type	GPS Coordinates	Traps and Bait Type (H/P/Z/C)
Bossou	575	forest	N7.6444° W8.4994°	18 (6/6/6/0)
Seringbara	660	forest	N7.6444° W8.4386°	8 (4/0/0/4)
Made Camp	685	forest	N7.6497° W8.4231°	16 (4/4/4/4)
SMFG	875	forest	N7.6991° W8.3976°	20 (10/0/0/10)
Kalazeyeila Plateau	1165	Forest-grass mosaic	N7.6288° W8.4192°	16 (4/4/4/4)
Protea	1185	savanna with scrub trees	N7.6778° W8.3781°	10 (5/0/0/5)
Richard-Molard	1615	grassland	N7.6991° W8.3792°	19 (9/0/0/10)

H human dung, *P* pig dung, *Z* chimpanzee dung, *C* cow dung

forest and half in grassland), a very high elevation grassland, and what was named "Protea Savanna" that contained a species of this plant genus. The Seringbara site is named after a village near this sampling location and is comprised of low elevation (660 m) forest that is slightly disturbed in the vicinity of this populated site via a less dense canopy.

Collection

Dung beetles were collected with conventional dung-baited pitfall traps (Halffter and Favila 1993; Spector 2006) set at elevations between 575 and 1615 m (Table 1). Traps consisted of 16-ounce plastic food containers that were placed in the soil with the brim level with the substrate. Water and several drops of dish soap (to act as a surfactant) were added to the container to a depth of about four centimeters to trap and kill the beetles. To attract the beetles, the dung bait (either cow, pig, human, or chimpanzee) was placed in 2-ounce plastic cups and suspended above the trap using a wooden kebab stick. The bait cups were pierced with the stick near the upper rim on both sides, and the opposite end was pushed into the soil at an angle (~45°) so that the bait was held aloft over the pitfall. A plastic food plate was suspended above the trap using two kebab sticks (piercing the plate on opposite sides) as posts to create a rain roof. While setting the trap, small canals were made in the soil surrounding the trap to divert rain-water away from the trap.

Traps were placed at least 50 m apart and alternating the bait type that was available during the time of field work. Eight to 20 traps were placed at each site and samples were collected after 48 h (see Table 1 for trap number/site). Due to limitations in space and time, sites varied in number of traps set. Samples were placed in alcohol (70% ethanol) inside plastic sample bags (Whirlpacs) during field collecting.

Analysis

In the lab, collected samples were first sorted by removing dung beetles, and allowing them to dry slightly before mounting on either pins or cardboard points or cards. Specimens were sorted and identified to species through use of dichotomous keys, voucher specimens, species descriptions (d'Orbigny 1913; Cambefort and Bordat 2003) and by comparison with museum material.

Dung beetle species abundance and diversity was then counted for each trap catch and compared across sites and differing elevations. Due to the unequal sampling effort, average capture rates per trap were calculated to compare dung preference and abundance across sites more accurately. Dung beetle species diversity data were analyzed with EstimateS version 9.1.0 software (Colwell 2013) to compute diversity estimates and indices including Chao (1 and 2), Jackknife (1 and 2), ACE, Shannon, and Simpson across sites. The Chao 1 and 2 were calculated using the classic option in the diversity settings. For details in the differences between these indices, see the discussions in Colwell (2013) and Magurran (2004). The Berger-Parker Dominance Index was also calculated that emphasizes the numerical importance of the most abundant species: $d = N_{max}/N$ where Nmax is the number of individuals in the most abundant species, and N is the total number of individuals in the sample. The reciprocal of the index, 1/d, was used, so that an increase in the value of the index accompanies an increase in diversity and a reduction in dominance.

Morisita-Horn and Chao-Jaccard indices were also calculated for pairwise comparisons of species composition of sites using 1000 randomizations. The former indicates overall similarity in species present; therefore, a score of 1.00 indicates they share all taxa, while 0.50 indicates they share half of their species. The latter compares samples but takes into consideration the proportion of individuals in each sample as well. The ecological roles and habitat preferences of species were also considered in making conclusions on the biotic integrity of the study area as in Cambefort and Bordat (2003) and Cambefort (1991). To help visualize the level of similarity of the samples from the different elevations as well as type of dung used as bait, nonmetric multidimensional scaling (MDS) ordination was performed in the statistical package R. $N = 2$ was chosen to optimize the object locations for a two-dimensional scatterplot.

Table 2 Average number of individuals of each species per trap at each site sampled with omnivore dung (human, pig, and chimpanzee). A total of 70 traps were set using this type of dung and a total of 757 beetles were captured

Species	Total collected	Bossou	Serinbara	Made Camp	SMFG	Kalaz. Plateau	Protea	Richard-Molard
Chalconotus cupreus	9	0.22	1.25	0	0	0	0	0
Caccobius auberti	5	0.17	0	0	0	0.08	0.20	0
Caccobius mirabilepunctatus	1	0	0	0	0	0	0.20	0
Caccobius sp. protea J	1	0	0	0	0	0	0.20	0
Copris carmelita	8	0	0	0	0	0	1.00	0.33
Diastellopalpus noctis	7	0	0.25	0.50	0	0	0	0
Diastellopalpis pluton	6	0	0	0.50	0	0	0	0
Diastellopalpus tridens	10	0.39	0	0	0	0	0.20	0.22
Epidrepanus caelatus	20	0	0	0	0	0	2.20	1
Garreta azureus	1	0	0	0	0	0	0.20	0
Heliocopris dianae	4	0	0.25	0.25	0	0	0	0
Jossonthophagus curtipilis	1	0	0	0	0	0	0.20	0
Milichus inaequalis lamottei	170	0	42.5	0	1.20	0	0	0
Odontoloma relicta	1	0	0	0	0	0	0.20	0
Onthophagus alluaudi	35	0	3	0.67	1.50	0	0	0
Onthophagus atridorsis	35	0.06	0	0	0	0	6.80	0
Onthophagus bimarginatus	3	0	0	0	0	0	0.60	0
Onthophagus cyanochlorus	2	0.11	0	0	0	0	0	0
Onthophagus densepilis	1	0	0	0	0.10	0	0	0
Onthophagus denudatus endroedyi	12	0	2.75	0	0.10	0	0	0
Onthophagus depilis	6	0	0	0	0.60	0	0	0
Onthophagus feai	22	0	0	0	1.30	0.58	0.20	0.11
Onthophagus fimetarius	2	0.06	0	0	0	0	0.20	0
Onthophagus flaviclava	53	0	0	0	0	0	10.60	0
Onthophagus funestus	15	0	3	0	0.30	0	0	0
Onthophagus fuscatus	15	0.06	2	0.50	0	0	0	0
Onthophagus jonathani	70	2.06	1	1.08	1	0.50	0	0
Onthophagus liberanius	3	0	0.25	0	0.20	0	0	0
Onthophagus longipilis	71	0	0	0	0	0	14.00	0.11
Onthophagus mucronatus	4	0	0	0	0	0.08	0.60	0
Onthophagus pullus	2	0.11	0	0	0	0	0	0
Onthophagus rufopygus	2	0	0	0	0.20	0	0	0
Onthophagus semiviridis	4	0.06	0.25	0.17	0	0	0	0
Onthophagus sinuosus	2	0	0	0.08	0	0.08	0	0
Onthophagus tripartitus	1	0	0	0	0.10	0	0	0
Onthophagus ugoi	1	0	0.25	0	0	0	0	0
Onthophagus sp. N5	2	0	0.25	0	0.10	0	0	0
Onthophagus sp. J5	3	0	0.75	0	0	0	0	0
Onthophagus sp. J8	3	0	0	0	0	0	0.60	0
Onthophagus sp. protea I	6	0	0	0	0	0	0.80	0.22
Onthophagus sp. protea K	1	0	0	0	0	0	0.20	0
Pseudopedaria grossa	3	0	0.25	0.17	0	0	0	0
Sisyphus africanus africanus	88	0.17	0	0.33	0	0.08	16.00	0
Sisyphus angulicollis	31	0	0.25	1	1.80	0	0	0
Sisyphus arboreus	3	0	0	0.08	0.10	0	0	0.11
Sisyphus cf. latus	12	0	1.75	0	0.40	0	0	0.11

Because the cow dung baited traps contributed little additional diversity and abundance data compared to other dung sources, diversity metrics for the Seringbara, SMFG, Protea, and Richard-Molard sites were also calculated with only omnivore dung capture data for these analyzes. Pairwise shared species diversity indices (Chao-Jaccard similarity and Morisita-Horn Overlap) were calculated only with omnivore dung data too.

Results

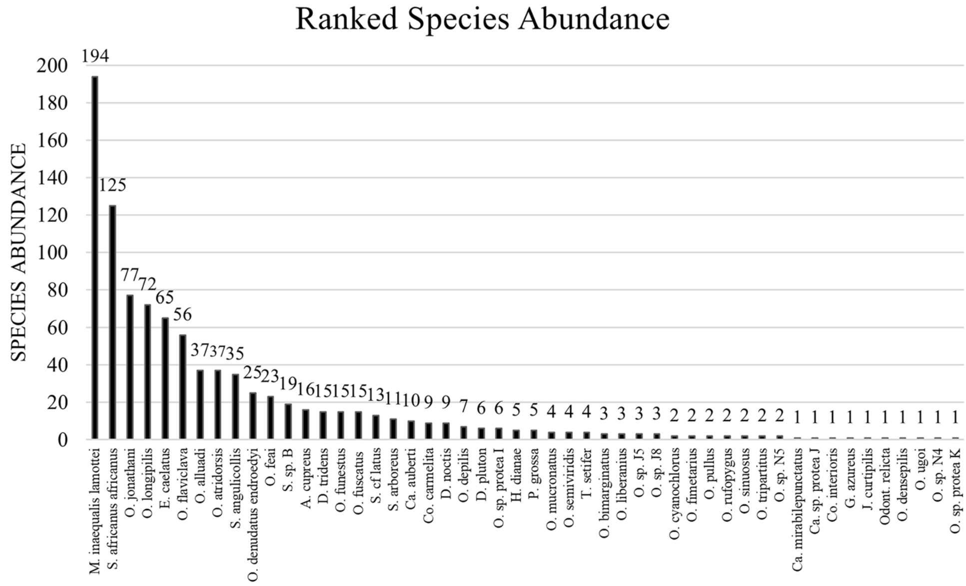
Fifty species, eight of which lack specific names, were observed in the 955 individuals collected (Tables 2 and 3). Species of *Onthophagus* dominated, contributing 28 of the 50 species and comprising 42.7% of the total catch (Fig. 3). The most abundant species was *Milichus inaequalis lamottei* with 194 individuals captured, most of which (182) were sampled at Seringbara and the remainder (12) at SMFG, representing 24.3% of the total catch. *Sisyphus africanus africanus* was also prevalent, making up 14.7% of the specimens, with the majority (117) captured in the Protea site and the remainder (8) in Bossou and Made Camp. The most abundant *Onthophagus* species were *O. jonathani* and *O. longipilis* with 77 and 72 individuals captured respectively. Other relatively numerous species sampled were *O. flaviclava* (56 individuals) and *O. alluaudi* and *O. atridorsis* (37 individuals of each). Notably the collections were very uneven among the collection sites; while *O. jonathani* was collected in five sites (absent from two) all of the other species were collected in only one to three sites (Supplementary Figs. 1–7).

The large-bodied roller *Chalconotus cupreus*, was found only in two low elevation sites (Bossou and Seringbara). Three species of the large tunneler genus, *Diastellopalpus*, were collected, and one species, *D. tridens*, was found in six of seven sites. *Diastellopalpus noctus* was present at three sites while *D. pluton* was the only present at the single site of Made. Two sites (Seringbara and Made) still have *Heliocopris dianae*, the largest tunneler known from West African wet and moist forests.

Table 3 Average number of individuals of each species per trap at each site sampled with cow (ruminant) dung. A total of 37 traps were set using this type of dung and a total of 198 beetles were captured

Species	Total collected	Bossou	Sering-bara	Made Camp	SMFG	Kalaz. Plateau	Protea	Richard-Molard
Chalconotus cupreus	**7**	0	1.75	0	0	0	0	0
Caccobius auberti	**5**	0	0	0	0	0	1.00	0
Copris carmelita	**1**	0	0	0	0	0	0.20	0
Copris interioris	**1**	0	0	0	0	0	0.20	0
Diastellopalpus noctis	**2**	0	0	0	0.20	0	0	0
Diastellopalpus tridens	**5**	0	0	0	0.10	0.75	0.20	0
Epidrepanus caelatus	**45**	0	0	0	0.10	0	8.80	0
Heliocopris dianae	**1**	0	0.25	0	0	0	0	0
Milichus inaequalis lamottei	**24**	0	3	0	1.20	0	0	0
Onthophagus alluaudi	**2**	0	0	0	0.20	0	0	0
Onthophagus atridorsis	**2**	0	0	0	0	0	0.40	0
Onthophagus denudatus endroedyi	**13**	0	2.75	0	0.20	0	0	0
Onthophagus depilis	**1**	0	0.25	0	0	0	0	0
Onthophagus feai	**1**	0	0	0	0	0.25	0	0
Onthophagus flaviclava	**3**	0	0	0	0	0	0.60	0
Onthophagus jonathani	**7**	0	0	0	0	1.75	0	0
Onthophagus longipilis	**1**	0	0	0	0	0	0.20	0
Onthophagus tripartitus	**1**	0	0	0	0.10	0	0	0
Onthophagus sp. N4	**1**	0	0	0	0.10	0	0	0
Pseudopedaria grossa	**2**	0	0.25	0	0	0.25	0	0
Sisyphus africanus africanus	**37**	0	0	0	0	0	7.40	0
Sisyphus angulicollis	**4**	0	0	0.50	0.20	0	0	0
Sisyphus arboreus	**8**	0	0	0	0	0	1.60	0
Sisyphus cf. latus	**1**	0	0.25	0	0	0	0	0
Sisyphus sp. B	**19**	0	0	0	0	0	3.80	0
Tiniocellus setifer	**4**	0	0	0	0	0	0.80	0

Fig. 3 Ranked species abundance observed in dung beetle species surveys on the Nimba Mountain Range and the nearby Bossou forest



The relatively high elevation Protea savanna site had both the highest species diversity with 24 taxa and the highest abundance with 402 individuals captured (Table 4). The next most diverse sites, also with high catches, were the mid-elevation forested sites of Seringbara and SMFG. The former produced 18 species and 274 individuals, while the latter had 19 species and 102 individuals.

The two least productive sites both in terms of species and abundance were the highest elevation habitat Richard-Molard site and the relatively high Kalazeyeila Plateau; in each only eight species were collected from a catch of 20 and 29 individuals, respectively (Table 4). The highest elevation site of Richard-Molard included the species *Copris carmelita*, *Diastellopalpus tridens*, *Epidrepanus caelatus*, three species of *Onthophagus*, and two species of *Sisyphus* (Table 2). All of these species were also found at lower elevations.

Sampling at Protea savanna and the Seringbara site had the highest average capture rate with about 40 and 34 specimens captured per trap, respectively (Table 4). All other sites had dramatically lower capture rates of about 1–5 beetles per trap, with the lowest at the highest site of Richard-Molard. This capture rate varied even more when dung type was used to separate the catch (Table 5). For example, the average capture rate per trap using human dung varied from a low of less than one to more than 61 beetles captured per trap; the rate was lowest (0.25) at the high elevation Kalazeyeila Plateau while the highest site of Richard-Molard is a comparatively high 2.22 capture rate. While pig and chimpanzee dung capture rates were similar to the levels seen in some of the human baited traps, the cow dung attracted low numbers (0.5–8.5) in all but the Protea Savanna as one might expect (e.g. Kunz and Krell 2011), where the capture rate increased to 19 beetles per trap.

Other notable records include a single *Sisyphus cf. latus*, a species described as being found in moist forests, that was observed at the highest elevation Richard-Molard site where only a few scattered trees are present in some areas. Additionally, *Onthophagus atridorsis*, *O. fimetarius*, and *O. pullus* were observed in the forested Bossou site but are recorded

Table 4 Elevation of each site with observed dung beetle species diversity, abundance, and average capture rate (ACR)

Site	Elevation (m asl)	Diversity	Abundance	Average Capture Rate
Bossou	575	11	62	3.389 ± 3.514
Seringbara	660	18	274	34.25 ± 32.824
Made Camp	685	11	66	4.188 ± 4.978
SMFG	875	19	102	5.1 ± 6.935
Kalazeyeila Plateau	1165	8	29	1.813 ± 3.264
Protea	1185	24	402	40.2 ± 24.722
Richard-Molard	1615	8	20	1.053 ± 2.305

Table 5 Dung preference as shown through average capture rates made with different dung types at each site. The number of traps for each dung type is indicated in parentheses

Site	Human	Pig	Chimpanzee	Omnivores total	Cow
Bossou	3.00 ± 3.46 (6)	5.33 ± 4.11 (6)	1.83 ± 1.34 (6)	3.44 (18)	-
Seringbara	60.00 ± 28.64 (4)	-	-	60.00 (4)	8.50 ± 2.96 (4)
Made	4.50 ± 2.06 (4)	9.00 ± 7.28 (4)	2.75 ± 1.48 (4)	5.33 (12)	0.50 ± 0.87 (4)
Kalazeyeila	0.25 ± 0.43 (4)	3.25 ± 2.86 (4)	0.75 ± 0.43 (4)	1.42 (12)	3.00 ± 5.20 (4)
SMFG	9.00 ± 8.05 (10)	-	-	9.00 (10)	1.20 ± 0.98 (10)
Protea	61.40 ± 13.59 (5)	-	-	61.40 (5)	19.00 ± 11.78 (5)
Richard-Molard	2.22 ± 2.94 (9)	-	-	2.22 (9)	0.00 (10)

as savanna species by Cambefort and Bordat (2003). But in contrast, Krell and Kunz (2011) found these species in both savannah and forest habitats, so these three species appear to be habitat generalists. The high elevation Kalazeyeila Plateau grassland- forest mosaic and the Richard-Molard grassland sites were found to be a blend of both savannah and forest species (Table 6).

Estimates of diversity were higher than were sampled for all sites, suggesting species were missed during sampling (Table 7). Additionally, when cow dung traps were excluded, at two sites (Protea Savanna and Seringbara) both the Chao and ACE diversity estimates increased, with one nearly doubling (Chao 1, Seringbara). In contrast, at the SMFG and Kalazeyeila Plateau sites, the diversity estimations and indices decreased after excluding cow dung data. The Made Camp and Richard-Molard sites were either the same or had only slight differences when cow dung traps were excluded.

The Shannon diversity indices did not show a great deal of range (1.41–2.44) while the Simpson indices had more variance (1.92–8.71). While the highest elevation Richard-Molard had the lowest number of species captured, the Simpson Index was higher there compared to that found for three other sites. The Protea Savanna had the highest number of species, but the Simpson index gave higher diversity values for both the Made Camp and the SMFG site. Regression analysis showed no evidence of an elevational trend in Shannon or Simpson indices ($r = 0.138$, $r^2 = 0.019$, $p = 0.768$; $r = 0.199$, $r^2 = 0.040$, $p = 0.668$, respectively, Table 7), even after excluding cow dung data ($r = 0.151$, $r^2 = 0.023$, $p = 0.746$; $r = 0.220$, $r^2 = 0.049$, $p = 0.635$, respectively).

Shared species analysis using the Chao-Jaccard and Morisita-Horn indices revealed some similarity in species composition between the Seringbara and the SMFG sites (Table 8). More unusual is the high similarity between the savannah sites of Bossou and the high Kalazeyeila Plateau found with the Chao-Jaccard but not with the Morisita-Horn index. The highest elevation unforested Richard-Molard site was most similar to the Protea Savanna in both indices. Lastly, the results from the two indices sometimes gave

Table 6 Forest and grassland or savannah species present at the two high elevation sites of the Richard-Molard savannah and the Kalazeyeila grassland-forest mosaic. Note that for the Kalazeyeila site, traps were set in both grassland and forest locations in equal numbers. Species that are either primarily savannah or forest species indicated by a "+" symbol and species absent indicated with a "-" symbol

Species	Kalazeyeila Savannah	Kalazeyeila forest	Richard-Molard savannah	Richard-Molard forest
Caccobius auberti	+	-	-	-
Copris carmelita	-	-	+	-
Diastellopalpus tridens	-	+	-	+
Epidrepanus caelatus	-	-	+	-
Onthophagus feai	-	+	-	+
Onthophagus jonathani	-	+	-	-
Onthophagus longipilis	-	-	+	-
Onthophagus mucronatus	+	-	-	-
Onthophagus sinuosus	-	+	-	-
Onthophagus sp. protea I	-	-	+	-
Onthophagus sinuosus	-	+	-	-
Pseudopedaria grossa	-	+	-	-
Sisyphus arboreus	-	-	+	-
Sisyphus africanus africanus	+	-	-	-
Sisyphus cf. latus	-	-	-	+

Table 7 Diversity estimates and indices for each site. These are calculated excluding the cow dung as indicated with "-C"

Site	Obs. Diversity	Chao1	Chao2	Jack1	Jack2	ACE	Shannon	Simpson	Berger-Parker
Bossou	11	12.96	14.14	15.72	18.49	14.75	1.51	2.62	1.68
Seringbara	18	24.97	24.3	25.87	30.05	29.78	1.41	2.19	1.51
Seringbara-C	17	44.88	27.31	25.25	29.75	42.77	1.26	1.92	1.41
Made Camp	11	11.00	11.18	12.87	11.35	11.36	2.16	7.45	4.71
Made Camp-C	11	11.00	11.18	12.83	11.46	11.36	2.18	7.69	5.08
SMFG	19	23.45	24.06	26.60	28.68	26.72	2.44	8.71	5.10
SMFG-C	15	21.18	20.51	21.30	24.05	22.17	2.26	7.81	5.00
Kalazeyeila	8	17.65	22.06	13.62	18.87	23.03	1.53	3.4	2.23
Kalazeyeila-C	6	11.64	11.50	9.66	13.00	13.47	1.39	3.24	2.43
Protea	24	41.95	34.80	32.10	37.87	34.48	2.13	6.03	3.44
Protea-C	23	67.85	41.00	31.00	36.55	38.19	2.12	5.92	3.84
R-Molard	8	9.90	9.89	11.78	13.67	15.78	1.70	3.92	2.22
R-Molard-C	8	9.90	9.77	11.55	13.30	15.78	1.70	3.92	2.22

conflicting results; the Protea Savanna and the Kalazeyeila Plateau have high species similarity using the Chao-Jaccard index but low similarity using the Morisita-Horn index. This indicates very different abundances of the species that were found in each site as factored into the algorithm of the latter index. The ordination plot (Fig. 4) shows a wide separation in ordinal space of both the Protea and the Made Camp sites from all the other sites. The SMFG, Bossou, and Richard Molard form a tight cluster with the Seringbara and the Kalazeyeila Plateau sites relatively close to that small cluster.

Discussion

Regarding elevational trends in dung beetle diversity, an inverse relationship is usually expected with dung beetle species diversity decreasing at higher elevations (Mongyeh et al. 2018; Sukhdeo et al. 2019; Gebert et al. 2020). This trend was indeed found on the Nimba Mountain Range. The habitats at the highest sampled location (1615 m) in the Richard-Molard grassland and the Kalazeyeila Plateau grassland-forest mosaic (1165 m) had the lowest diversities with only eight species in each while other habitats sampled had 11–24 taxa (Table 4). Notably, species composition in these two areas was very dissimilar with only two species in common and all 14 species found in both areas combined were also present at lower elevations. The three dominant species in the isolated grassland-forest mosaic site of the Kalazeyeila Plateau (*Diastellopalpus tridens*, *Onthophagus feai*, and *O. johnsoni*) were also found in the lowland forest site SMFG. In contrast, the Richard-Molard grassland was more similar to the Protea savannah which may be due to the relative connectivity of these two open sites.

While no unique high elevation taxa were discovered in this sampling effort, dung beetle species have been reported as endemic in the Guinean Forest Highlands and specifically in the nearby Mont Tonkoui (near the town of Man, Cote d'Ivoire) that rises to 1150 m. Possible endemic taxa may include *Heliocopris eryx* (Fabricius), *Diastellopalpus pluton* d'Orbigny (collected in this study at Made), *Proagoderus nicolasi* Moretto, *Catharsius n. sp. cf. sesotris, Ametina n. sp.* and six other new species (Moretto et al. 2021). The 47 species sampled at Mont Tonkoui is a similar number

Table 8 Matrix showing pairwise shared species diversity statistics between sites listed in sequence as the Chao-Jaccard similarity index, the number of shared species (in bold), and the Morisita-Horn overlap index. The indices were calculated using only the omnivore dung data

Site	R-Mol.	Bossou	Seringbara	Made	SMFG	Kala
Bossou	0.055 **1** 0.035	---	---	---	---	---
Sering.	0.018 **1** 0.003	0.072 **4** 0.026	---	---	---	---
Made	0.011 **1** 0.003	0.329 **4** 0.497	0.117 **8** 0.045	---	---	---
SMFG	0.093 **3** 0.051	0.103 **1** 0.261	0.685 **9** 0.341	0.341 **4** 0.636	---	---
Kala.	0.046 **1** 0.072	0.389 **3** 0.631	0.016 **1** 0.014	0.212 **3** 0.349	0.237 **2** 0.452	---
Protea	0.321 **6** 0.153	0.183 **5** 0.058	0 **0** 0	0.053 **1** 0.108	0.003 **1** 0.003	0.252 **4** 0.073

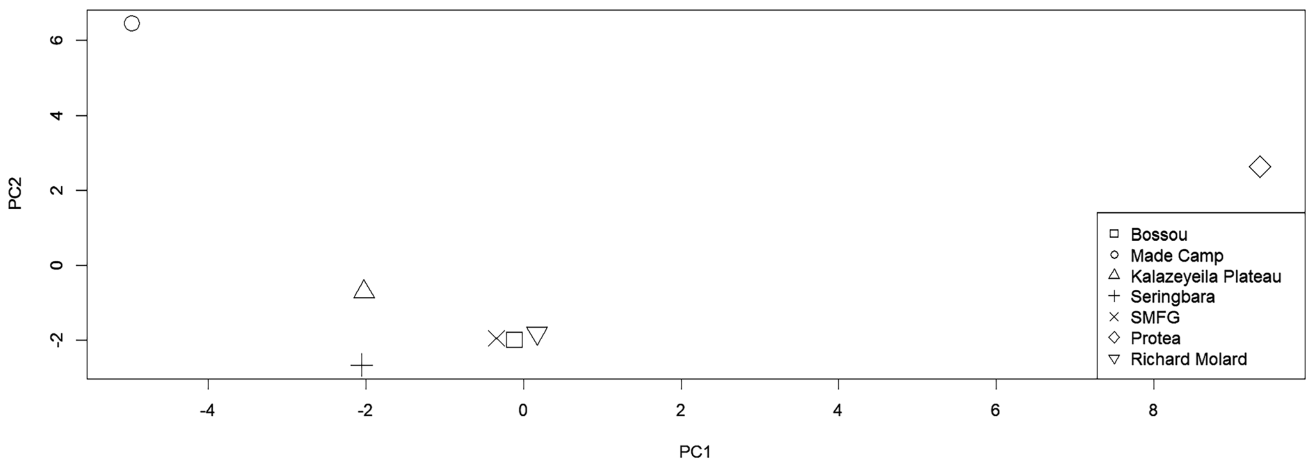


Fig. 4 Ordination plot showing study sites using nonmetric multidimensional scaling (MDS)

to what were collected in this study with 50 species; Excluding the eight myrmecophilous and termitophilous species they collected (none of these taxa were sampled in this study) and leaving 40 species, surprisingly less than half of these (18) overlapped with what were found in this Nimba study. The dung beetle fauna of the forest on Mount Tonkoui is the same as that in the forests of Nimba (Moretto, unpublished data). Hence some of the calculated diversity indices that indicate species diversity in the 30's or 40's for some sites may be considered more accurate than one might initially think.

Elevation alone may not explain the variation in dung beetle species diversity found on the Nimba Mountain Range. Variation may be due in part to a preference for open habitats for some species. This includes *Copris carmelita*, *Epidrepanus caelatus*, *Onthophagus longipilis*, and *Onthophagus* sp. "Protea I" that were only found in the areas with open habitats that included Richard-Molard, Kalazeyeila Plateau, and the Protea Savanna. As expected, the lowest abundance was also found at the highest elevation of Richard Molard with only 20 individuals captured. The high elevation Kalazeyeila Plateau, a grassland-forest mosaic, was the second lowest with only 29 species. Other areas ranged from a low of 62 to as many as 402 individuals collected in the Protea Savanna (Table 4).

At a relatively high elevation of 1185 m and using only 10 traps, the Protea Savanna had the highest diversity, abundance, and average capture rate compared to any of the other sites surveyed (Tables 4, 5 and 7). Additionally, the Protea site generally had the highest diversity estimates with one exception (Seringbara excluding cow dung data) and the third highest Shannon and Simpson indices (Table 7). This high diversity could potentially be explained by the habitats; African savannas can sometimes host higher diversity than do forests (e.g. Kunz and Krell 2011). However, counter to this pattern, other studies in Africa indicate a relatively high diversity of 120 species in Central African forests (Moretto 2010). The Protea site, with 24 species recorded, only shared five of these species with two other sites, and surprisingly, one of these, Bossou, is forested. One additional factor that may be affecting the Protea Savanna is that some lower elevation savannah species may have colonized this location. This site (with actually few *Protea* species plants compared to other scrub tree species) is probably the single natural relatively high-altitude savanna, which likely explains why it is the most species rich site. In contrast, the two higher savannahs of Richard-Molard and the Kalazeyeila Plateau are surrounded by forest and isolated from lower elevation savannahs as well. These two upland grassland or grassland-forest mosaic species are a blend of savanna and forest faunas (Table 6). Further, these two high elevation grasslands are thought to be ancient and natural and not a result of fires set by humans (Curry-Lindahl 1966). However, the range is certainly affected by periodic fires that occur due to pastoral, agricultural or poaching activities (Poilecot and Loua 2009). The highest elevations have fires triggered by lightning strikes (e.g. see Schäfer et al. 2022). These fires maintain the non-forest species dung beetle diversity in these open areas.

The Bossou site may be affected by small habitat size negatively influencing the dung beetle assemblage. This locality had the second lowest diversity and is a remnant small patch of forest isolated from the Nimba Range. Further, unfortunately its chimpanzee populations have been declining since the 1970's (Samani et al. 2023). In contrast, the SMFG and Seringbara had the second and third highest species diversities of 19 and 18, respectively, and may be representative of the species composition in the area when their faunas are combined (26 total taxa). One difference between the two sites was that Seringbara had an average capture rate that was nearly seven times that of SMFG. The cause is not obvious but may be due to the latter locality being closer to the primary mine camp and possibly lower mammal densities in the vicinity. The total diversity for both areas combined at 26 species is closer to some of the estimates from the Chao 1 and 2, Jacknife 1 and 2, and ACE for each area that generally ranged from 18 to 30 species. But surprisingly the estimates rose to 43–45 species when the cow dung traps were excluded for Seringbara. Hence, it appears these collections may have under-sampled the diversity present in all areas with the possible exception of the Made Camp. It also appears that some diversity indices are grossly overestimating the number of species present at some sites and are likely unrealistic. Hence the Simpson and Berger-Parker dominance indices (Table 7) are of some value as they emphasize dominance and may be providing clearer actual diversity numbers for comparisons with the dung beetle faunas of other regions.

The highest Shannon, Simpson, and Berger-Parker diversity indices for forest sites were found at Seringbara and SMFG. These may suggest somewhat robust assemblages present in relatively undisturbed forests. The Seringbara sampling site had a high average capture rate that may be due to its close proximity to the Seringbara village and the greater availability of human dung. Diversity indices were low at the relatively low elevation sites of Bossou and Made Camp. While the former may be explained by small habitat size and species loss, the latter may be due to relatively high bush meat hunting pressures at this low elevation site reducing local mammal abundance and diversity and the concomitant decline in dung beetle populations.

Bush meat hunting and deforestation are widely acknowledged as threats to biodiversity in this region as previously mentioned. In order to preserve this biological wealth, the local mammal and habitat resources must be protected. Fauna and Flora International published a case study in 2009 discussing conservation at the Nimba Mountain Range, emphasizing improving quality of life for local inhabitants. The study stated a method for reducing bush meat hunting by giving viable alternative protein sources and offering alternate sources of income for those relying on hunting and trade. Support for reforesting programs and conservation NGOs was also allocated in hope of establishing programs to protect and improve the environment. Notably, there is hope for the preservation of this ecosystem; Conservation International's Critical Ecosystem Partnership Fund invested $8.3 million USD in the Guinean Forests of West Africa from 2001 to 2012 and started a new investment in 2016 supporting the area with $10 million USD (Conservation International 2021b).

In conclusion, these surveys document dung beetle species diversity on the Nimba Mountain Range and in the nearby Bossou forest in Guinea in 2010–2011. There were complications such as difficult access to high elevation sites and availability of different types of dung during the collection period. Another limitation was caused by unequal sampling either due to the number of traps or the dung used. For example, no traps at the Bossou site were baited with cow dung as it had yet to be procured during the available trapping period. Hence the conclusions that can be drawn are somewhat limited. Regardless, the data do suggest generally high variability among sites that are due to both elevational filtering at high elevations and habitat effects. The faunas may also reflect pressures from bush meat hunting, deforestation, and disturbance from mining activities. Unsustainable harvesting of wildlife and habitat destruction, particularly at the edge of the Mount Nimba Strict Nature Preserve, should be reduced as much as possible to preserve this unique biological treasure. Further monitoring of the biotic integrity of this unique and beautiful area is highly encouraged.

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Declarations

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