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Diversity of the Endemic Madagascan Dung Beetles (Coleoptera, Scarabaeidae, Scarabaeinae): New Records from Six Protected Areas

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Abstract: Dung beetles (Scarabaeidae, Scarabaeinae) are among the most cost-effective and informative biodiversity indicator groups, conveying rich information about the status of habitats and faunas of an area. In Madagascar, they are important elements in forest food chains and ecosystems where they originally evolved to decompose lemur excrements, but later many species shifted to utilize cattle dung and human feces. In the present contribution, we report the results of dung beetle sampling in six protected areas of northern and central Madagascar. In total, over 400 specimens of Scarabaeinae beetles belonging to three tribes, eight genera, and 26 species were collected. All species are endemic to the island and most of them belong to the endemic genus *Helictopleurus* d'Orbigny. *Nanos neoelectrinus* Montreuil and Viljanen, recently synonymized with *N. humeralis* Paulian, is revalidated based on the new material.

Keywords: coprophages; scarabaeines; Montagne d'Ambre range; Andasibe-Mantadia; Manjakatompo Ankaratra

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1. Introduction

Biodiversity hotspots are regions containing exceptional concentrations of biota endemism and experiencing high rates of habitat loss [1]. Of the 25 originally identified hotspots, Madagascar is ranked first in terms of the five most important factors, including endemic taxa per area ratio and percentage of remaining primary vegetation. Madagascar is known for its unique biota characterized by an exceptionally high level of endemism at all taxonomic levels [2]. Species-level endemism reaches 100% in many taxa, and there are many families and tribes that are found only in Madagascar. For example, all native amphibians and land mammals in Madagascar are endemic [3]. Due to its exceptional endemism and generally high species diversity, Madagascar is considered one of the most important biodiversity hotspots in the world [1] yet its biodiversity is highly underestimated [4].

Scarab beetles of the subfamily Scarabaeinae, the dung beetles, are a marquee focal group for global efforts to assess the status of biodiversity. They are among the most cost-effective and informative biodiversity indicator groups [5,6]. Dung beetles provide rich information about the status of habitats and faunas of an area [7–9]. The world fauna of dung beetles is estimated at more than 6200 species in 267 genera [10] with highest diversity found in Africa [11].

In Madagascar, dung beetles are important elements in forest food chains and ecosystems where they originally evolved and diversified to decompose lemur excrements [12]. The fauna of the island is very diverse but highly biased. Of the five tribes found in Madagascar (Onthophagini, Scarabaeini, Ateuchini, Helictopleurini and Epilissini), the first three are represented by only a few species [13,14]. In contrast, the endemic monotypical tribe Helictopleurini includes around sixty species [15]. The last tribe is the most diversified with over 220 species in 14 genera [13,14], although some genera are still in need of taxonomic revision.

Increasing anthropogenic pressure reduces forest habitats, where the bulk of dung beetles reside, and the population of lemurs, which are the original producers of food for dung beetles. This forces dung beetles to switch to other food sources, not available previously: human feces and cattle dung. This, in turn, may drastically affect distribution ranges and population size, and leads to a global rewiring in tropical food chains [16–18].

Despite a reasonable number of publications dealing with Madagascan dung beetles, the fauna of the island needs further research. The available publications are devoted to specific questions of the population ecology [16,19–21], phylogeny of lineages [12,22,23], and classification of separate taxa [13,24–27], yet the comprehensive surveys of the fauna are missing. In the course of a project investigating trophic associations and diet shift in endemic Madagascan dung beetles, one of us (A.F.) surveyed six protected areas and nearby localities in February 2022. Despite heavy rains in most localities during most of the survey period, an unexpectedly large number of species was collected. The goal of the present study is to report the new data that will contribute to our better understanding of the distribution, habitat preferences, and seasonal activities of the members of this group.

2. Materials and Methods

2.1. Sampling Areas

Six protected areas were surveyed in northern and central Madagascar in February 2022 (Table 1, Figures 1 and 2).

Table 1. Study sites in six Madagascan protected areas.

No.	Name	Administrative Division	Latitude	Longitude	Elevation	Biotope
1	Montagne d'Ambre N.P., site 1	Antsiranana	12°31′30″ S	49°10′20″ E	1049 m	humid primary forest
2	Montagne d'Ambre N.P., site 2	Antsiranana	12°30′54″ S	49°10′50″ E	995 m	humid primary forest
3	Forêt d'Ambre S.R.	Antsiranana	12°28′16″ S	49°13′4″ E	503 m	subhumid primary forest
4	Ankarana S.R., site 1	Antsiranana	12°51′54″ S	49°13′31″ E	290 m	subhumid primary forest
5	Ankarana S.R., site 2	Antsiranana	12°51′54″ S	49°13′24″ E	295 m	savannah
6	Analamazaotra S.R., site 1	Toamasina	18°55′59″ S	48°25′12″ E	963 m	humid primary forest
7	Analamazaotra S.R., site 2	Toamasina	18°56′7″ S	48°24′58″ E	940 m	humid bamboo forest
8	Mantadia N.P., site 1	Toamasina	18°49′47″ S	48°25′56″ E	969 m	humid primary forest
9	Mantadia N.P., site 1	Toamasina	18°49′32″ S	48°26′5″ E	977 m	humid primary forest
10	Ankaratra, site 1	Antananarivo	19°22′29″ S	47°21′15″ E	1603 m	grassland
11	Ankaratra, site 2	Antananarivo	19°21′20″ S	47°18′18″ E	1869 m	humid primary forest
12	Ankaratra, site 2	Antananarivo	19°21′30″ S	47°18′45″ E	1742 m	edge of subhumid forest

2.1.1. Montagne d'Ambre National Park

Montagne d'Ambre National Park occupies a major part of Montagne d'Ambre range at the extreme northern tip of Madagascar. The mountain range is volcanic in origin, with elevations from 200–300 m at the foot to ca. 1500 m at the summit, and with the annual precipitation much higher than in the surrounding areas [28]. The vegetation of Montagne d'Ambre is rainforest, with moist montane forest above 800 m and lowland rainforest below 800 m [29].

2.1.2. Forêt d'Ambre Special Reserve

The Forêt d'Ambre is situated on the north-eastern foothills of the Montagne d'Ambre mountain range. It is a part of the subhumid bioclimatic zone and is subject to marked seasonal variation, with a distinct and relatively long dry season followed by a wet season lasting from December to April [30,31]. The annual precipitation at this location is higher than that in the areas north of the reserve, but lower than at the adjacent Montagne d'Ambre National Park [28]. The vegetation of the Forêt d'Ambre Special Reserve is mesic and has been described as transitional between lowland rainforest (at higher elevations) and dry deciduous western forest (at lower elevations) [29,32]. Despite the close proximity to the much larger Montagne d'Ambre National Park, the Forêt d'Ambre Special Reserve has endemic vertebrate species [33].

2.1.3. Ankarana Special Reserve

Ankarana is a Special Reserve situated south of the Montagne d'Ambre mountain range. It is a small limestone massif and an "island" of pinnacle karst and semi-deciduous dry tropical forest surrounded by savannah [34]. The central part of the limestone has been eroded into spectacular razor-sharp ridges and pinnacles called "tsingy". A somewhat isolated part east of the national route RN6 is a degraded forest surrounded by the savannah.

2.1.4. Mantadia National Park

Mantadia National Park is in the northern part of the Andasibe-Mantadia protected area. It is covered mostly by a primary humid forest, but also comprises a range of vegetation types. The altitude of the area is 850–1100 m; it receives an average rainfall of 1700 mm per year, and has a mean temperature of 19 °C [35].

2.1.5. Analamazaotra Special Reserve

The Analamazaotra Special Reserve is a smaller part of the Andasibe-Mantadia protected area and is located south of Mantadia National Park [36]. The reserve is 810 ha in extent and consists of evergreen rain forest with altitudes ranging from 850 m to 1100 m above sea level [37]; mean annual rainfall in the region is 1700 mm with an average temperature of 18 °C.

2.1.6. Manjakatompo Ankaratra

Manjakatompo Ankaratra is a protected area on the eastern slopes of the Ankaratra Massif on the Central Plateau. The reserve covers 8130 ha and has a range in altitude starting from about 1500 m to 2643 m. The moist and evergreen forested parts are mostly between 1600 and 2000 m, and above 2000 m extensive grasslands extend with some pockets of ericoid thicket and bushes, heathland, and montane wetlands [38]. The forest is degraded due to high anthropogenic pressures.

The exact collecting localities are given in Table 1.

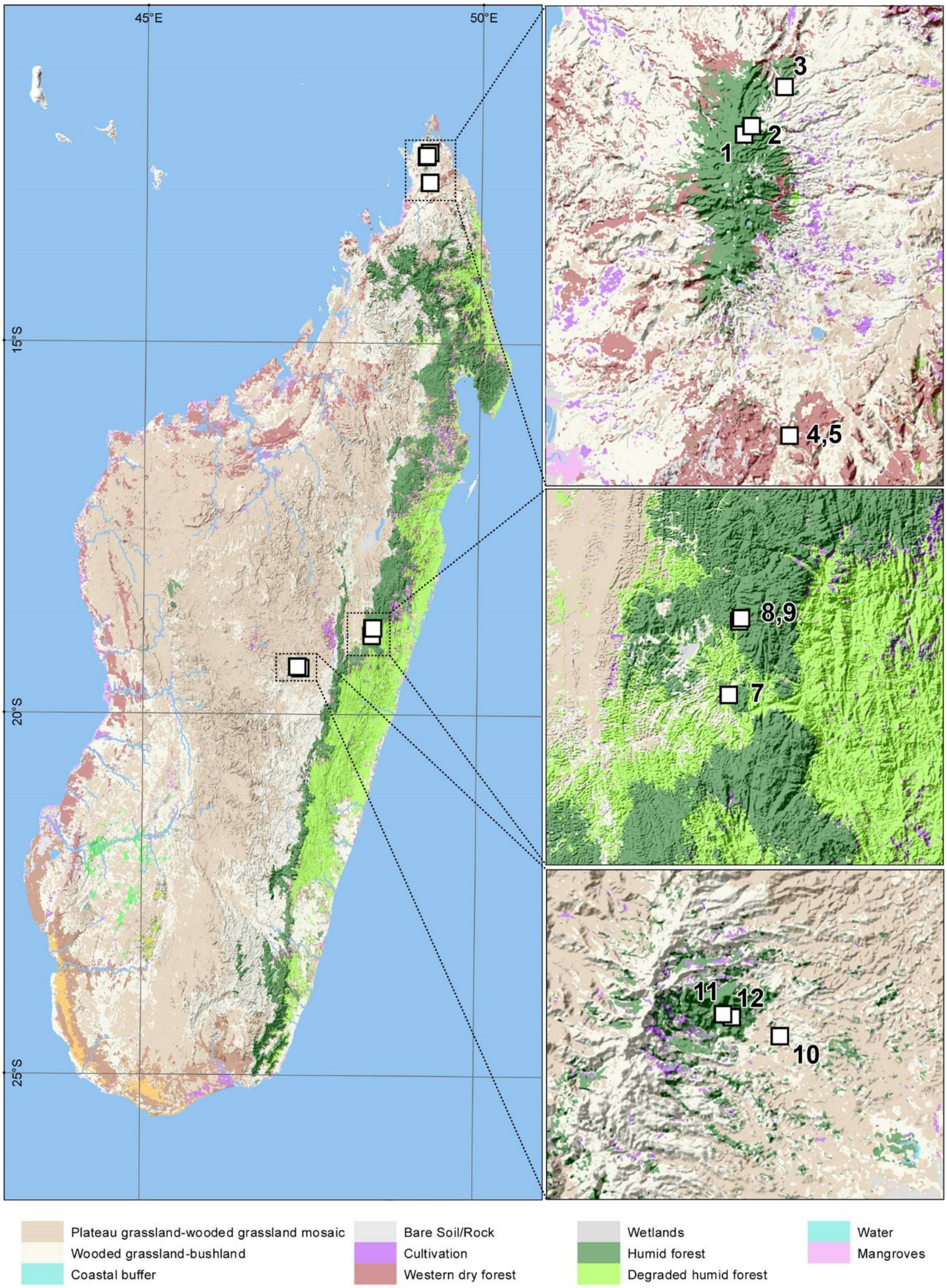

Figure 1. Locality map based on the Atlas of the Vegetation of Madagascar [39]. Numbers represent site numbers in Table 1.

Figure 2. Sampling biotopes. Site numbers (Table 1) in brackets. **1**—Montagne d'Ambre N.P., humid primary forest (1); **2**, **4**—Ankarana S.R., subhumid primary forest (4); **3**—Ankarana S.R., savannah (5); **5**, **6**—Analamazaotra S.R., humid primary forest (6); **7**–**9**—Mantadia N.P., humid primary forest (9); **10**, **11**—Ankaratra, humid primary forest (11); **12**—Ankaratra, disturbed grassland (10).

2.2. Field Sampling Methods

The beetles were collected by standard pitfall traps [40] baited with human feces. Three traps were set in each locality at a distance of about 3 m from each other. The traps compromised a 1-L plastic container ca. 10 cm in diameter buried in the soil. Bait was placed in a 5 cm diameter cup wrapped in gauze and suspended by a wire above a collecting container. To avoid the flooding of traps, they were covered with plastic lids attached about 4 cm above the ground. The collecting containers were filled to 1/3 of their total capacity with a 50% solution of propylene glycol or a preservation solution with SDS and EDTA [41]. In other pitfall traps, we used funnels over the collecting jars, so the beetles attracted to the traps fell into the jars and stayed alive until retrieval; these traps were exposed overnight. In a few localities, the beetles were manually picked from cow dung pads. After retrieval, the beetles were placed in containers with 96% ethanol and transported to the laboratory after two or three weeks at room temperature; the alcohol was changed twice.

2.3. Specimen Deposition, Digitalization, Mapping, and Biogeographical Analysis

The examined specimens are deposited in the following organizations:

MNHN—National Museum of Natural History, Paris, France;
ZIN—Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia;
UMAM—University of Antananarivo, Antananarivo, Madagascar.

The specimens for habitus photographs were cleaned in an ultrasonic bath in a detergent solution, rinsed in distilled water, and pinned. Habitus photographs were taken with a Canon D100 camera equipped with a EF-S 60 macro lens. Partially focused serial images were combined using Helicon Focus 3.2 software (Helicon Soft Ltd., Kharkov Ukraine) to produce completely focused images. Helicon Focus was used with default settings (method B “depth map”, radius 8, smoothing 4), and the number of the stack images varied from 20 to 40. Stacking artefacts were not retouched, and only general image enhancing (levels, background elimination, and slight sharpening) was applied. Locality maps were generated with ArcGIS software 8.1 (ESRI Ltd., Redlands, CA, USA). Co-ordinates of the localities were recorded in the field with a handheld GPS device. Similarities in species composition among the studied sites were evaluated using Jaccard similarity indices [42]. Cluster analysis of the fauna of sites was performed using Statistica 10 software (StatSoft, Tulsa, OK, USA) based on dissimilarity indices complementary to Jaccard indices.

3. Results

In total, over 400 specimens of Scarabaeinae beetles belonging to three tribes, eight genera, and 26 species were collected (Figure 3). The list of species, distribution of the species among the collecting localities (Table 2), Jaccard similarity indices (Table 3), and graphical results of cluster analysis (Figure 4) are given below.

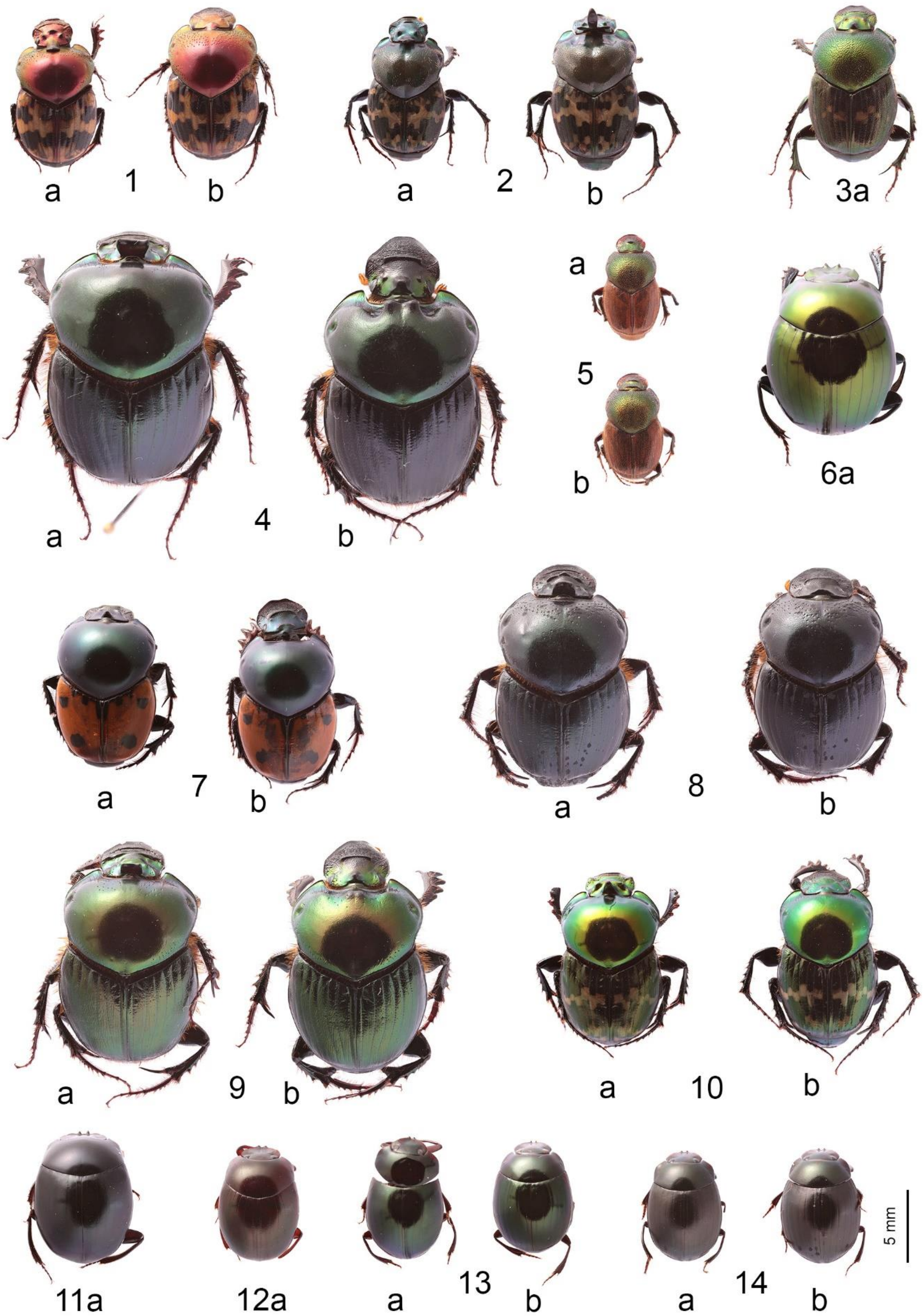

Figure 3. Madagascan Scarabaeinae, dorsal habitus. **1**—Helictopleurus splendidicollis; **2**—H. fissicollis; **3**—H. rudicollis; **4**—H. giganteus; **5**—H. viridiflavus; **6**—Epilissus splendidus; **7**—H. quadripunctatus; **8**—H. marsyas; **9**—H. coruscus; **10**—H. politicollis; **11**—Epilissus morio; **12**—Nanos dubitatus; **13**—N. agaboides; **14**—Pseudarachnodes hanskii; **a**—male, **b**—female.

Table 2. List and abundance of species in different collecting sites. For site numbers see Table 1.

Species\Site No.	1	2	3	4	5	6	7	8	9	10	11	12
O. pipitzi					6							
E. planatus				4								
E. splendidus						29			5			
E. apotolamproides						7						
E. morio										6		
Epactoides sp.									1			
A. quadrinotatus									1			
A. saprinoides	26											
Arachnodes sp. 1	17											
Arachnodes sp. 2				3					5			
Ps. hanskii						9						
N. agaboides			43									
N. dubitatus						6						
N. hanskii			1									
N. neoelectrinus	9											
H. giganteus						12		3	1	1	13	10
H. marsyas										15	5	
H. splendidicollis	6			7								
H. fissicollis	36	9	12									
H. viridiflavus						64			5			
H. coruscus						3			1			
H. neoamplicollis										1		
H. clouei					3							
H. quadripunctatus										5	1	
H. rudicollis						2	3	1	3			
H. politicollis	11	2										
Total species (specimens)	6 (105)	2 (11)	3 (56)	3 (14)	2 (9)	8 (132)	1 (3)	2 (4)	8 (22)	5 (28)	3 (19)	1 (10)

Table 3. Jaccard similarity indices. For site numbers see Table 1.

Site No.	1	2	3	4	5	6	7	8	9	10	11	12
1												
2	0.33											
3	0.13	0.25										
4	0.25	0.20	0.17									
5	0.00	0.00	0.00	0.00								
6	0.00	0.00	0.00	0.00	0.00							
7	0.00	0.00	0.00	0.00	0.00	0.13						
8	0.00	0.00	0.00	0.00	0.00	0.25	0.50					
9	0.00	0.00	0.00	0.09	0.00	0.45	0.13	0.25				
10	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.17	0.08			
11	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.25	0.10	0.60		
12	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.50	0.13	0.20	0.33	

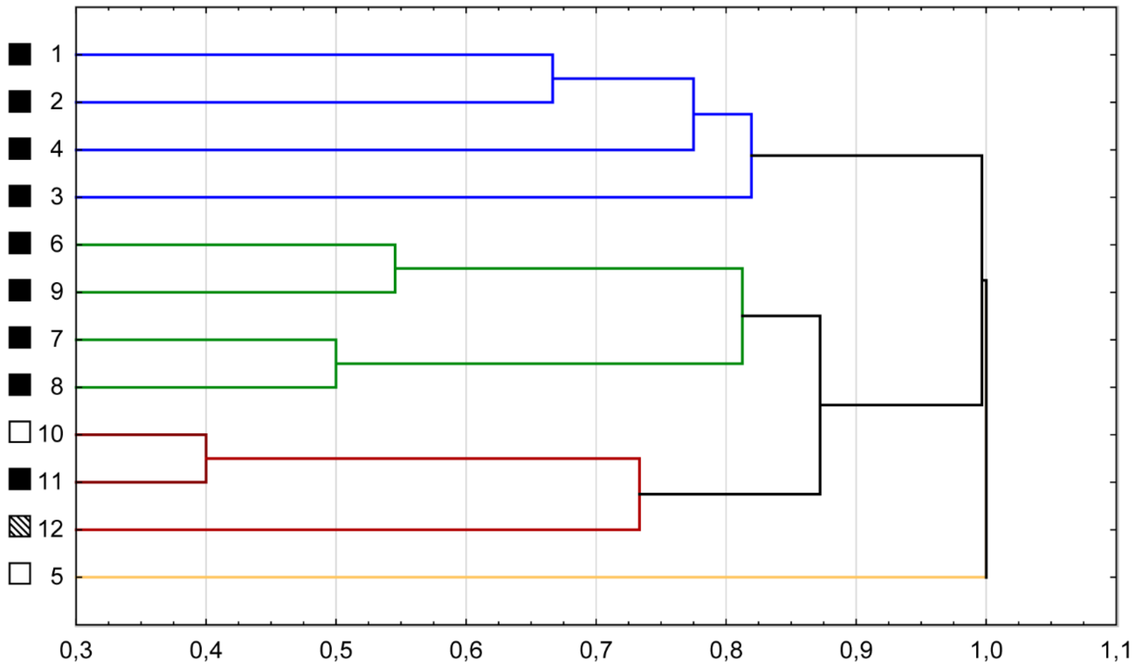

Figure 4. Diagram for 12 sites based on dissimilarity indices, complementary to Jaccard similarity indices (Table 3); method of clustering—joining, unweighted pair-group average. Y-axis: site number (Table 1), X-axis: linkage distance. ■—closed biotope (humid, subhumid, bamboo forest), □—open biotope (grassland, savannah), ▧—ecotone (between forest and grassland). Different colors depict clusters discussed in the text.

Tribe Oniticellini
Genus *Helictopleurus* d'Orbigny, 1915
***Helictopleurus splendidicollis* (Fairmaire, 1893)**
Figure 3. 1.

MADAGASCAR. Antsiranana: • Ankarana Special Reserve, subhumid forest near Manongarivo, 12°51′54″ S 49°13′31″ E, pitfall traps baited with human feces, 6–12.II.2022, A.V.Frolov leg., one male (ZIN), two females (MNHN), and two females (UMAM) • Montagne d'Ambre National Park, near camping site, humid forest, 12°31′30″ S 49°10′20″ E, pitfall traps baited with human feces, 5–10.II.2022, A.V.Frolov leg., one female (ZIN), three females (MNHN), and two females (UMAM).

***Helictopleurus fissicollis* (Fairmaire 1895)**
Figure 3. 2.

MADAGASCAR. Antsiranana: • Forêt d'Ambre Special Reserve, subhumid forest, 12°28′16″ S 49°13′4″ E, pitfall traps baited with human feces, 7–10.II.2022, A.V.Frolov leg., one male and two females (ZIN), two males and three females (MNHN), two males and three females (UMAM) • Montagne d'Ambre National Park, near camping site, humid forest, 12°31′30″ S 49°10′20″ E, pitfall traps baited with human feces, 5–10.II.2022, A.V.Frolov leg., five males and ten females (MNHN), five males and five females (UMAM), two males and nine females (ZIN) • Montagne d'Ambre National Park, humid forest, near entrance to park, 12°30′54″ S 49°10′50″ E, human feces, 5.II.2022, A.V.Frolov leg., one male and eight females (MNHN).

***Helictopleurus rudicollis* (Fairmaire 1898)**
Figure 3. 3.

MADAGASCAR. Toamasina: • Analamazaotra Special Reserve, primary forest, 18°55′59″ S 48°25′12″ E, pitfall traps baited with human feces, 17–20.II.2022, A.V.Frolov leg., one female (ZIN) • Mantadia National Park, humid forest, 18°49′47″ S 48°25′56″ E, pitfall traps baited with human feces, 17–20.II.2022, A.V.Frolov leg., one female (MNHN) • Mantadia National Park, humid forest, 18°49′32″ S 48°26′5″ E, pitfall traps baited with human feces, 18–20.II.2022, A.V.Frolov leg., two males and one female (MNHN) • Analamazaotra Special Reserve, bamboo forest, 18°56′7″ S 48°24′59″ E, pitfall traps baited with human feces, 18–20.II.2022, A.V.Frolov leg., three males (MNHN).

***Helictopleurus giganteus* (Harold 1869)**

Figure 3. 4.

MADAGASCAR. Toamasina: • Analamazaotra Special Reserve, primary forest, 18°55′59″ S 48°25′12″ E, pitfall traps baited with human feces, 17–20.II.2022, A.V.Frolov leg., three males and five females (ZIN), one male and two females (MNHN) • Mantadia National Park, humid forest, 18°49′47″ S 48°25′56″ E, pitfall traps baited with human feces, 17–20.II.2022, A.V.Frolov leg., three females (ZIN) • Mantadia National Park, humid forest, 18°49′32″ S 48°26′5″ E, pitfall traps baited with human feces, 18–20.II.2022, A.V.Frolov leg., one female (ZIN). Antananarivo: • Ankaratra massif, NW of Andraraly village, road along subhumid forest, 19°21′30″ S 47°18′45″ E, cow dung, 25.II.2022, A.V.Frolov leg., two males and eight females (ZIN) • Foothills of Ankaratra massif, near Andraraly village, open area, 19°22′29″ S 47°21′15″ E, cow dung, 23–24.II.2022, A.V.Frolov leg., one female (ZIN) • Ankaratra massif, NW of Andraraly village, humid forest, 19°21′20″ S 47°18′18″ E, pitfall traps with human feces, 23–26.02.2022, A.V.Frolov leg., two males and one female (MNHN), five males and five females (ZIN).

***Helictopleurus viridiflavus* (Fairmaire 1898)**

Figure 3. 5.

MADAGASCAR. Toamasina: • Analamazaotra Special Reserve, primary forest, 18°55′59″ S 48°25′12″ E, pitfall traps baited with human feces, 17–20.II.2022, A.V.Frolov leg., 25 males and 21 females (MNHN), 6 males and 3 females (ZIN), 5 males and 5 females (UMAM) • Mantadia National Park, humid forest, 18°49′32″ S 48°26′5″ E, pitfall traps baited with human feces, 18–20.II.2022, A.V.Frolov leg., two males and two females (MNHN).

***Helictopleurus quadripunctatus* (Olivier 1789)**

Figure 3. 7.

MADAGASCAR. Antananarivo: • Foothills of Ankaratra massif, near Andraraly village, open area, 19°22′29″ S 47°21′15″ E, cow dung, 23–24.II.2022, A.V.Frolov leg., one male and two females (MNHN), one male and one female (UMAM) • Ankaratra massif, NW of Andraraly village, humid forest, 19°21′20″ S 47°18′18″ E, pitfall traps with human feces, 23–26.02.2022, A.V.Frolov leg., one female (MNHN).

***Helictopleurus marsyas* (Olivier 1789)**

Figure 3. 8.

MADAGASCAR. Antananarivo: • Foothills of Ankaratra massif, near Andraraly village, open area, 19°22′29″ S 47°21′15″ E, cow dung, 23–24.II.2022, A.V.Frolov leg., three males and 12 females (ZIN) • Ankaratra massif, NW of Andraraly village, humid forest, 19°21′20″ S 47°18′18″ E, pitfall traps with human feces, 23–26.02.2022, A.V.Frolov leg., one male and three females (MNHN), one female (ZIN).

***Helictopleurus coruscus* D'Orbigny 1915**

Figure 3. 9.

MADAGASCAR. Toamasina: • Analamazaotra Special Reserve, primary forest, 18°55′59″ S 48°25′12″ E, pitfall traps baited with human feces, 17–20.II.2022, A.V.Frolov leg., two females (MNHN), two females (ZIN) • Mantadia National Park, humid forest, 18°49′32″ S 48°26′5″ E, pitfall traps baited with human feces, 18–20.II.2022, A.V.Frolov leg., one female (ZIN).

***Helictopleurus neoamplicollis* Krell 2000**

MADAGASCAR. Antananarivo: • Foothills of Ankaratra massif, near Andraraly village, open area, 19°22′29″ S 47°21′15″ E, cow dung, 23–24.II.2022, A.V.Frolov leg., one female (MNHN).

***Helictopleurus clouei* Harold (Harold 1869)**

MADAGASCAR. Antsiranana: • Ankarana Special Reserve, open area near Manongarivo, 12°51′55″ S 49°13′24″ E, cow dung, 6.II.2022, A.V.Frolov leg., one female (MNHN), one male (UMAM), and one female (ZIN).

***Helictopleurus politicollis* (Fairmaire 1902)**

Figure 3. 10.

MADAGASCAR. Antsiranana: • Montagne d'Ambre National Park, near camping site, humid forest, 12°31′30″ S 49°10′20″ E, pitfall traps baited with human feces, 5–10.II.2022, A.V.Frolov leg., three males and six females (MNHN), two females (ZIN) • Montagne d'Ambre National Park, humid forest, near entrance to park, 12°30′54″ S 49°10′50″ E, human feces, 5.II.2022, A.V.Frolov leg., two females (MNHN).

Tribe Onthophagini

Genus *Onthophagus*

***Onthophagus pipitzi* Ancey, 1883**

MADAGASCAR. Antsiranana: • Ankarana Special Reserve, open area near Manongarivo, 12°51′55″ S 49°13′24″ E, cow dung, 6.II.2022, A.V.Frolov leg., one male and five females (MNHN).

Tribe Epilissini

Genus *Epilissus* Reiche, 1841

***Epilissus planatus* (Montreuil, 2006)**

MADAGASCAR. Antsiranana: • Ankarana Special Reserve, subhumid forest near Manongarivo, 12°51′54″ S 49°13′31″ E, pitfall traps baited with human feces, 6–12.II.2022, A.V.Frolov leg., one female (ZIN), one male and one female (MNHN).

***Epilissus splendidus* Fairmaire, 1889**

Figure 3. 6.

MADAGASCAR. Toamasina: • Analamazaotra Special Reserve, primary forest, 18°55′59″ S 48°25′12″ E, pitfall traps baited with human feces, 17–20.II.2022, A.V.Frolov leg., six males and seven females (MNHN), three females (ZIN), four females (UMAM) • Mantadia National Park, humid forest, 18°49′32″ S 48°26′5″ E, pitfall traps baited with human feces, 18–20.II.2022, A.V.Frolov leg., two females (ZIN), five females (MNHN).

***Epilissus apotolamproides* (Lebis, 1961)**

MADAGASCAR. Toamasina: • Analamazaotra Special Reserve, primary forest, 18°55′59″ S 48°25′12″ E, pitfall traps baited with human feces, 17–20.II.2022, A.V.Frolov leg., three males and one female (MNHN), three females (ZIN).

***Epilissus morio* Harold, 1879**

Figure 3. 11.

MADAGASCAR. Antananarivo: • Foothills of Ankaratra massif, near Andraraly village, open area, 19°22′29″ S 47°21′15″ E, cow dung, 23–24.II.2022, A.V.Frolov leg., two males (MNHN), one male and one female (ZIN), one male (UMAM).

Genus *Nanos* Westwood, 1842

***Nanos dubitatus* (Lebis, 1953)**

Figure 3. 12.

MADAGASCAR. Toamasina: • Analamazaotra Special Reserve, primary forest, 18°55′59″ S 48°25′12″ E, pitfall traps baited with human feces, 17–20.II.2022, A.V.Frolov leg., five males (MNHN).

***Nanos agaboides* (Boucomont, 1937)**

Figure 3. 13.

MADAGASCAR. Antsiranana: • Forêt d'Ambre Special Reserve, subhumid forest, 12°28′16″ S 49°13′4″ E, pitfall traps baited with human feces, 7–10.II.2022, A.V.Frolov leg., 13 males and 10 females (MNHN).

***Nanos hanskii* Montreuil and Viljanen, 2007**

MADAGASCAR. Antsiranana: • Forêt d'Ambre Special Reserve, subhumid forest, 12°28′16″ S 49°13′4″ E, pitfall traps baited with human feces, 7–10.II.2022, A.V.Frolov leg., one male (MNHN).

***Nanos neoelectrinus* Montreuil and Viljanen, 2007, stat. rest.**

MADAGASCAR. Antsiranana: • Montagne d'Ambre National Park, near camping site, humid forest, 12°31′30″ S 49°10′20″ E, pitfall traps baited with human feces, 5–10.II.2022, A.V.Frolov leg., six males and three females (MNHN).

Genus *Epactoides* Olsoufieff, 1947

***Epactoides* sp.**

MADAGASCAR. Toamasina: • Mantadia National Park, humid forest, 18°49′32″ S 48°26′5″ E, pitfall traps baited with human feces, 18–20.II.2022, A.V.Frolov leg., one female (MNHN).

Genus *Apotolamprus* Olsoufieff, 1947

***Apotolamprus quadrinotatus* (Boucomont, 1937)**

MADAGASCAR. Toamasina: • Mantadia National Park, humid forest, 18°49′32″ S 48°26′5″ E, pitfall traps baited with human feces, 18–20.II.2022, A.V.Frolov leg., one male (MNHN).

Genus *Arachnodes* Westwood, 1842

***Arachnodes saprinoides* (Fairmaire, 1889)**

MADAGASCAR. Antsiranana: • Montagne d'Ambre National Park, near camping site, humid forest, 12°31′30″ S 49°10′20″ E, pitfall traps baited with human feces, 5–10.II.2022, A.V.Frolov leg., ten males and six females (MNHN), five males and five females (UMAM).

***Arachnodes* sp. 2**

MADAGASCAR. Antsiranana: • Ankarana Special Reserve, subhumid forest near Manongarivo, 12°51′54″ S 49°13′31″ E, pitfall traps baited with human feces, 6–12.II.2022, A.V.Frolov leg., one male and two females (MNHN). Toamasina: • Mantadia National Park, humid forest, 18°49′32″ S 48°26′5″ E, pitfall traps baited with human feces, 18–20.II.2022, A.V.Frolov leg., two males and three females (MNHN).

***Arachnodes* sp. 1**

MADAGASCAR. Antsiranana: • Montagne d'Ambre National Park, near camping site, humid forest, 12°31′30″ S 49°10′20″ E, pitfall traps baited with human feces, 5–10.II.2022, A.V.Frolov leg., 13 males and 4 females (MNHN).

Genus *Pseudarachnodes* Lebis, 1953

***Pseudarachnodes hanskii* Montreuil, 2003**

Figure 3. 14.

MADAGASCAR. Toamasina: • Analamazaotra Special Reserve, primary forest, 18°55′59″ S 48°25′12″ E, pitfall traps baited with human feces, 17–20.II.2022, A.V.Frolov leg., nine females (MNHN).

Nomenclatorial remarks

Nanos neoelectrinus Montreuil and Viljanen, 2007, was recently synonymized with *N. humeralis* Paulian, 1975 [43]. However, based on the new material it is revalidated here because the two species show significant differences in pronotal punctuation and were described from different regions.

Epactoides Olsoufieff and part of the *Arachnodes* Westwood species were identified to morphospecies because these genera need further taxonomic treatment which is outside the scope of the present contribution.

Biogeographical analysis

Jaccard similarity indices (Table 3) are low for most localities. There are four clusters of sites (Figure 4). One site, a savannah in northeastern Ankarana Special Reserve (No 5), has no similarity with other sites because the species we collected there were not found in other localities. The three other clusters are those combining (1) sites in Montagne d'Ambre mountain range and a forest site northeastern Ankarana Special Reserve, (2) sites in Andasibe-Mantadia protected area, and (3) sites in Manjakatompo Ankaratra.

The maximum species number per locality was eight (primary forests in Montagne d'Ambre National Park and Analamazaotra Special Reserve). Most localities yielded two to six species per site. At the same time, the species differed among the distant conservation areas. The species composition of Montagne d'Ambre National Park and Ankarana Special Reserve, Andasibe-Mantadia protected area, and Manjakatompo Ankaratra were different.

The notable exception is the largest *Helictopleurus* species—*H. giganteus*, which was found in different biotopes in Andasibe-Mantadia protected area and Manjakatompo Ankaratra, separated by over 120 km.

4. Discussion

In Madagascar, dung beetles are important elements in forest food chains and ecosystems and the recent fauna originally evolved to decompose the excrements of lemurs [12,21,22,27,44,45]. Madagascan dung beetles have been the subject of a number of studies. In particular, it has been shown that the present day diversity of Madagascan scarabaeines is a result of four big radiations after at least eight independent overseas colonization events [12]. Despite the absence of large native herbivores and, in general, relatively poor mammal diversity on the island, Madagascar has an exceptionally diverse dung beetle fauna. In terms of the number of genera, Madagascar is comparable to the Palaearctic region and is richer than the Nearctic region. The tropical islands of New Guinea and Borneo have larger areas than Madagascar but only about 120 species of dung beetles each, with species endemism varying from 38 to 83 percent [46]. In total, these two islands have less species of dung beetles than Madagascar. The latter has over 300 described species and new species continue to be described.

The majority of Madagascan dung beetles species, more than 200 species of Epilissini, and about 55 species of Helictopleurini inhabit forested areas. In contrast, the number of open area dwellers is rather small [16]: Onthophagini (six species), Scarabaeini (three species), some Helictopleurini (nine species), and a few Epilissini (four species) were recorded at the time of this study from cattle dung and human feces in open areas. As all Madagascan Onthophagini and Scarabaeini species are open area specialists, they were probably already living in open biotopes before human's arrival to Madagascar 11,000 years ago [47] and were feeding upon the dung of the then existing megafauna inhabited open and semi-open area (mammals, birds: [48,49]). In such biotopes, they could shift to human feces and cow dung after the extinction of megafauna due to human activity and the introduction of cattle about 1000 years ago [50].

On the other hand, Helictopleurini and Epilissini went through adaptive radiation along with lemurs [44]. Most of the species of these groups live in forested areas and depend on lemur feces and carrion. Of the nine Helictopleurini species registered in open areas, three (*H. giganteus*, *H. rudicollis*, and *H. situaticornis*) are still mostly found in forest areas. We could hypothesize that for these species, the shift to open areas is in progress. The six remaining species are only found in open habitats. This suggests that the shift from forest to open areas was either already completed after the extinction of megafauna, which is less probable [16,49], or that it happened long time ago during initial radiation of the tribe.

In our survey, too, a much higher number of species was found in closed forest biotopes than in open areas. Only 7 out of 26 species were found in open biotopes. These include the only onthophagine species (*Onthophagus pipitzi*), belonging to the group occurring mostly in open areas. All other species belong to helictopleurines and canthonines, which are predominantly forest dwellers. Except for *O. pipitzi*, two species were found only in open biotopes: *H. clouei* in Ankarana Special Reserve and *Epilissus morio* in Ankaratra massif. This is probably because of the insufficient sampling.

It has been suggested that the relatively low alpha diversity of dung beetles in a given biotope is compensated for by an exceptionally high regional turnover in species composition [23]. Our results support this assumption. There was commonly found for all the studied sites. Most of the species were limited in distribution to one protected area. The larger range of *H. giganteus* may be due to their diet shift to cattle dung and human feces and a secondary expansion of the range of this species. We found this species both in humid forests (attracted to the pitfall traps baited with human feces) and in open areas in cattle dung pads. However, despite both their food sources being easily available throughout the island, the species range does not cover all this area. This may be a result of the interspecific interactions that restrict the number of locally co-existing species [20,21].

Seasonality is one of the key niche dimensions in tropical forest dung beetle communities [46,51]. Peaks in activity occur during seasonally favorable warm and wet conditions, and the activity declines during seasonally unfavorable cooler and drier weather. In Afrotropics, there are a few principal seasonal patterns, including bimodal rainfall, with the highest peak of diversity and abundance occurring in the first period of longer rains [11]; the subequatorial rainforests are seasonal but have high temperatures and rainfall that are favorable for beetle activity year-round. Madagascan rainforests are seasonal with a wet season (December–February) and a dry season (June–August). The multiyear study in Ranomafana National Park and Masoala National Park showed that although the beetle abundance was generally higher during the wet season, there was no obvious seasonality in the occurrence of species [21].

It is interesting to note that the heavy rains encountered during this survey period did not apparently effect the activity of dung beetles. Two cyclones passed via northern Madagascar in February 2022, which resulted in almost continuous rains in the Montagne d'Ambre range, yet the dung beetles of different species were observed flying around and small canthonines rolling their balls. Previous studies suggested that canthonines, as opposed to helictopleurines, are nocturnal [21]. We think that prolonged showers may shift the activity of some canthonine species to day hours.

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