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Dung Beetle (Scarabaeinae) Diversity of the Highest Elevation in West Africa: The Nimba Mountain Range

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DUNG BEETLE (SCARABAEINAE) DIVERSITY OF THE HIGHEST ELEVATION IN WEST AFRICA: THE NIMBA MOUNTAIN RANGE

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By

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ABSTRACT

The Nimba Mountain Range in Guinea, Ivory Coast, and Liberia is within the Upper Guinean Forests, a critical biodiversity hotspot highly threatened by various human activities. The region is home to many endemic species including the viviparous Nimba toad, Nimba otter-shrew, and the discrete Bossou chimpanzee population. Dung beetles can act as a focal taxon from which extrapolation to the diversity of other taxa and ecosystem health can be made. Elevational trends in dung beetle diversity were investigated on the Nimba Mountain Range and in the nearby Bossou Chimpanzee reserve in Guinea. Dung beetle species diversity surveys aimed to document the dung beetle species diversity of the area, investigate elevational trends in diversity, and assess the biotic integrity of this unique ecosystem and World Heritage Site. Conventional dung baited pitfall traps were set at selected sites along an elevational gradient in the Bossou Chimpanzee Preserve and the Mount Nimba Strict Nature Preserve. Evidence did not reveal a strong trend in lower diversity at higher elevations. Comparatively lower diversity than what was expected at low elevations potentially reflect a declining ecosystem due to declining mammal populations brought on by bush meat hunting and deforestation pressures. Ecosystem preservation will require protection from human activities and viable alternatives to bush meat hunting.

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INTRODUCTION

At 1,752 meters above sea level, Mount Richard-Molard is the highest peak of the Nimba Mountain Range and one of the highest elevations in the Guinean Forests of West Africa (UNEP-WCMC 2008). The Nimba Mountain Range is situated on the border between Guinea and west-central Côte d'Ivoire and extends into Liberia. The range in elevation offers a variety of habitats including lowland forest, open savanna, and disturbed habitats that can be found on the lower elevations typically between 500 and 600 m asl. Guinean montane forests are present between 550 and 1,000 m asl. At nine hundred meters above sea level and higher is predominantly composed of cloud forest, while between 1,000 m and 1,600 m asl montane grasslands separated by gallery forests within ravines occur.

The Guinean Forests of West Africa, or the Upper Guinean Forest, is considered a critical biodiversity hotspot by multiple sources as it has a high concentration of endemic species and is highly threatened (Myers et al. 2000, Mittermeier et al. 2004, Fauna & Flora International 2009, Conservation International 2021a). The Western African Forests, defined similarly to the Guinean Forests of West Africa, retains only 10% of its primary vegetation and contains 2,250 endemic vascular plant species (Conservation International 2021b, Myers et al. 2000). The Nimba Mountain Range also contains notable threatened animal 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 West African Nimba toad, (Monadjem, Richards, &

Denys 2016, Bryson-Morrison et al. 2017, Sandberger-Loua, Müller, & Rödel 2017, Monadjem et al. 2019, Birdlife International 2021). Moreover, the range acted as forest refugia during glacial periods, further lending to its biodiversity value (Cotillon & Tappan 2016).

The Nimba Mountain Range region is highly threatened by human activities that both alter or fragment habitats, and the assaults include agriculture, mining, and logging (Lebbie 2001). Two studies focusing on the effects of deforestation on dung beetle assemblages in Western 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 & Philips 2005, Davis & Philips 2009). Bush meat hunting and trade, provoked by economic hardship brought on by conflict and political instability (Fauna & 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 (Lebbie 2001, Davis & Philips 2005, Davis & Philips 2009). 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 2001-2012 and started a $9 million USD investment goal in 2016 supporting the area that is projected to be reached by 2021 (Conservation International 2021b).

Dung beetle (*Scarabaeidae: Scarabaeinae*) diversity surveys were conducted in 2010 and 2011 to assess the biotic integrity of the Nimba Mountain Range. Dung beetles were chosen as the focal taxon for extrapolation to other taxa for their easy and standard sampling methods, taxonomic accessibility, response to environmental change, ecological importance through nutrient cycling, and tightly linked relationships with vegetation and dung type, as well as to mammal abundance and diversity (Cambefort 1982, 1991; Cambefort & Walter 1991, Halffter & Favila 1993, Davis 1994, 1996; McGeoch et al. 2002, Spector 2006). The primary goals of these surveys were to document the dung beetle species diversity of the Nimba Mountain Range in Guinea, to estimate and extrapolate from diversity data the biotic integrity and uniqueness of the area, and to acquire baseline data for tracking and monitoring changes in this Nimba ecosystem.

Further, elevational trends in dung beetle species abundance and diversity were investigated for the purpose of studying general trends as well as trends specific to dung beetles in the Nimba Mountain Range. It has been suggested that studying the abiotic and biotic gradients on mountains will grant insight into species diversity and give information valuable to conservation (McCain & Grytnes 2010, Sanders & Rahbek 2012). The most influential factors that cause variability across elevational gradients are thought to be climatic and affect varying taxa differently (McCain & Grytnes 2010). Considering this, montane communities should change as the climatic factors affecting diversity are altered via the effects of climate change (McCain & Grytnes 2010). More research is recommended to understand elevational species diversity trends and one study emphasized the importance of preserving montane gradients for conservation and future research (McCain & Grytnes 2010).

Researching elevational gradients in species diversity on mountains is more convenient and potentially more appropriate for gaining insight into causes of spatial variation of diversity than studying latitudinal gradients (Sanders & Rahbek 2012). Mountains and ranges can act as replicates for study, variables can be manipulated on the ascent of mountains, and it is more convenient to collect data across gradients due to the relatively smaller two dimensional extent of mountains, that is 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.

As for elevational trends in dung beetle diversity, it is generally an inverse relationship, with dung beetle species diversity typically decreasing with elevation. This is supported at Bioko Island, Equatorial Guinea, in the eastern block of the Upper Guinean region by Sukhdeo et al. (2019); however and in contrast, diversity was discovered to be highest at mid-elevation on Mt Cameroon (Mongyeh et al, 2018). These authors hypothesize that the studied assemblages, and the divergence from the general elevational trend found on Mt Cameroon, indicate a greater influence of mammal dung resource and availability on dung beetle diversity than in intact ecosystems. This led to the conclusion that the dung beetle species diversity trends indicate the negative effects of bush meat hunting pressures on dung beetle assemblages at lower elevations. It is predicted that the data collected by the surveys conducted on Mount Nimba will show lower dung beetle species abundance and diversity at low elevations in response to bush meat hunting and habitat destruction pressures. If this hypothesis is supported, the data could be extrapolated from to conclude that other taxa of the region, primarily mammals, are also suffering from the negative effects of human activity.

METHODS AND MATERIALS

Study Sites

Data was collected on the Nimba Mountain Range located in the Nzéré Koré region, southeast Guinea, West Africa. The Bossou, Made Camp, and Kalazeyeila Plateau sites were sampled through July 20-25, 2010. The Seringbara, SMFG, Protea, and Richard-Molard sites were sampled through May 30 - June 7, 2011. These sites were chosen for their relative elevations as well as for their environmental and habitat conditions (Figure 1). Habitat types sampled included *Protea* savanna, high elevation grassland, and both high and low elevation moist forests. The Seringbara site is named after a village near this study site and is comprised of low elevation (660 m asl) slightly disturbed forest.

Figure 1. Map of the Nimba Mountain Range study area and the relative positions of the study sites (Google Maps, 2021).

Figure 2. The Bossou site is named after the nearby village, and was chosen for its low elevation (575 m asl), moist forest habitat, and its close proximity to the Bossou chimpanzee population. It is isolated from the mountain range by grassland and farms.

Figure 3. The Made Camp site is a bush camp in low elevation (685 m asl) moist forest.

Figure 4. The SMFG site is near a Société des Mines de fer du Nimba camp, and represents low elevation (875 m asl) moist forest.

Figure 5. The Kalazeyeila Plateau site is comprised of high elevation (1165 m asl) grassland and forest.

Figure 6. The Protea site is at high elevation (1185 m asl) with protea and other unidentified tree species.

Figure 7. The Richard-Molard site is high elevation (1615 m asl) grassland, and has habitat for the endemic viviparous Nimba toad.

Collection

Dung beetles were collected through the use of conventional dung baited pit fall traps (Halffter & Favila 1993, Spector 2006, Figure 8) set at elevations between 575 m and 1615 m. Traps were constructed of 16-ounce plastic food containers that were placed in the soil with the brim level with the substrate. Once the food container is placed, water and 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, dung was placed in 2-ounce condiment cups and suspended above the trap with a wooden kebab stick. The small bait cup is pierced with the wooden kebab skewer, and the opposite end of the kebab skewer is pushed into the soil at an angle 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) to create a rain roof. While setting the trap, small canals are made in the soil surrounding the trap to divert rain runoff away from the rim of the trap.

Figure 8. A conventional pitfall trap with a rain roof created using kebab sticks and a plastic plate.

Traps were placed at least 50 m apart, alternating the bait type (two or more of human, pig, cow and/or, chimpanzee). Eight to 20 traps were placed at each site and samples were collected after 48 hours (Table 1). Due to limitations in space, time, and bait availability, sites varied in number of traps and bait type. Samples were placed in alcohol (70% ethanol) inside plastic sample bags (Whirlpacs) during the field collecting.

Table 1. Site elevation, coordinates, and number of traps set of each dung type. H: baited with human dung. P: baited with pig dung. Z: baited with chimpanzee dung. C: baited with cow dung.

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

<u>Analysis</u>

In the lab, collected samples were first sorted by removing dung beetles. Specimens were then allowed to dry slightly and prepared for study by mounting on pins or glued onto small cardboard points on pins and placed in unit trays with foam-filled bottoms. Specimens were appropriately labeled to site (locality, date, dung type, trap number, coordinates, collector) to avoid mistaking when, where, and how they were collected. Specimens were sorted to species by morphological traits and through use of dichotomous keys, voucher specimens, and species descriptions (d'Orbigny 1913, Cambefort & Bordat 2003).

Dung beetle species abundance and diversity was then counted and compared across sites and differing elevations. Due to unequal sampling effort, average capture rates per trap were calculated in order to compare dung preference and abundance across sites more accurately. Dung beetle species diversity data were also analyzed with EstimateS v9.1.0 software (Colwell 2013) to compute diversity estimates and indices including Chao (1 and 2), Jackknife (1 and 2), ACE, Shannon, and Simpson across sites. Morisita-Horn and Chao-Jaccard indices were also calculated for pairwise comparisons of species composition of sites. 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 & Bordat (2003).

RESULTS

Fifty species, eight of which lack specific names, were observed out of the 955 individuals collected (Table 2—see Appendix). Species in the *Onthophagus* genus dominated the catch, contributing 28 of the 50 species observed and comprising 42.7% of the total catch. The most abundant species observed was *Milichus inaequalis lamottei* with 194 individuals captured, most of which were sampled at Seringbara, representing 24.3% of the total catch. *Sisyphus africanus africanus* was also prevalent, making up 14.7% of the specimens. *Diastellopalpus tridens*, one of the most common dung beetle species in dry to moist forests, was observed from 575 – 1615 m asl. *D. tridens* was recorded in the most sites, and was only absent in the Made Camp and Seringbara sites. *Onthophagus jonathani* was observed from 575 – 1165 m asl. *Onthophagus feai* seemed to prefer higher elevations as it was only observed from 875 – 1615 m asl. Surprisingly, a single *Sisyphus cf. latus* individual, a species described as being found in moist forests, was observed at the highest elevation Richard-Molard site. *Onthophagus feai,* another forest species, was also observed in high elevation grasslands. *Copris interioris* is tightly linked with cattle; however, a single individual was found in the Protea savanna site. *Anachalcos cupreus,* a species described as often found in savanna or near forests, was observed in the Bossou and Seringbara sites. Similarly, *Onthophagus atridorsis*, *Onthophagus fimetarius,* and *Onthophagus pullus*, are other savanna species observed in the Bossou catch.

Study sites surveyed in 2011 generally collected more dung beetle individuals and species than those surveyed in 2010 (Table 3). Forested sites had higher average capture rates than did the grassland areas. The Kalazeyeila Plateau and Richard-Molard high elevation sites had the lowest observed abundances and diversity. The Protea site, another high elevation site, surprisingly had the highest observed dung beetle species abundance and diversity out of the study sites and with only 10 traps. The Seringbara site had a high average capture rate considering its close proximity to the Seringbara village.

Table 3. Elevation of each site with observed dung beetle species diversity, abundance, and average capture rate.

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
Total	---	50	955	---

Based on the capture data for differing dung types in the 2010 catch, it seems there was a preference for pig dung (51.6% of the total catch) over human (23.6%), chimpanzee (15.9%), and cow dung (8.9%, Table 4). Because the cow dung baited traps contributed little to the 2010 and 2011 catches (17.7% of total catch in 2011, Table 5) compared to other dung sources, diversity metrics for the Seringbara, SMFG, Protea, and Richard-Molard sites were also calculated with only human dung capture data.

Table 4. Dung preference shown through average capture rates with differing dung types in 2010.

Site	Human	Pig	Chimpanzee	Cow
Bossou	3 ± 3.4641	5.333 ± 4.1096	1.833 ± 1.3437	---
Made Camp	4.5 ± 2.0616	9 ± 7.2801	2.75 ± 1.4790	0.5 ± 0.8660
Kalazeyeila	0.25 ± 0.4330	3.25 ± 2.8614	0.75 ± 0.4330	3 ± 5.1962

Table 5. Dung preference as shown through captures made with human and cow dung and their average capture rates (ACR) at the Seringbara, SMFG, Protea, Richard-Molard sites.

Site	Human	Cow	Human ACR	Cow ACR
Seringbara	240	34	60 ± 28.636	8.5 ± 2.958
SMFG	90	12	9 ± 8.050	1.2 ± 0.980
Protea	307	95	61.4 ± 13.588	19 ± 11.781
Richard-Molard	20	0	2.222 ± 2.936	0

All estimates of diversity were higher than that observed for the sites, suggesting species were possibly missed in the sampling (Table 6). Additionally, at most sites the Chao and ACE diversity estimates increased, some doubling, if data collected with cow dung was excluded. The SMFG site's diversity estimations and indices decreased after excluding cow dung data, most likely due to the large presence of *Epidrepanus caelatus* in the cow capture. The Made Camp also had slight increases in diversity estimates. Diversity metrics for the Richard-Molard site did not differ greatly after excluding cow dung data as no data were collected with cow dung at this site. After excluding cow dung data, most of the relative diversity relationships remained the same.

The Made Camp and SMFG sites had the highest diversity indices of the sites surveyed, suggesting the dung beetle assemblages here are more equally distributed and robust than those of the other sites. The Protea site had unusually high diversity indices considering its high elevation. The Bossou and Seringbara sites had the lowest diversity indices, suggesting assemblages here have relatively unequal distributions and are poor in diversity. 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 6), 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).

Table 6. Diversity estimates and indices for each site. The diversity estimates and indices for sites as calculated excluding cow dung data (-C) are also included.

Site	Obs. Diversity	Chao1	Chao2	Jack1	Jack2	ACE	Shannon	Simpson
Bossou	11	12.96	14.14	15.72	18.49	14.75	1.51	2.62
Seringbara	18	24.97	24.3	25.87	30.05	29.78	1.41	2.19
Seringbara-C	17	44.88	27.31	25.25	29.75	42.77	1.26	1.92
Made Camp	11	11	11.18	12.87	11.35	11.36	2.16	7.45
Made Camp-C	11	11	11.18	12.83	11.46	11.36	2.18	7.69
SMFG	19	21.97	22.8	26.6	28.68	26.72	2.44	8.71
SMFG-C	15	18.3	17.7	20.4	22.35	20.89	2.19	7.06
Kala. Plateau	8	17.65	22.06	13.62	18.87	23.03	1.53	3.4
Kala. Plateau-C	6	11.64	11.5	9.66	13	13.47	1.39	3.24
Protea	24	41.95	34.8	32.1	37.87	34.48	2.13	6.03
Protea-C	23	67.85	41	31	36.55	38.19	2.12	5.92
R-Molard	8	9.9	9.89	11.78	13.67	15.78	1.7	3.92
R-Molard-C	8	9.9	9.77	11.55	13.30	15.78	1.7	3.92

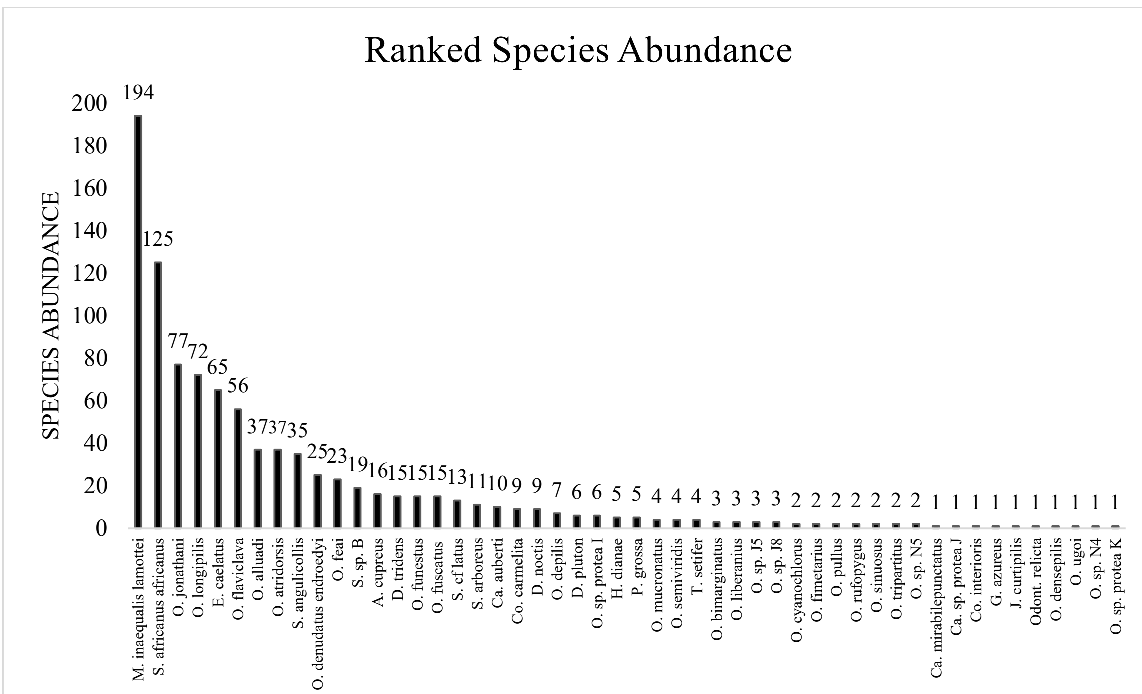

Figure 9. Ranked species abundance observed in dung beetle species surveys on the Nimba Mountain Range.

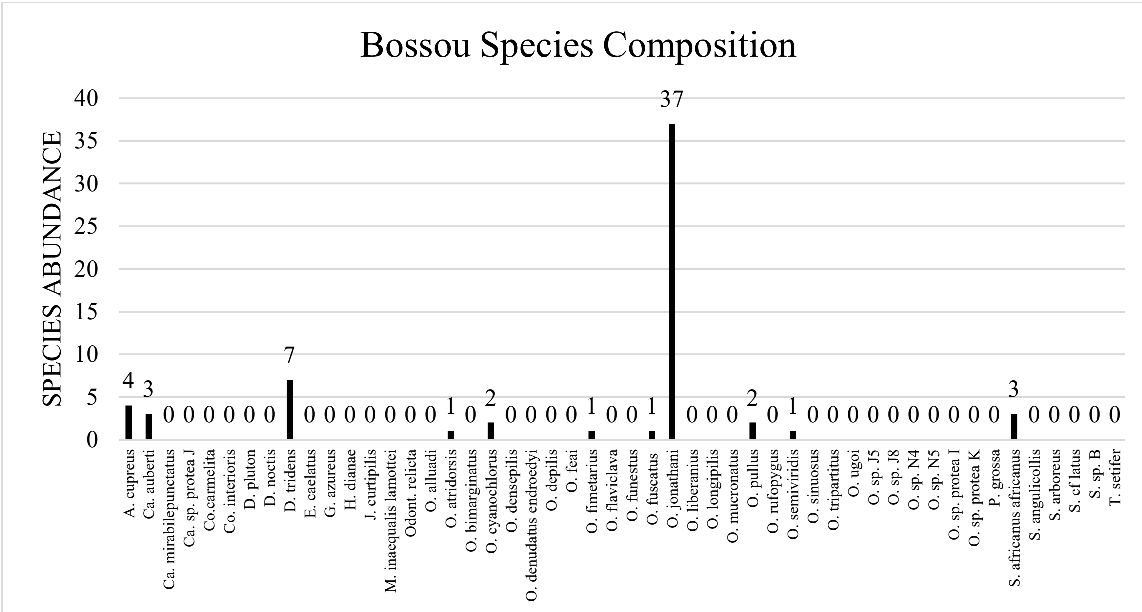

Figure 10. Species composition observed at the Bossou site.

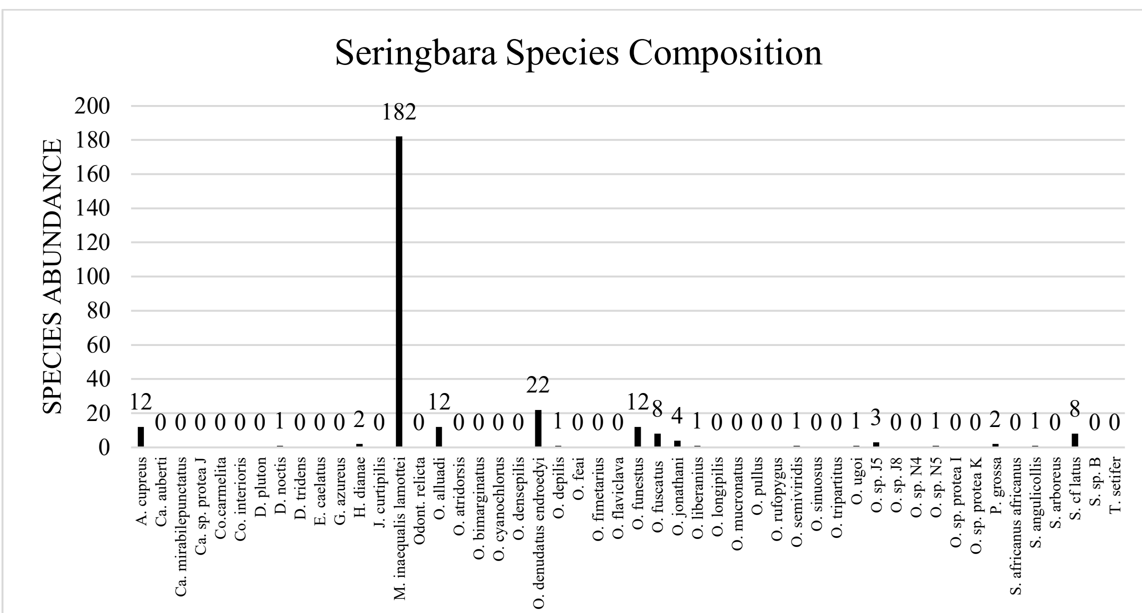

Figure 11. Species composition observed at the Seringbara site.

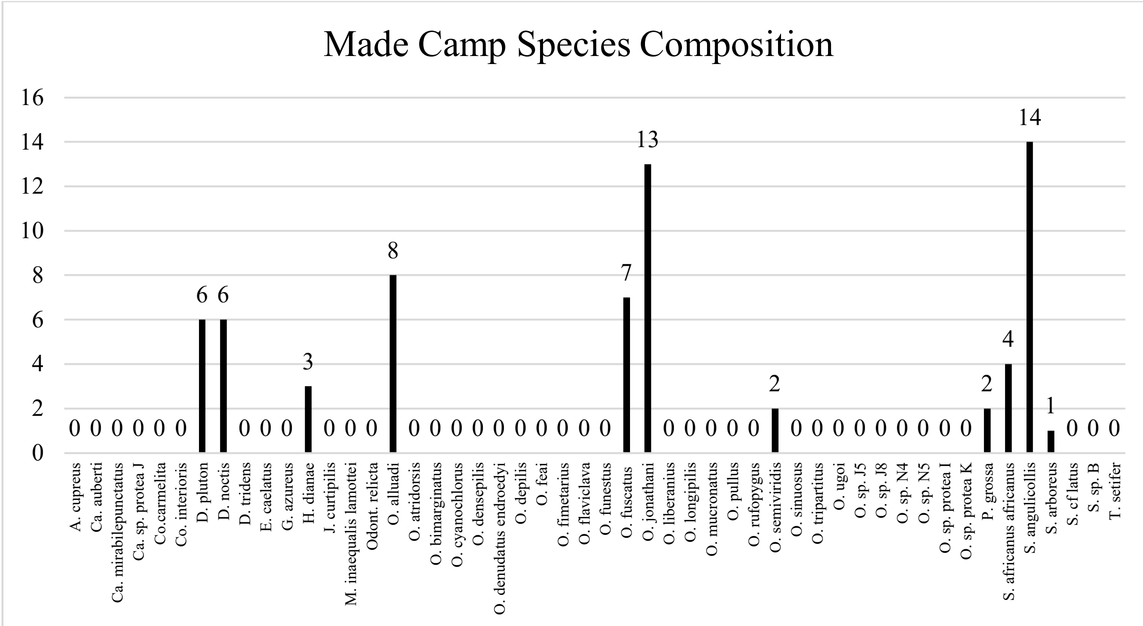

Figure 12. Species composition observed at the Made Camp site.

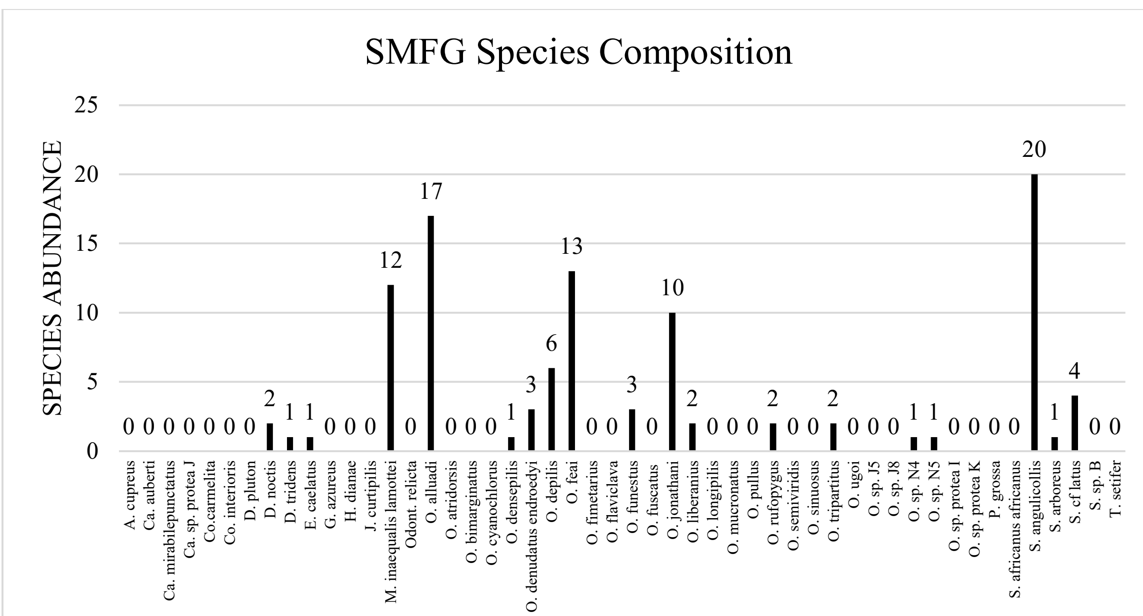

Figure 13. Species composition observed at the SMFG site.

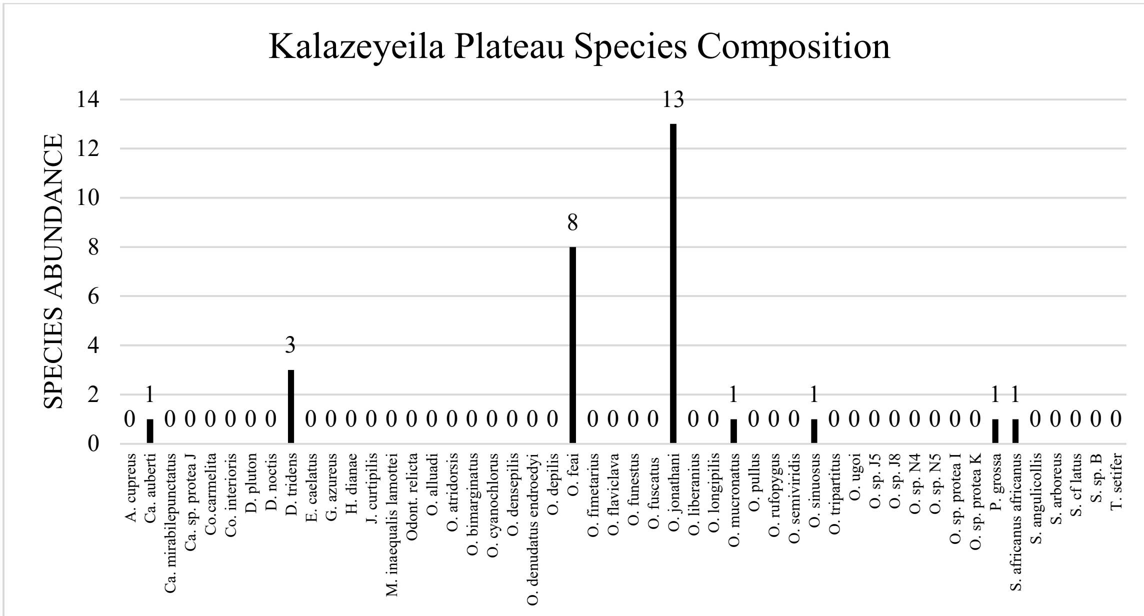

Figure 14. Species composition observed at the Kalazeyeila Plateau site.

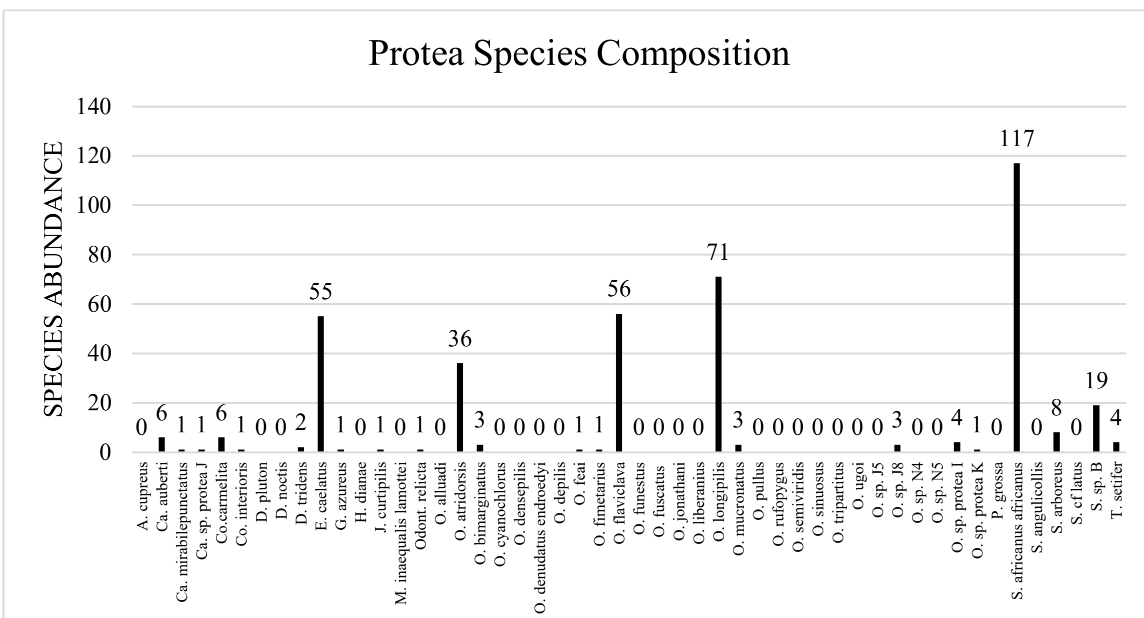

Figure 15. Species composition observed at the Protea site.

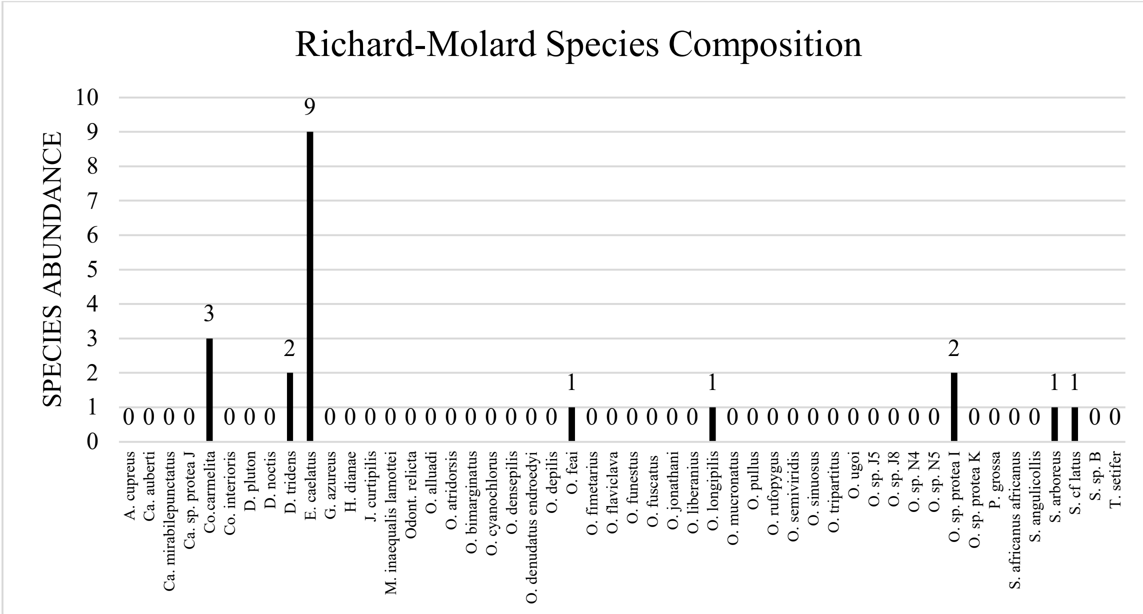

Figure 16. Species composition observed at the Richard-Molard site.

Shared species analysis revealed no similarity in composition between the Seringbara and Protea sites (Figures 11, 15; Table 7—see Appendix). The Chao-Jaccard and Morisita-Horn indices suggest differing relative similarities between pairwise comparisons. The Chao-Jaccard indices calculated for these abundance data indicate that the compositions of the Seringbara and SMFG sites are most similar, while Morisita-Horn indices show the compositions of the Bossou and Kalazeyeila Plateau sites are most similar (Figure 10, 11, 13, 14). The Bossou and Seringbara sites, which have the lowest diversity indices, had relatively dissimilar assemblages (Figure 10, 11). Also notable, the Made Camp and SMFG sites, which have the highest diversity indices, had more similar compositions (Figure 12, 13).

DISCUSSION

No elevational trend was found in dung beetle diversity on the Nimba Mountain Range. Elevation alone may not be able to explain the variation in dung beetle species diversity found on the ascent of the Nimba Mountain Range. This is contrary to the general global trend in dung beetle elevational diversity, decreasing diversity with elevation. This could indicate a disturbance influencing the assemblage (Mongyeh et al. 2018, Sukhdeo et al. 2019). When the 2010 and 2011 data sets are analyzed separately, both have their lowest observed diversity at their highest elevations (Kalazeyeila Plateau and Richard-Molard), as expected; however, one notable contradiction is the high abundance and diversity recorded for the Protea site.

At 1185m asl with only 10 traps set, the Protea site collected the highest abundance and diversity out of all sites surveyed. Additionally, the Protea site had relatively high diversity indices. This high diversity could potentially be explained by the habitat; savanna could host higher diversity than do forests because it can host savanna restricted species. The protea savanna habitat has characteristic flora that could offer a unique range of conditions for dung beetle species that the forest alone does not. Alternatively, the habitat might harbor such high diversity because it is nearly untouched by human activity.

The high diversity indices nearer low elevation (Made Camp and SMFG) could suggest robust assemblages in relatively undisturbed forests (Figure 12, 13). These sites are in close proximity to minor human development, a bush camp in the case of Made Camp and a small complex of buildings for the SMFG. The disturbance at these sites could be less than that of the lower elevation sites near larger disturbances (villages). Diversity indices were alarmingly low at low elevation (Bossou and Seringbara), suggesting assemblages comprised of highly abundant and scarce species, potentially at-risk populations (Figure 10, 11). This could be explained by bush meat hunting pressures reducing local mammal abundance and diversity, thus leading to declines in associated dung beetle populations. In addition, several savanna species were observed at these sites, which could indicate the decline of the forest habitat through deforestation.

As discussed before, bush meat hunting and deforestation are already acknowledged as threats to biodiversity in this region. In order to preserve this biological wealth, the local mammal and habitat resources must be protected. Fauna & Flora International published a case study in 2009 discussing conservation at the Nimba Mountain Range. In this case study, there was an emphasis on improving quality of life for locals. The case study stated a method for reducing bush meat hunting could be found in producing viable alternative protein sources and offering alternate sources of income for those relying on bush meat hunting and trade. Support for reforesting programs and conservation NGOs was allocated in hopes of establishing programs to protect and improve the environment.

Unfortunately, there were many complications during data collection that limit any conclusions that can be drawn. One major limitation is caused by unequal sampling. Because of time constraints, no traps at the Bossou site were baited with cow dung as it had yet to be procured during the available trapping period. There was not enough space available at the Kalazeyeila site to allow for traps to be 50 m apart; instead, they were placed within 30 m of each other. There is also a temporal difference between the surveys as a year had passed between sampling periods and it is possible that slight variations in rainfall may have affected dung beetle activity. Additionally, the data discussed above were collected almost 10 years prior to the publishing of this thesis. In order to continue monitoring and improve conclusions made on the biotic integrity of this unique ecosystem, future sampling must occur. Future surveys minimizing error caused by unequal sampling efforts can collect more data and possibly reveal more accurate relationships between elevation and species abundance and diversity. Future surveys can also be designed such that they can test whether declines in dung beetle populations are associated with bush meat hunting and deforestation. Conducting more surveys can reduce the influence of biases in previous samples and the biotic integrity of this area can be more accurately reflected and monitored over time.

In conclusion, these surveys documented dung beetle species diversity on the ascent of the Nimba Mountain Range in Guinea. The data collected suggest low elevation dung beetle assemblages are being negatively affected, possibly by bush meat hunting and deforestation; however, more evidence is needed to support this hypothesis. This next statement is made with a bias towards caution: Unsustainable harvesting of wildlife and habitat destruction need be reduced in order to preserve this unique biological treasure. Further monitoring of this area's biotic integrity, as well as focused monitoring of local mammal and dung beetle diversity, is highly encouraged.

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APPENDIX

Table 2. Total abundance of each species observed and at each site.

Species	Total	Bossou	Ser. Vill.	M. Camp	SMFG	K. Plat.	Protea	Mt. R-M.
Anachalcos cupreus	16	4	12	0	0	0	0	0
Caccobius auberti	10	3	0	0	0	1	6	0
Caccobius mirabilepunctatus	1	0	0	0	0	0	1	0
Caccobius sp. protea J	1	0	0	0	0	0	1	0
Copris carmelita	9	0	0	0	0	0	6	3
Copris interioris	1	0	0	0	0	0	1	0
Diastellopalpus noctis	9	0	1	6	2	0	0	0
Diastellopalpis pluton	6	0	0	6	0	0	0	0
Diastellopalpus tridens	15	7	0	0	1	3	2	2
Epidrepanus caelatus	65	0	0	0	1	0	55	9
Garreta azureus	1	0	0	0	0	0	1	0
Heliocopris dianae	5	0	2	3	0	0	0	0
Jossonthophagus curtipilis	1	0	0	0	0	0	1	0
Milichus inaequalis lamottei	194	0	182	0	12	0	0	0
Odontoloma relicta	1	0	0	0	0	0	1	0
Onthophagus alluadi	37	0	12	8	17	0	0	0
Onthophagus atridorsis	37	1	0	0	0	0	36	0
Onthophagus bimarginatus	3	0	0	0	0	0	3	0
Onthophagus cyanochlorus	2	2	0	0	0	0	0	0
Onthophagus densepilis	1	0	0	0	1	0	0	0
Onthophagus denudatus endroedyi	25	0	22	0	3	0	0	0
Onthophagus depilis	7	0	1	0	6	0	0	0
Onthophagus feai	23	0	0	0	13	8	1	1
Onthophagus fimetarius	2	1	0	0	0	0	1	0
Onthophagus flaviclava	56	0	0	0	0	0	56	0
Onthophagus funestus	15	0	12	0	3	0	0	0
Onthophagus fuscatus	15	1	8	6	0	0	0	0
Onthophagus jonathani	77	37	4	13	10	13	0	0
Onthophagus liberanius	3	0	1	0	2	0	0	0
Onthophagus longipilis	72	0	0	0	0	0	71	1
Onthophagus mucronatus	4	0	0	0	0	1	3	0
Onthophagus pullus	2	2	0	0	0	0	0	0
Onthophagus rufopygus	2	0	0	0	2	0	0	0
Onthophagus semiviridis	4	1	1	2	0	0	0	0
Onthophagus sinuosus	2	0	0	1	0	1	0	0
Onthophagus tripartitus	2	0	0	0	2	0	0	0
Onthophagus ugoi	1	0	1	0	0	0	0	0
Onthophagus sp. N4	1	0	0	0	1	0	0	0
Onthophagus sp. N5	2	0	1	0	1	0	0	0
Onthophagus sp. J5	3	0	3	0	0	0	0	0
Onthophagus sp. J8	3	0	0	0	0	0	3	0
Onthophagus sp. protea I	6	0	0	0	0	0	4	2
Onthophagus sp. protea K	1	0	0	0	0	0	1	0
Pseudopedaria grossa	5	0	2	2	0	1	0	0
Sisyphus africanus africanus	125	3	0	4	0	1	117	0
Sisyphus angulicollis	35	0	1	14	20	0	0	0
Sisyphus arboreus	11	0	0	1	1	0	8	1
Sisyphus cf latus	13	0	8	0	4	0	0	1
Sisyphus sp. B	19	0	0	0	0	0	19	0
Tiniocellus setifer	4	0	0	0	0	0	4	0
Total	955	62	274	66	102	29	402	20

Table 7. Matrix showing pairwise shared species diversity statistics between sites listed as number of shared species, Chao-Jaccard similarity index, and Morisita-Horn overlap index.

Site	Bossou	S. Vill.	Made	SMFG	Kala.	Protea
S. Vill.	4, 0.117, 0.028	---	---	---	---	---
Made	4, 0.422, 0.476	8, 0.113, 0.044	---	---	---	---
SMFG	2, 0.104, 0.240	11, 0.895, 0.325	5, 0.389, 0.667	---	---	---
Kala.	4, 0.581, 0.837	2, 0.025, 0.018	3, 0.278, 0.427	3, 0.228, 0.392	---	---
Protea	5, 0.199, 0.061	0, 0, 0	2, 0.065, 0.119	4, 0.166, 0.013	5, 0.526, 0.052	---
R-M	1, 0.056, 0.035	1, 0.024, 0.004	1, 0.017, 0.003	5, 0.448, 0.076	2, 0.131, 0.087	7, 0.501, 0.357