Biodiversity Data Journal 11: e96101
doi: 10.3897/BDJ.11.e96101

Taxonomy & Inventories

Dung beetles from two sustainable-use protected forests in the Brazilian Amazon

Edrielly C. Carvalho[‡,§], Maria Eduarda Maldaner[|], Vinicius Costa-Silva[‡,¶], Heivanice Sehn[#], Carol Franquini[‡], Vinicius O. Campos[‡], Vinicius P. Seba[‡], Laís F. Maia[¤], Fernando Z. Vaz-de-Mello[‡], Filipe Machado França[¤,«]

‡ Departamento de Biologia e Zoologia, Instituto de Biociências, Universidade Federal de Mato Grosso. Laboratório de Scarabaeoidologia. Instituto de Biociências - UFMT, Cuiabá, Brazil
§ Programa de Pós-Graduação em Entomologia. Instituto Nacional de Pesquisas da Amazônia – INPA, Manaus, Brazil
| Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade (PPGECB), Universidade Federal de Mato Grosso - UFMT, Cuiaba, Brazil
¶ Laboratory of Integrative Entomology, Department of Animal Biology, Institute of Biology, University of Campinas, Campinas, Brazil
# Programa de Pós-Graduação em Zoologia. Instituto de Biociências, Universidade Federal de Mato Grosso - UFMT, Cuiabá, Brazil
¤ School of Biological Sciences, University of Bristol, Queens Road, BS8 1QU, UK, Bristol, United Kingdom
« Programa de Pós-Graduação em Ecologia (PPGECO), Universidade Federal do Pará, Belém, PA, 66075-110, Brazil, Belém, Brazil

Corresponding author: Edrielly C. Carvalho (edrielly.carol@gmail.com)

Academic editor: Matthias Seidel

Received: 07 Oct 2022 | Accepted: 14 Feb 2023 | Published: 16 Mar 2023

Citation: Carvalho EC, Maldaner ME, Costa-Silva V, Sehn H, Franquini C, Campos VO, Seba VP, Maia LF, Vaz-de-Mello FZ, França FM (2023) Dung beetles from two sustainable-use protected forests in the Brazilian Amazon. Biodiversity Data Journal 11: e96101. https://doi.org/10.3897/BDJ.11.e96101

Abstract

Background

The Amazon Forest is one of the world's most biodiverse ecosystems and yet its protected areas are understudied concerning insects and other invertebrates. These organisms are essential for tropical forests due to their ecological processes, with some species being very sensitive to habitat disturbances. Dung beetles (Coleoptera, Scarabaeidae, Scarabaeinae) have been used as bioindicators for more than 30 years and were surveyed to assess the insect biodiversity of two sustainable-use forest reserves in the Brazilian Amazon.

New information

We report inventories of dung beetles from two Amazonian forest reserves in Pará State, Brazil: the Tapajós National Forest and the Carajás National Forest. Surveys were carried out with baited-pitfall traps installed in 2010, 2016, 2017 and 2019. We collected a total of 3,772 individuals from 19 genera and 96 species. We highlight the importance of Amazonian protected areas as refugia for insect biodiversity, particularly dung beetles, which contribute to many key ecosystem processes.

Keywords

Amazonia, biodiversity, Coleoptera, dung beetles, Scarabaeinae, sustainable-use forests, tropical ecosystems

Introduction

The Amazon Forest has global importance for biodiversity, being amongst the world's most diverse tropical ecosystems (Barlow 2018). The region's warm and humid climate makes Amazonian forests a unique ecosystem with extraordinary biodiversity levels, particularly for insects (Fearnside 2008, Sobral-Souza and Lima-Ribeiro 2017).

With the human footprint and climate extremes increasing within tropical regions (França et al. 2020a), protected areas are increasingly becoming the final refuges for biodiversity, including many restricted-range and highly threatened species (Rylands and Brandon 2005 , Sollmann et al. 2008). Until 2009, around 54% of the remaining Amazon Forest in Brazil was part of a protected area network, ranging from strictly protected areas and indigenous lands to sustainable use forests (Soares-Filho et al. 2010). The importance of these protected areas goes beyond biodiversity conservation by sustaining local livelihoods (Naughton-Treves et al. 2005, Spinola et al. 2020), preventing climate-tipping points (Walker et al. 2009) and supporting the mitigation of climate changes through carbon accumulation and reduction of Greenhouse Gases (GHG) emissions from deforestation (Soares-Filho et al. 2010, Walker et al. 2020).

Despite the unparalleled contribution of insects to the totality of biodiversity (Zhang 2011) and their important role in many critical ecological functions (Nichols et al. 2008, Campbell et al. 2012, Dangles and Casas 2019), insects are understudied when compared to vertebrates (Dornelas and Daskalova 2020). For example, only 1.67% of the known invertebrate species have been assessed by the IUCN Red List of threatened species compared with 68.9% of all vertebrates (Kitching et al. 2020). The lack of studies with insects and invertebrates is also evidenced within Amazonian protected areas.

Dung beetles (Coleoptera, Scarabaeinae) are a key group of detritivore insects frequently used in ecological research linking biodiversity and ecosystem functioning (França et al. 2018, Griffiths et al. 2015). Through feeding and nesting in mammal dung, carrion or rotten fruits, dung beetles play important roles in nutrient cycling and other ecosystem functions (Halffter and Matthews 1966, Nichols et al. 2008). Given their quick responses to environmental degradation by anthropogenic and climatic disturbances (e.g. França et al. 2020a, França et al. 2020b), since the 1990s, dung beetles have been used as an efficient indicator of environmental quality in tropical forests (Halffter and Favila 1993, Davis et al. 2004, Larsen and Forsyth 2005, Spector 2006, Nichols et al. 2007, Gardner et al. 2008, Nichols et al. 2008, Culot et al. 2013). In general, anthropogenic activities lead to changes in dung beetle 'fitness' (through physiological stress: for example, França et al. (2016), Salomao et al. (2018)), species richness and abundance (Klein and Bert 1989, Halffter and Arellano 2002, Escobar et al. 2007).

Here, we: (1) present a list of dung beetle species surveyed at two sustainable-use protected forests in the Brazilian Amazon – the Tapajós National Forest and the Carajás National Forest (FLONAS); and (2) discuss insights associated with the species distribution and previous recordings in literature.

Materials and methods

Study region

The Tapajós National Forest and Carajás National Forest (hereafter 'Tapajós' and 'Carajás', respectively) cover 527,319 ha and 411,948 ha of Amazonian forests, respectively, spread across multiple municipalities in the State of Pará, Brazil (Fig. 1). These FLONAS are located in two Amazonian biogeographical regions with distinct socio-environmental contexts. Specifically, the Tapajós region has a more recent history of agriculture expansion and lower deforestation rates than the Carajás region (Braz 2016), with FLONA Carajás located within a mosaic of federal and state forest reserves, national parks and indigenous protected lands (Piló et al. 2015). The climate is characterised as hot-humid (Köppen's classification) and the annual average temperature is 25-26°C in both regions, which have short dry seasons in August-November (average precipitation [mm]: Tapajós = 1405.8) and July-September (Xingu = 84.8). Surveyed sites are within the 'terra-firm' forests, with vegetation varying depending on soil and relief.

Sampling design

Dung beetles were sampled within a total of 13 forest sites (Carajás = 3 and Tapajós = 10). We surveyed Carajás in February–March 2019, while Tapajós forests were surveyed in June-July 2010, June–July 2016, March–April 2017 and Feb–March 2019. These field sites are part of the Long-Term Ecological Research Program of the Sustainable Amazon Network (PELD-RAS). At each of our forest sites, dung beetles were sampled at three sampling points (0, 150 and 300 m) along a 300-m transect. As in França et al. (2020b), we used three dung-baited pitfall traps arranged at the ends of a 2-m equilateral triangle at each sampling point, resulting in a total of 117 traps (21 and 96 pitfalls in Carajás and Tapajós, respectively). Pitfall traps were 1-litre plastic containers (14 cm in diameter; 9 cm deep) buried in the ground with the opening at ground level and protected from rain with a plastic lid suspended 15 cm above the surface. Each trap was part-filled with a saline killing solution, had a bait container with 35 g of dung (4:1 pig to human ratio, following Marsh et al. (2013)) supported by a wire above the trap and was left in the field for 48 hours.

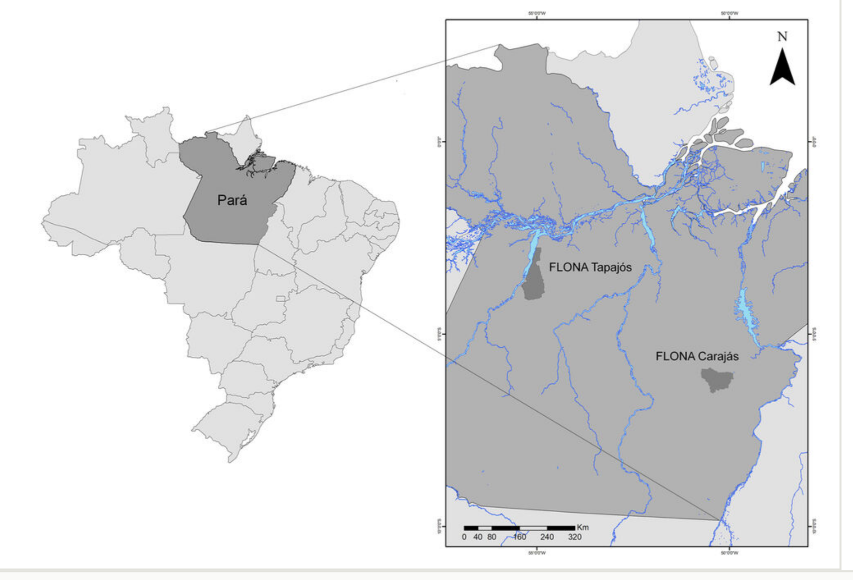

Figure 1. doi

Map showing the localities of Tapajós National Forest (FLONA Tapajós) and Carajás National Forest (FLONA Carajás; both in dark grey) in Pará State (medium grey), in the north of Brazil (light grey).

Data resources

All trapped dung beetles were collected and taken to the laboratory, where they were sorted, mounted and identified to species (using identification key or descriptions) or morphospecies. Voucher specimens were deposited at the Entomological Section of the Zoological Collection (CEMT) at the Federal University of Mato Grosso, Brazil (UFMT). Specimens were photographed using the Leica M250C Photomontage Equipment (UFMT/Finep) and an Olympus SZX16 stereomicroscope with expandable stream motion imaging software v. 2.5 (UoB/Liv Sidse Hansen Foundation). The morphospecies identification numbers are not indicating the amount of species collected at the sites and are purely reference numbers for species across multiple projects. The abbreviations *aff.*, *cf.* and *gp.* are qualifiers used in taxonomy to indicate different degrees of uncertainty of identification. The use of *aff.* and *cf.* follows Lucas (2012) and *gp.* indicates species group affinity.

The map showing the localities of Tapajós National Forest and Carajás National Forest was prepared using ArcGIS 10.8 software. Dung beetle data can be found at http://www.gbif.org/tools/data-validator/f1e2a538-5fea-4258-9b0e-27805b684404 (GBIF 2022).

List and abundance of species present in FLONA Tapajós and Carajás

Subfamily Scarabaeinae Latreille, 1802

Notes: We collected 3,772 dung beetles from 96 species and 19 genera. Only 14 of the 96 identified species were found in both FLONAS (Table 1). *Canthidium deyrollei* was the most abundant species, with exclusive records from FLONA Tapajós. The three most diverse genera comprise distinct functional strategies in dung beetles: *Eurysternus* (endocoprids – i.e. residents in the dung resource); *Dichotomius* (paracoprids – i.e. tunnellers, where all species mostly dig tunnels close to or immediately below the resource) and *Canthon* (telecoprids – i.e. rollers), which could be an indicator of whole exploitation of dung resources in Amazonian forests. However, if abundance is considered, small paracoprids (especially *Onthophagus* species) were the most abundant functional group, which is expected for the Amazon Region (FVM, pers. obs). We discuss below the current knowledge about the distribution and ecology of each identified genera.

Table 1.

List and abundance of species present in FLONA Tapajós and Carajás.

Species	Abundance	
	FLONA Tapajós	FLONA Carajás
Anomiopus aff. *pereirai*	1	-
Anomiopus sp. 2	1	-
Anomiopus sp. 3	1	-
Anomiopus sp. 4	1	-
Anomiopus sp. 5	-	1
Ateuchus globulus (Balthasar, 1938)	1	-
Ateuchus sp. 2	14	-
Ateuchus sp. 3	10	-
Ateuchus gp. *pygidialis*	-	1
Ateuchus cf. *murrayi*	113	-
Ateuchus sp. 4	64	-
Ateuchus semicupreus (Harold, 1868)	-	18
Ateuchus sp. 1	-	39
Ateuchus substriatus (Harold, 1868)	12	-
Canthidium deyrollei Harold, 1867	283	-
Canthidium melanocephalum (Olivier, 1789)	31	-
Canthidium sp. 1	-	13

Species	**Abundance**	
	FLONA Tapajós	**FLONA Carajás**
Canthidium sp. 2	1	-
Canthidium sp. 3	-	3
Canthidium sp. 4	-	29
Canthidium sp. 5	84	-
Canthidium sp. 6	6	-
Canthidium sp. 7	6	-
Canthidium sp. 9	1	-
Canthidium sp. 10	86	-
Canthidium sp. 11	4	-
Canthidium sp. 12	5	-
Canthidium sp. 13	-	2
Canthidium sp. 14	-	346
Canthidium sp. 15	128	-
Canthidium sp. 18	15	-
Canthidium sp. 19	3	-
Canthidium sp. 20	1	-
Canthidium sp. 21	1	-
Canthidium sp. 22	-	2
Canthidium sp. 25	-	4
Canthidium sp. 26	-	1
Canthidium sp. 33	-	3
Canthon aff. *histrio*	34	-
Canthon aff. *sericatus*	1	-
Canthon aff. *xanthopus*	9	-
Canthon conformis Harold, 1868	1	-
Canthon fulgidus Redtenbacher, 1868	235	29
Canthon histrio (Lepeletier de Saint-Fargeau & Audinet-Serville, 1828)	-	35
Canthon subhyalinus (Rivera-Cervants & Halffter, 1999)	2	-
Canthon semiopacus Harold, 1868	6	0
Canthon triangularis (Drury, 1770)	-	3
Coprophanaeus degallieri Arnaud, 1997	1	-
Coprophanaeus jasius (Olivier, 1789)	3	-
Coprophanaeus lancifer (Linnaeus, 1767)	27	18
Cryptocanthon campbellorum Howden, 1973	4	3
Deltochilum enceladus Kolbe, 1893	4	-

Species	Abundance	
	FLONA Tapajós	FLONA Carajás
Deltochilum gp. *aspericolle*	156	-
Deltochilum gp. *guyanense*	13	45
Deltochilum gp. *sextuberculatum*	6	-
Deltochilum orbiculare Van Lansberge, 1874	2	27
Deltochilum orbignyi amazonicum Bates, 1887	5	-
Deltochilum sp. 1	3	-
Dichotomius aff. *batesi*	225	36
Dichotomius aff. *lucasi* 1	137	50
Dichotomius aff. *lucasi* 2	112	-
Dichotomius cuprinus (Felshe, 1901)	-	1
Dichotomius mamillatus (Felshe, 1901)	-	5
Dichotomius melzeri (Luederwaldt, 1922)	2	-
Dichotomius nisus (Olivier, 1789)	-	51
Dichotomius pelamon (Harold, 1869)	5	1
Dichotomius worontzowi (Pereira, 1942)	3	2
Eurysternus arnaudi Génier, 2009	8	-
Eurysternus atrosericus Génier, 2009	192	-
Eurysternus balachowskyi Halffter & Halffter, 1977	4	-
Eurysternus caribaeus (Herbst, 1789)	163	86
Eurysternus cavatus Génier, 2009	-	3
Eurysternus cayennensis Castelnau, 1840	10	-
Eurysternus cyclops Génier, 2009	-	1
Eurysternus fallaciosus Génier, 2009	-	2
Eurysternus foedus Guérin-Méneville, 1844	-	12
Eurysternus hamaticollis Balthasar, 1939	2	1
Eurysternus hypocrita Balthasar, 1939	1	-
Eurysternus plebejus Harold, 1880	5	-
Eurysternus wittmerorum Martínez, 1988	47	44
Eutrichillum sp. 1	1	-
Hansreia oxygona (Perty, 1830)	-	17
Isocopris imitator (Felsche, 1901)	3	-
Isocopris nitidus (Luederwaldt 1922)	2	-
Ontherus carinifrons Luederwaldt, 1930	13	-
Onthophagus digitifer Boucomont, 1932	1	-
Onthophagus gp. *rubrescens*	91	147

Species	Abundance	
	FLONA Tapajós	FLONA Carajás
Onthophagus onthochromus Arrow, 1913	-	1
Onthophagus osculatii Guérin-Méneville, 1855	70	10
Oxysternon macleayi Nevinson, 1892	26	11
Oxysternon silenus Castelnau, 1840	1	3
Scybalocanthon sp. 1	-	2
Sulcophanaeus faunus (Fabricius, 1775)	1	-
Sylvicanthon candezei (Harold, 1869)	1	-
Sylvicanthon proseni (Martínez, 1949)	116	-
Uroxys cf. *minutus*	29	8

Genus *Anomiopus* Westwood, 1842

Notes: *Anomiopus* is a Neotropical genus with most species occurring in South America. The latest revision has 48 described species (Canhedo 2004, Canhedo 2006). Most *Anomiopus* species are collected with flight interception traps (FIT), Malaise traps, pitfalls baited with human dung (Canhedo 2006), light traps and bird faeces (Martinez 1959). Some species were observed in the Colombian Amazon landing on leaves during the day (Canhedo 2006). In our study, we found five species: *Anomiopus* aff. *pereirari*, *Anomipus* sp. 2, *Anomiopus* sp. 3, *Anomiopus* sp. 4 and *Anomiopus* sp. 5.

Genus *Ateuchus* Weber, 1801

Notes: With around 100 species described, this genus needs urgent revision. The last revision of Brazilian *Ateuchus* species was done by Harold (1868), while Balthasar (1939) represents the last identification key for the genus. Most species occur in North America, Costa Rica and Mexico (Kohlmann 1984, Kohlmann 1997, Génier 2000, Kohlmann and Vaz-de-Mello 2018) and appear to be copro-necrophagous, including species from open areas and species that live associated with ant nests (Vaz-de-Mello et al. 1998). Nine species were identified in our study: *Ateuchus globulus* (Balthasar, 1938), *A.* cf. *pygidialis*, *A.* cf. *murrayi*, *A. semicupreus* (Harold, 1868), *A. substriatus* (Harold, 1868) and *Ateuchus* sp. 1, *Ateuchus* sp. 2, *Ateuchus* sp. 3 and *Ateuchus* sp. 4 (Fig. 2A-G).

Genus *Canthidium* Erichson, 1847

Notes: This is one of the most diverse dung beetle genera, comprising around 180 described species (Génier and Cupello 2018, Schoolmeesters 2022). Numerous species were described in small revisions, synopses and regional studies (e.g. Boucomont (1928), Balthasar (1939), Martínez et al. (1964), Howden and Young

(1981), Solis and Kohlmann (2004), Kohlmann and Solís (2006)), while new species are expected to be described (Cupello 2018, Kohlmann et al. 2018, Santana et al. 2019). *Canthidium* species have been recorded within Neotropical forests and intra-Amazonian savannahs (e.g. França et al. (2016)). Although little is known about most species' habits, specimens are easily collected in traps baited with faeces, rotten fruit and/or light traps (e.g. Medri and Lopes (2001), Silva and Audino (2011), Silva et al. (2014)), while some species were observed feeding on fungus (Falqueto et al. 2005). The specimens were identified from comparison with the original types and descriptions, which were analysed by one of the authors. Two species were identified to the species level in our survey in FLONA Tapajós: *Canthidium deyrollei* Harold, 1867 and *C. melanocephalum* (Olivier, 1789) (Fig. 2H-I). Other 22 species are present, but could not be identified.

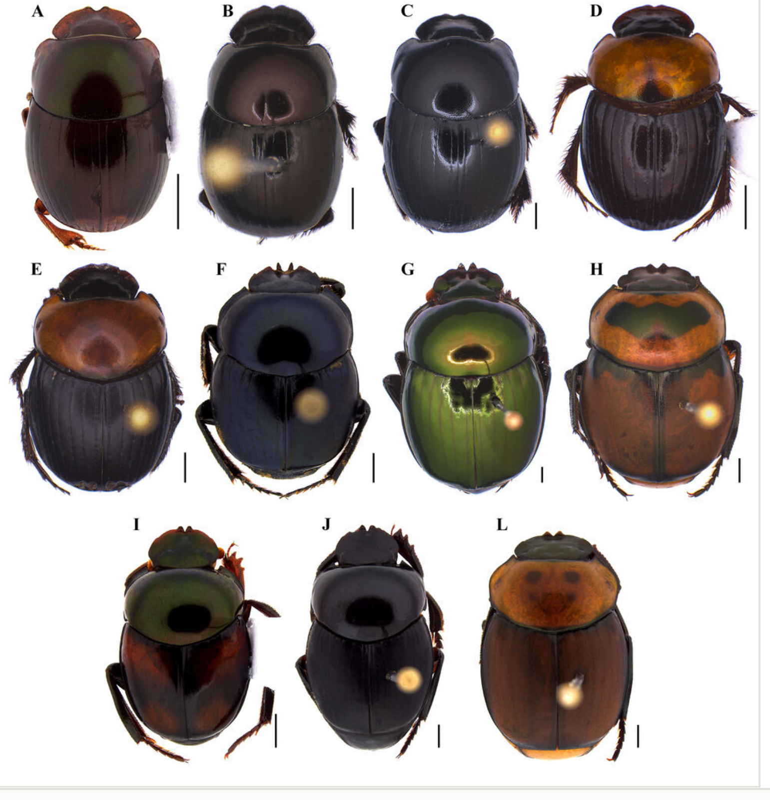

Figure 2. doi

Dorsal habitus of dung beetle species collected in the Tapajós National Forest and/or Carajás National Forest **A** *Ateuchus globulus* (Balthasar, 1938); **B** *Ateuchus semicupreus* (Harold, 1868); **C** *Ateuchus substriatus* (Harold, 1868); **D** *Canthidium deyrollei* Harold, 1867; **E** *Canthidium melanocephalum* (Olivier, 1789); **F** *Canthon conformis* Harold, 1868; **G** *Canthon fulgidus* Redtenbacher, 1868; **M** *Canthon histrio* (Lepeletier de Saint Fargeau & Audinet-Serville, 1828); **I** *Canthon subhyalinus* (Rivera-Cervants & Halffter, 1999); **J** *Canthon semiopacus* Harold, 1868; **L** *Canthon triangularis* (Drury, 1770). Scale bar: 1 mm.

Genus *Canthon* Hoffmannsegg, 1817

Notes: This is also a very diverse genus, comprising more than 170 described species (Halffter and Martinez 1977). Most species are considered copro-necrophagous, although some exhibit predatory behaviour – for example, hunting ants (Halffter and Matthews 1966) – or use dead insects and millipedes (Villalobos et al. 1988, Silva et al. 2014), rotten fruits and fungus as food resources (Vaz-de-Mello 1999). This genus is endemic to the Americas and its distribution ranges from the USA to Uruguay and northern Argentina. Recent revisions have been made for some *Canthon* subgenera (Nunes et al. 2018, Nunes et al. 2020). Typically, these species are abundant in lowland forest environments, with individuals found perching on leaves exposed to light (Nunes et al. 2018). Another important point to be discussed is the population of *Canthon fulgidus* Redtenbacher, 1868 with green colour living in eastern Amazonia. According to Nunes et al. (2018), the population with green colour, named *Canthon fulgidus martinezi* Nunes et al., 2018, is restricted to the western Amazon, while the populations from Carajás and Tapapós regions were expected to have a red metallic colour (named by the authors as *Canthon fulgidus pereirai* Nunes et al., 2018). This new finding (both green and red populations collected in the same region) suggests that Nunes et al. (2018) may have overlooked the green specimens from eastern Amazonia, as previously mentioned by Cupello et al. (2021), who discuss the colour variation and geographical distribution of distinct Scarabaeinae beetles. For the identification of species, the following works were mainly used: Nunes et al. (2018), Nunes et al. (2020). Nine species were identified: *Canthon* aff. *histrio*, *C.* aff. *sericatus*, *C.* aff. *xanthopus*, *C. conformis* Harold, 1868, *C. fulgidus* Redtenbacher, 1868, *C. histrio* (Lepeletier de Saint-Fargeau & Audinet-Serville, 1828), *C. subhyalinus* (Rivera-Cervants & Halffter, 1999), *C. semiopacus* Harold, 1868 and *C. triangularis* (Drury, 1770) (Fig. 2J-P).

Genus *Coprophanaeus* d'Olsoufieff, 1924

Notes: A Neotropical genus with approximately 51 known species (Schoolmeesters 2022), which are easily identified using the taxonomic keys published by Edmonds and Zidek (2010). This genus is known to be attracted to carcasses and be captured in flight intercept traps (Vaz-de-Mello 1999). Usually found in fresh carrion at dusk periods (Halffter and Matthews 1966). For the identification of species, the following works were mainly used: Edmonds and Zidek (2010). Three species were identified in our study: *Coprophanaeus degallieri* Arnaud, 1997, *C. jasius* (Olivier, 1789) and *C. lancifer* (Linnaeus, 1767) (Fig. 3A-C).

Genus *Cryptocanthon* Balthasar, 1942

Notes: This genus comprises around 43 species occurring from Brazil to Mexico (Arias and Medina 2014, Martínez-Revelo et al. 2020, Giraldo-Mendonza 2022). The only available information about their habitat describes specimens inhabiting the leaf litter of humid and tropical forests, both in mountains and low altitudes (Cook 2002). For the identification of the species, the following works were mainly used: Cook (2002). *Cryptocanthon campbellorum* Howden, 1973 (Fig. 3D) was the only species, which is usually collected in leaf litter, with flight interception and pitfall traps baited with human faeces (Cook 2002).

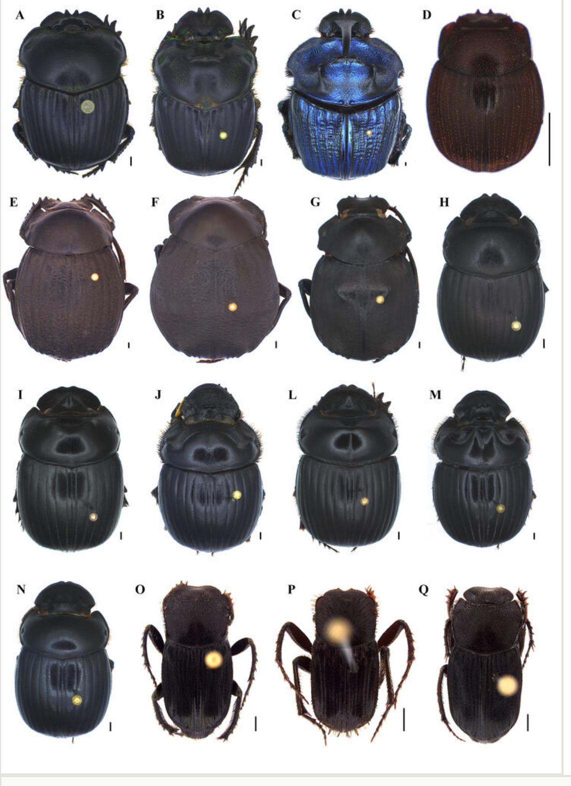

Figure 3. doi

Dorsal habitus of dung beetle species collected in the Tapajós National Forest and/or Carajás National Forest. **A** *Coprophanaeus degallieri* Arnaud, 1997; **B** *Coprophanaeus jasius* (Olivier, 1789); **C** *Coprophanaeus lancifer* (Linnaeus, 1767); **D** *Cryptocanthon campbellorum* Howden, 1973; **E** *Deltochilum anceladus* Kolbe, 1893; **F** *Deltochilum orbiculare* Lansberge, 1874; **G** *Deltochilum orbignyi amazonicum* Bates, 1887; **H** *Dichotomius cuprinus* (Felsche, 1901); **I** *Dichotomius mamillatus* (Felsche, 1901); **J** *Dichotomius melzeri* (Luederwaldt, 1922); **L** *Dichotomius nisus* (Olivier, 1789); **M** *Dichotomius pelamon* (Harold, 1869); **N** *Dichotomius worontzowi* (Pereira, 1942); **O** *Eurysternus arnaudi* Génier, 2009; **P** *Eurysternus atrosericus* Génier, 2009; **Q** *Eurysternus balachowski* Halffter & Halffter, 1977. Scale bar: 1 mm.

Genus *Deltochilum* Eschscholtz, 1822

Notes: This is a very diverse genus of the Americas, with approximately 115 described species (González-Alvarado and Vaz-de-Mello 2021). *Deltochilum* individuals are mostly nocturnal and often found in temperate, tropical and subtropical forests (Halffter and Matthews 1966). *Deltohyboma* is currently the most challenging subgenus, which has been recently revised with several new species (González-Alvarado and Vaz-de-Mello 2021). For the identification of the species, the following works were mainly used: González-Alvarado and Vaz-de-Mello (2021). Seven species were identified through our study: *Deltochilum enceladus* Kolbe, 1893, *D.* gp. *aspericolle*, *D.* gp. *guyanense*, *D.* gp. *sextuberculatum*, *D. orbiculare* van Lansberge, 1874, *D. orbignyi amazonicum* Bates, 1887 and *Deltochilum* sp. 1 (Fig. 3E-G).

Genus *Dichotomius* Hope, 1838

Notes: According to the most recent taxonomic revision from one of the subgenera of *Dichotomius*, this Neotropical genus comprises around 190 species widely distributed from the USA to Argentina (Nunes and Vaz-de-Mello 2019). The four subgenera are either being revised or were recently revised (Nunes et al. 2016, Valois et al. 2017, Maldaner et al. 2018, Nunes and Vaz-de-Mello 2019). *Dichotomius* species occur in all Brazilian biomes and can be collected in pastures, savannahs or forests. The genus as a whole is considered paracoprid – i.e. tunnellers (Nunes and Vaz-de-Mello 2019). For the identification of the species, the following works were mainly used: Nunes et al. (2016), Valois et al. (2017), Maldaner et al. (2018), Nunes and Vaz-de-Mello (2019). We collected nine species: *Dichotomius* aff. *batesi*, *D.* aff. *lucasi* 1, *D.* aff. *lucasi* 2, *D. cuprinus* (Felshe, 1901), *D. mamillatus* (Felshe, 1901), *D. melzeri* (Luederwaldt, 1922), *D. nisus* (Olivier, 1789), *D. pelamon* (Harold, 1869) and *D. worontzowi* (Pereira, 1942) (Fig. 3H-N).

Genus *Eurysternus* Dalman, 1824

Notes: A Neotropical genus with 53 described species (Génier 2009) that are mostly endocoprids (Halffter and Matthews 1966, Cupello and Vaz-de-Mello 2018). *Eurysternus* species are easily collected in pitfalls baited with faeces, occurring in forests and frequently abundant in flooding-prone areas (Génier 2009). Génier (2009) was used for species identification. Thirteen species were recorded in our surveys: *Eurysternus arnaudi* Génier, 2009, *E. atrosericus* Génier, 2009, *E. balachowskyi* Halffter & Halffter, 1977, *E. caribaeus* (Herbst, 1789), *E. cavatus* Génier 2009, *E. cayannensis* Castelnau, 1840, *E. cyclops* Génier, 2009, *E. fallaciosus* Génier, 2009, *E. foedus* Guérin-Méneville, 1844, *E. hamaticollis* Balthasar, 1939, *E. hypocrita* Balthasar, 1939, *E. plebejus* Harold, 1880 and *E. wittmemorum* Martínez, 1988 (Fig. 3O-Q, Fig. 4 A-J).

Genus *Eutrichilum* Martínez, 1969

Notes: This genus presents a group of species that inhabit South American lowlands, east of the Andes as far south as Buenos Aires in Argentina; one species in Costa Rica (Vaz-De-Mello 2008). Species of this genus are frequently necrophagous and are often attracted to light (Vaz-De-Mello 2008). *Eutrichillum* sp. 1 was the only species recorded within the Tapajós region.

Genus *Hansreia* Halffter & Martínez, 1977

Notes: This is an Amazonian genus with six species distributed across Brazil, French Guiana and Venezuela (Halffter and Martinez 1977); recently revised by Valois et al. (2015). Valois et al. (2015) was used for species identification. There is not much ecological information about *Hansreia* dung beetles (Hadara et al. 2020). Only the species *Hansreia oxygona* (Perty, 1830) was recorded within the Carajás region (Fig. 4L).

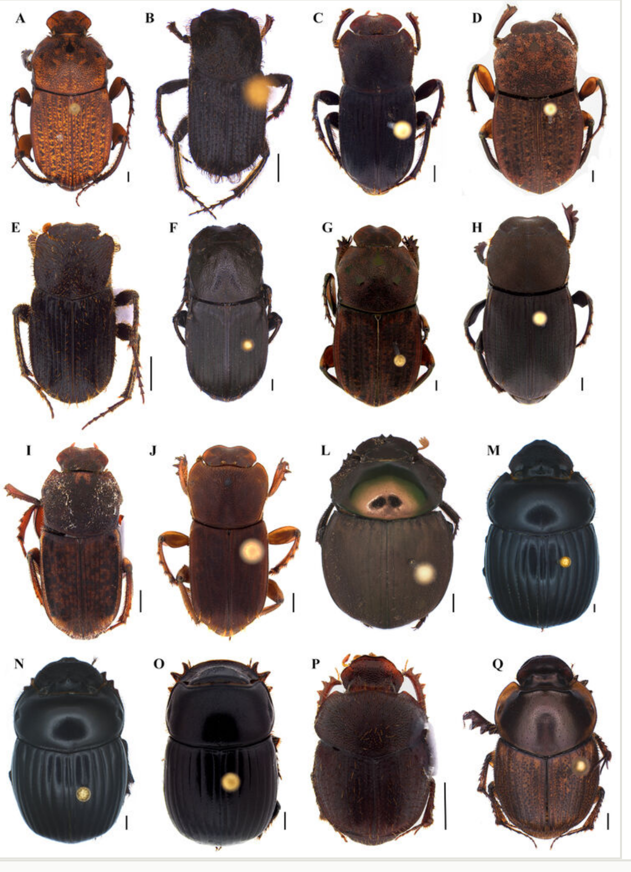

Figure 4. doi

Dorsal habitus of dung beetle species collected in the Tapajós National Forest and/or Carajás National Forest. **A** *Eurysternus caribaeus* (Herbst, 1789); **B** *Eurysternus cavatus* Génier, 2009; **C** *Eurysternus cayennensis* Castelnau, 1840; **D** *Eurysternus cyclops* Génier, 2009; **E** *Eurysternus fallaciosus* Génier, 2009; **F** *Eurysternus foedus* Guérin-Méneville, 1844; **G** *Eurysternus hamaticollis* Balthasar, 1939; **H** *Eurysternus hypocrita* Balthasar, 1939; **I** *Eurysternus plebejus* Harold, 1880; **J** *Eurysternus wittmerorum* Martinez, 1988; **L** *Hansreia oxygona* (Perty, 1830); **M** *Isocopris imitator* (Felsche, 1901); **N** *Isocopris nitidus* (Luederwaldt, 1922); **O** *Ontherus carinifrons* Luederwaldt, 1930; **P** *Onthophagus digitifer* Boucomont, 1932; **Q** *Onthophagus onthochromus* Arrow, 1913. Scale bar: 1 mm.

Genus *Isocopris* Pereira e Martínez, 1960

Notes: This Neotropical genus, frequently misidentified as *Dichotomius*, comprises seven known species recently revised by Rossini and Vaz-de-Mello (2017), the same work being used to identify the species. No biological information for the genus was found. Two species were identified in our study: *Isocopris imitator* (Felsche, 1901) and *I. nitidus* (Luederwaldt, 1922) (Fig. 4M-N).

Genus *Ontherus* Erichson, 1847

Notes: Occurring from Argentina to Mexico, this genus has approximately 60 species (Génier 1996, Génier 1998). Although most species are considered coprophagous or saprophagous, some complex associations with ants have been previously recorded (Génier 1996). For the identification of the species, the following works were mainly used: Génier (1996). One species was found in the Tapajós region: *Ontherus carinifrons* Luederwaldt, 1930 (Fig. 4O). This species belongs to a group called *appendiculatus*, which is widely distributed in South America (Génier 1996). Species from this group are usually collected in human or cattle dung, also using flight or light traps in sandy habitats (Génier 1996).

Genus *Onthophagus* Latreille, 1802

Notes: Considered a megadiverse and cosmopolitan genus with approximately 2,000 described species (Tarasov and Kabakov 2010). Some species have been recently revised (Rossini et al. 2018a, Rossini et al. 2018b), while others are under current revision. The species mentioned here have been recorded mainly in primary and secondary forests, through the use of both flight interception traps and pitfalls baited with dung or carrion (Korasaki et al. 2012). For the identification of the species, the following works were mainly used: Rossini et al. (2018a), Rossini et al. (2018b). Four species were identified in our study: *Onthophagus digitifer* Boucomont, 1932, *O.* gp. *rubrescens*, *O. onthochromus* Arrow, 1913 and *O. osculatii* Guérin-Méneville, 1855 (Fig. 5A).

Genus *Oxysternon* Castelnau, 1840

Notes: This Neotropical genus comprises 11 species according to the last taxonomic revision by Edmonds and Zídek (2004) which was used for species identification. *Oxysternon* beetles are usually found in primary and secondary forests (Gigliotti et al. 2011). The literature on the biology of the genus is scarce, but most species are considered as coprophagous and inhabit moist forests (Edmonds and Zídek 2004). Two species were recorded in this study: *Oxysternon macleayi* Nevinson, 1892 and *O. silenus* Castelnau, 1840 (Fig. 5B-C).

Genus *Scybalocanthon* Martínez, 1948

Notes: *Scybalocanthon* is a widespread genus occurring in South and Central America (Pereira and Martínez 1956, Silva and Valois 2019). The genus comprises 24 valid species, most of which are diurnal and inhabit either moist or dry forests in the Amazon Region, Atlantic Rainforest and the Yungas (Silva and Valois 2019, Silva and Génier 2019). Only the species *Scybalocanthon* sp. 1 was reported to the Carajás region.

Genus *Sulcophanaeus* d'Olsoufieff, 1924

Notes: This Neotropical genus has approximately 15 described species (Edmonds 2000). Morelli et al. (1996)Noriega (2001) bring information about the life cycle of some *Sulcophanaeus* species. *Edmonds (2000)* was used for species identification. *Sulcophanaeus faunus* (Fabricius, 1775) was the only species recorded in this study (Fig. 5D).

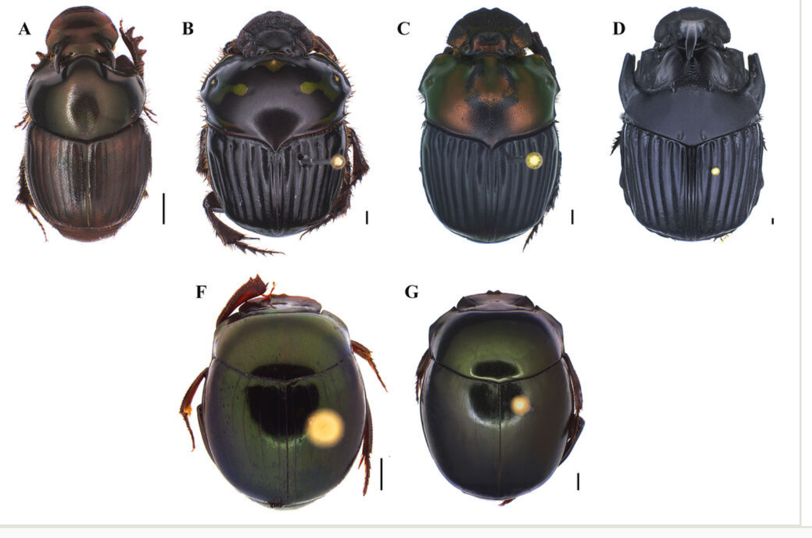

Figure 5. doi

Dorsal habitus of dung beetle species collected in the Tapajós National Forest and/or Carajás National Forest. **A** *Onthophagus osculatii* Guérin-Méneville, 1855; **B** *Oxysternon macleayi* Nevison, 1892; **C** *Oxysternon silenus* Castelnau, 1840; **D** *Sulcophanaeus faunus* (Fabricius, 1775); **E** *Silvycanthon candezei* (Harold, 1869); **F** *Sylvicanthon proseni* (Martínez, 1949). Scale bar: 1 mm.

Genus *Sylvicanthon* Halffter & Martínez, 1977

Notes: This genus has 15 species, broadly occurring in the Neotropics and was recently revised by Cupello and Vaz-de-Mello (2018). Some species are widespread in the Amazon Basin (Cupello and Vaz-de-Mello 2018). All known species are nocturnal, with most of them considered coprophagous feeding on primate, pig and cattle dung (

Cupello and Vaz-de-Mello 2018). For the identification of the species, the following works were mainly used: Cupello and Vaz-de-Mello (2018). Two species were identified in our study: *Sylvicanthon candezei* (Harold, 1869) and *S. proseni* (Martínez, 1949) (Fig. 5E-F).

Genus *Uroxys* Westwood, 1842

Notes: *Uroxys* is an exclusively Neotropical genus with more than 50 described species (Vaz-De-Mello 2008, Korasaki et al. 2012). This genus has species that can be found in grasslands and within primary and secondary forests; it also includes species specialised in sloth (Bradypodidae) dung (Korasaki et al. 2012). *Uroxys* cf. *minutus* was the only species reported in this study.

Discussion

The knowledge of biodiversity is key to providing information for conservation and management strategies, particularly within the hyperdiverse tropics (Barlow 2018). Our dung beetle surveys within FLONA Tapajós and Carajás highlight the importance of Amazonian Sustainable-Use protected forests for conserving insect biodiversity in the tropics. Protected areas have a key role as a thermal buffer against climate changes (Xu et al. 2022) and for the long-term maintenance of Amazonian biodiversity (Laurance 2005). However, Brazilian protected forests are largely underfunded, particularly in Amazonia (Silva et al. 2021) – which hinders their efficacy in protecting biodiversity and raises the urgency for new policies and funding mechanisms to enhance their efficacy.

Acknowledgements

We are grateful to all the farmers for collaborating to the Long-Term Ecological Research Project of the Sustainable Amazon Network (PELD-RAS); to Victor Hugo de Oliveira, Rodrigo Braga, Julio Louzada, Gilson de Oliveira, Marcos de Oliveira, Elivan Santos, Jaiane da Silva, Janitoni Lima, Renilson de Freitas and Josivan Oliveira for invaluable help during fieldwork and dung beetle identification; and to the Large Scale Biosphere-Atmosphere Program (INPA-LBA) and to Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio CR-03-Santarém and Carajás) for all provided support. FF acknowledges funding provided by [1] CNPq (National Council for Scientific and Technological Development) through the National Institute of Science and Technology (INCT) “Syntheses of Amazonian Biodiversity (CNPq/INCT 406767/2022-0 [SinBiAm]), PELD-RAS (CNPq-CAPES 441659/2016-0 and 441573/2020-7), SEM-FLAMA (CNPq-PrevFogo-IBAMA 441949/2018-5), and RESFLORA (MCIC-CNPq 420254/2018-8); and [2] NERC (UK Natural Environment Research Council (NERC, NE/P004512/1 [AFIRE]). EC thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001 and Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) - POSGRAD/scholarship/ financial support. VCS thanks UNICAMP for providing the licence to use the software ArcGIS (process nº 20-P-21727/2021/Contract nº

161/2021). We would like to thank all members of the Rede Amazônia Sustentável (RAS Network) for their support, in particular Joice Ferreira, Jos Barlow, Erika Berenguer and Fernando Elias Silva for their commitment to establish and maintain the long-term research plots in Santarém and Carajás.

Author contributions

Fieldwork was conducted by FMF (2016, 2017 and 2019) and LFM (2016 and 2017). Dung beetles were sorted and mounted by CFGC, VOC, VPS, HS with key support from EC and MEM (2019). Beetle identification was conducted by LFM (2016, 2017) and MEM and EC (2019). FZVM revised and validated all dung beetle identifications (2010, 2016, 2017 and 2019). FF contributed for funding acquisition and supervision. All dung beetle photos were made by VCS. The manuscript was written by EC, MEM, FF and VCS. All authors gave final approval for publication.

References

- Arias J, Medina C (2014) Tres nuevas especies de *Cryptocanthon* Balthasar, 1942 (Coleoptera: Scarabaeidae: Scarabaeinae) para Colombia. Caldasia 36 (1): 165-180. https://doi.org/10.15446/caldasia.v36n1.43898
- Balthasar V (1939) Neue *Canthidium*-Arten. (Beitrag zur Kenntniss der Scarabaeiden der neotrop. Region). Entomologiches Nachrichtenblatt 13: 111-140.
- Barlow J, et al. (2018) The future of hyperdiverse tropical ecosystems. Nature 559 (7715): 517-526. https://doi.org/10.1038/s41586-018-0301-1
- Boucomont A (1928) Coprophages d'Amérique du Sud nouveaux ou peu connus. Bulletin de la Société Entomologique de France 12: 186-194, 202. https://doi.org/10.3406/bsef.1928.28008
- Braz L, et al. (2016) A situação das áreas de endemismo da Amazônia com relação ao desmatamento e às áreas protegidas. Boletim de Geografia 34 (3): 45-62. https://doi.org/10.4025/bolgeogr.v34i3.30294
- Campbell AJ, Biesmeijer JC, Varma V, Wackers FL (2012) Realising multiple ecosystem services based on the response of three beneficial insect groups to floral traits and trait diversity. Basic and Applied Ecology 13 (4): 363-370. https://doi.org/10.1016/j.baae.2012.04.003
- Canhedo VL (2004) *Anomiopus* Westwood (Coleoptera, Scarabaeidae): novas espécies do grupo virescens. Revista Brasileira de Entomologia 48 (4): 449-458. https://doi.org/10.1590/S0085-56262004000400005
- Canhedo VL (2006) Revisão taxonômica do gênero *Anomiopus* Westwood, 1842 (Coleoptera, Scarabaeidae, Scarabaeinae). Arquivos de Zoologia 37 (4): 349-502. https://doi.org/10.11606/issn.2176-7793.v37i4p349-502
- Cook J (2002) A revision of the neotropical genus *Cryptocanthon* Balthasar (Coleoptera: Scarabaeidae: Scarabaeinae). The Coleopterists Bulletin 56: 3-96. https://doi.org/10.1649/0010-065X(2002)56

- Culot L, Bovy E, Vaz-de-Mello FZ, Guevara R, Galetti M (2013) Selective defaunation affects dung beetle communities in continuous Atlantic rainforest. Biological Conservation 163: 79-89. https://doi.org/10.1016/j.biocon.2013.04.004
- Cupello M (2018) On the types species of the New World dung beetle genus *Canthidium* Erichson, 1847 (Coleoptera: Scarabaeidae: Scarabaeinae), with an annotated checklist of species. Zootaxa 4388: 451-486. https://doi.org/10.11646/zootaxa.4388.4.1
- Cupello M, Vaz-de-Mello F (2018) A monographic revision of the Neotropical dung beetle genus *Sylvicanthon* Halffter & Martínez, 1977 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini), including a reappraisal of the taxonomic history of *Canthon* sensu lato. European Journal of Taxonomy 467 https://doi.org/10.5852/ejt.2018.467
- Dangles O, Casas J (2019) Ecosystem services provided by insects for achieving sustainable development goals. Ecosystem Services 35: 109-115. https://doi.org/10.1016/j.ecoser.2018.12.002
- Davis AL, Scholtz CH, Dooley PW, Bham N, Kryger U (2004) Scarabaeinae dung beetles as indicators of biodiversity, habitat transformation and pest control chemicals in agro-ecosystems. South African Journal of Science 100: 415-424.
- Dornelas M, Daskalova G (2020) Nuanced changes in insect abundance. Science 368 (6489): 368-369. https://doi.org/10.1126/science.abb6861
- Edmonds WD (2000) Revision of the Neotropical dung beetle genus *Sulcophanaeus* (Coleoptera: Scarabaeidae: Scarabaeinae). Folia Heyrovskyana Supplementum 6: 1-60.
- Edmonds WD, Zídek J (2004) Revision of the Neotropical dung beetle genus *Oxysternon* (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). Folia Heyrovskyana 11: 1-58.
- Edmonds WD, Zidek J (2010) A taxonomic review of the neotropical genus *Coprophanaeus* Olsoufieff, 1924 (Coleoptera: Scarabaeidae, Scarabaeinae). Insecta Mundi 0129: 1-111.
- Escobar F, Halffter G, Arellano L (2007) From forest to pasture: an evaluation of the influence of environment and biogeography on the structure of beetle (Scarabaeinae) assemblages along three altitudinal gradients in the Neotropical region. Ecography 30 (2): 193-208. https://doi.org/10.1111/j.0906-7590.2007.04818.x
- Falqueto SA, Vaz-de-Mello FZ, Schoereder J (2005) Are fungivorous Scarabaeidae less specialist. Ecología Austral 15: 17-22.
- Fearnside PM (2008) Amazon Forest maintenance as a source of environmental services. Anis da Academia Brasileira de Ciências 80 (1): 101-114. https://doi.org/10.1590/S0001-37652008000100006
- França F, Barlow J, Araujo B, Louzada J (2016) Does selective logging stress tropical forest invertebrates? Using fat stores to examine sublethal responses in dung beetles. Ecology and Evolution 6 (23): 8526-8533. https://doi.org/10.1002/ece3.2488
- França F, Louzada J, Barlow J (2018) Selective logging effects on 'brown world' faecal-detritus pathway in tropical forests: A case study from Amazonia using dung beetles. Forest Ecology and Management 410: 136-143. https://doi.org/10.1016/j.foreco.2017.12.027
- França FM, Benkwit CE, Peralta G, Robinson JP, Graham NA, Tylianakis JM (2020a) Climatic and local stressor interactions threaten tropical forests and coral reefs.

Philosophical Transactions of the Royal Society375-1794. https://doi.org/10.1098/rstb.2019.0116

- França FM, Ferreira J, Vaz-de-Mello FZ, Maia LF, Berenguer E, Palmeira AF (2020b) El Niño impacts on human-modified tropical forests: Consequences for dung beetle diversity and associated ecological processes. Biotropica 52 (2): 252-262. https://doi.org/10.1111/btp.12756
- Gardner TA, Barlow J, Araujo IS, Avila-Pires TC, Bonaldo AB, Costa JE (2008) The cost-effectiveness of biodiversity surveys in tropical forests. Ecology Letters 11 (2): 139-150. https://doi.org/10.1111/j.1461-0248.2007.01133.x
- GBIF (2022) GBIF Secretariat. http://www.gbif.org/tools/data-validator/f1e2a538-5fea-4258-9b0e-27805b684404. Accessed on: 2022-10-04.
- Génier F (1996) A revision of the neotropical genus *Ontherus* Erichson (Coleoptera: Scarabaeidae, Scarabaeinae). The Memoirs of the Entomological Society of Canada 128 (S170): 3-170. https://doi.org/10.4039/entm128170fv
- Génier F (1998) A Revision of the neotropical genus *Ontherus* Erichson (Coleoptera: Scarabaeidae, Scarabaeinae), Supplement 1. The Coleopteristis Bulletin 52 (3): 270-274. URL: https://www.jstor.org/stable/4009362
- Génier F (2000) A new North American *Ateuchus* Weber (Coleoptera: Scarabaeidae, Scarabaeinae). The Coleopterists Bulletin 54 (3): 341-346. https://doi.org/10.1649/0010-065X(2000)054[0341:ANNAAW]2.0.CO;2
- Génier F (2009) Le genre *Eurysternus* Dalman, 1824 (Scarabaeidae: Scarabaeinae: Oniticellini): Révision taxonomique et clés de détermination illustrées. Pensoft Series Faunistica 85: 1-430.
- Génier F, Cupello M (2018) *Canthidium alvarezi* Martínez and Halffter, 1986: a remarkable *Ateuchus* Weber, 1801 (Coleoptera: Scarabaeidae: Scarabaeinae). Insecta Mundi 0646: 1-4.
- Gigliotti M, Nunes R, Vaz-de-Mello F (2011) Distribuição extra-amazônica brasileira de Oxysternon (Oxysternon) conspicillatum (Weber, 1801) e Oxysternon (Oxysternon) silenus Castelnau, 1840 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). Anais do I Simpósio de Entomologia do Rio de Janeiro. I Simposio de Entomologia do Rio de Janeiro, Museu Nacional, UFRJ, Rio de Janeiro, 35-36 pp.
- Giraldo-Mendonza A (2022) A new species of the genus *Cryptocanthon* from Peru (Coleoptera: Scarabaeidae: Scarabaeinae). Acta zoológica mexicana 38: 1-11. https://doi.org/10.21829/azm.2022.3812443
- González-Alvarado A, Vaz-de-Mello FZ (2021) Towards a comprehensive taxonomic revision of the Neotropical dung beetle subgenus Deltochilum (Deltohyboma) Lane, 1946 (Coleoptera: Scarabaeidae: Scarabaeinae): Division into species-groups. PLOS One 16 (1). https://doi.org/10.1371/journal.pone.0244657
- Griffiths HM, Louzada J, Bardgett RD, Beiroz W, França F, Tregidgo D (2015) Biodiversity and environmental context predict dung beetle-mediated seed dispersal in a tropical forest field experiment. Ecology 96 (6): 1607-1619. https://doi.org/10.1890/14-1211.1
- Hadara LM, Araújo IS, Overal WL, Silva FA (2020) Comparison of dung beetle communities (Coleoptera: Scarabaeidae: Scarabaeinae) in oil palm plantations and native forest in the eastern Amazon. Brazil. Revista Brasileira de Entomologia 64 (1): 1-10.

- Halffter G, Matthews EG (1966) The natural history of dung beetles of the subfamily Scarabaeinae. Folia Entomologica Mexicana 12 (14): 1-312.
- Halffter G, Martinez A (1977) Revision monografica de los Canthonina Americanos IV clava para generos y subgeneros. Folia Entomologica Mexicana 38: 29-107.
- Halffter G, Favila ME (1993) The Scarabaeinae an animal group for analysing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. Biology International 27: 15-21.
- Halffter G, Arellano (2002) Response of dung beetle diversity to human-induced changes in a tropical landscape 1. Biotropica 34 (1): 144-154. https://doi.org/10.1111/j.1744-7429.2002.tb00250.x
- Harold E (1868) Dier arten der gattung *Choeridium* von Herausgeber. Coleopterologische Hefte 4: 32-76.
- Howden H, Young OP (1981) Panamanian Scarabaeinae: taxonomy, distribution, and habits (Coleoptera, Scarabaeidae). Entomological Institute 18 (1): 1-204.
- Kitching RL, Dahlsjo CA, Eggleton P (2020) Invertebrates and the complexity of tropical ecosystems. Biotropica 52 (2): 207-214. https://doi.org/10.1111/btp.12768
- Klein, Bert C (1989) Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. Ecology 70 (6): 1715-1725. https://doi.org/10.2307/1938106
- Kohlmann B (1984) Biosistemática de las especies norteamericanas del género Ateuchus (Coleoptera: Scarabaeidae: Scarabaeinae). Folia Entomologia Mexicana 60: 3-81.
- Kohlmann B (1997) The Costa Rican species of *Ateuchus* (Coleoptera: Scarabaeidae). Revista de Biología Tropical 43 (4): 177-192.
- Kohlmann B, Solís A (2006) El género *Canthidium* (Coleoptera: Scarabaeidae) en Norteamerica. Giornale Italiano di Entomologia 11: 235-295.
- Kohlmann B, Vaz-de-Mello F (2018) A new key for the species of *Ateuchus* Weber (Coleoptera: Scarabaeidae: Scarabaeinae) occurring in Mexico, with a description of the first North American inquiline species from a rodent burrow (Rodentia: Geomydae) and new distribution records. Revista Brasileira de Entomologia 62 (2): 131-134. https://doi.org/10.1016/j.rbe.2018.01.002
- Kohlmann B, Arriaga-Jiménez, Matthias R (2018) An unusual new species of *Canthidium* (Coleoptera: Scarabaeidae: Scarabaeinae) from Oaxaca, Mexico. Zootaxa 4378 (2): 273-278. https://doi.org/10.11646/zootaxa.4378.2.7
- Korasaki V, Vaz-de-Mello FZ, Braga RF, Zanetti R, Louzada J (2012) Taxocenose de Scarabaeinae (Coleoptera: Scarabaeidae) em Benjamin Constant, AM. Acta Amazonica 42: 423-432. https://doi.org/10.1590/S0044-59672012000300015
- Larsen TH, Forsyth A (2005) Trap spacing and transect design for dung beetle biodiversity studies 1. Biotropica: The Journal of Biology and Conservation 37 (2): 322-325. https://doi.org/10.1111/j.1744-7429.2005.00042.x
- Laurance W (2005) When bigger is better: the need for Amazonian mega-reserves. Trends in Ecology & Evolution 20 (12): 645-648. https://doi.org/10.1016/j.tree.2005.10.009
- Lucas S (2012) Proper syntax when using aff. and cf. in taxonomic statements. Journal of Vertebrate Paleontology 6 (2): -202. https://doi.org/10.1080/02724634.1986.10011613

- Maldaner ME, Valois M, Vaz-de-Mello F (2018) A revision of Dichotomius (Homocanthonides) Luederwaldt, 1929 (Coleoptera: Scarabaeidae: Scarabaeinae). Revista Brasileira de Entomologia 62 (3): 237-242. https://doi.org/10.1016/j.rbe.2018.05.001
- Marsh CJ, Louzada J, Beiroz W, Ewers RM (2013) Optimising bait for pitfall trapping of Amazonian dung beetles (Coleoptera: Scarabaeinae). PLOS One 8 (8): 73147. https://doi.org/10.1371/journal.pone.0073147
- Martinez A (1959) Catalogo de los Scarabaeidae argentinos (Coleoptera). Revista del Museu Argentino de Ciencias Naturales “Bernardino Rivadavia" 5 (1): 1-126.
- Martínez A, Pereira G, Halffter E (1964) Notes on the genus *Canthidium* and allied genera. Studia Entomologica 7: 161-178.
- Martínez-Revelo D, Torres E, Neita-Moreno J (2020) El género *Cryptocanthon* (Coleoptera: Scarabaeidae) en Colombia: descripción de especies nuevas, distribución geográfica y conservación. Revista mexicana de biodiversidad 91: 2-28. https://doi.org/10.22201/ib.20078706e.2020.91.3156
- Medri IM, Lopes J (2001) Scarabaeidae (Coleoptera) do Parque Estadual Mata dos Godoy e de área de pastagem, no norte do Parana. Brasil. Revista Brasileira de Zoologia 18: 135-141. https://doi.org/10.1590/S0101-81752001000500011
- Morelli E, Gonzalez-Vainer P, Canziani C (1996) Nidificación, ciclo de vida y estadios preimaginales de *Sulcophanaeus menelas* (Laporte, 1840) (Coleoptera: Scarabaeidae). Elytron 10: 11-22.
- Naughton-Treves L, Holland MB, Brandon K (2005) The role of protected areas in conserving biodiversity and sustaining local livelihoods. Annual Review of Environment and Resources 30: 219-252. https://doi.org/10.1146/annurev.energy.30.050504.164507
- Nichols E, Larsen T, Spector S, Davis A, Escobar F (2007) Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. Biological Conservation 137 (1): 1-19. https://doi.org/10.1016/j.biocon.2007.01.023
- Nichols E, Spector S, Louzada J, Larsen T, Amezquita S, Favila M (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation 141 (6): 1461-1474. https://doi.org/10.1016/j.biocon.2008.04.011
- Noriega JA (2001) Aportes a la biología del escarabajo sudarericano *Sulcophanaeus leander* (Waterhouse, 1891) (Coleoptera: Scarabaeidae). Acta Zoológica Mexicana 87: 67-82.
- Nunes LG, Nunes RV, Vaz-De-Mello FZ (2018) Taxonomic revision of the South American subgenus Canthon (Goniocanthon) Pereira & Martínez, 1956 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini). European Journal of Taxonomy 437: 1-31.
- Nunes LG, Nunes RV, Vaz-De-Mello FZ (2020) Taxonomic revision of the South American subgenus Canthon (Peltecanthon) Pereira, 1953 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini). European Journal of Taxonomy 594: 1-27. https://doi.org/10.5852/ejt.2020.594
- Nunes RV, Carvalho MS, Vaz-De-Mello FZ (2016) Taxonomic review of the Dichotomius (Luederwaldtinia) assifer (Eschscholtz) species-group (Coleoptera: Scarabaeidae). Zootaxa 1: 230-244. https://doi.org/10.11646/zootaxa.4078.1.21
- Nunes RV, Vaz-de-Mello FZ (2019) Taxonomic revision of Dichotomius (Cephagonus) Luederwaldt, 1929 and the taxonomic status of remaining *Dichotomius* Hope, 1838

subgenera (Coleoptera: Scarabaeidae: Scarabaeinae: Dichotomiini). Journal of Natural History 53 (37-38): 2231-2351. https://doi.org/10.1080/00222933.2019.1692088

- Pereira FS, Martínez A (1956) Os gêneros de Canthonini Americanos (Col. Scarabaeidae). Revista Brasileira de Entomologia 6: 91-192.
- Piló L, Auler A, Martins F (2015) Carajás National Forest: Iron ore plateaus and caves in southeastern Amazon. In Landscapes and landforms of Brazil. Springer273-283.
- Rossini M, Vaz-de-Mello FZ (2017) A taxonomic review of the genus *Isocopris* Pereira and Martínez, 1960 (Coleoptera: Scarabaeidae: Scarabaeinae), with description of a new Brazilian species. Journal of Natural History 20: 1091-1117. https://doi.org/10.1080/00222933.2017.1319517
- Rossini M, Vaz-de-Mello FZ, Zunino M (2018a) Toward a comprehensive taxonomic revision of the “hirculus” group of American *Onthophagus* Latreille, 1802 (Coleoptera, Scarabaeidae, Scarabaeinae). European Journal of Taxonomy 432: 1-21.
- Rossini M, Vaz-de-Mello FZ, Zunino M (2018b) A taxonomic revision of the New World *Onthophagus* Latreille, 1802 (Coleoptera: Scarabaeidae: Scarabaeinae) of the osculatii species-complex, with description of two new species from South America. Journal of Natural History 52 (9-10): 541-586. https://doi.org/10.1080/00222933.2018.1437230
- Rylands AB, Brandon K (2005) Brazilian protected areas. Conservation Biology 19 (3): 612-618. https://doi.org/10.1111/j.1523-1739.2005.00711.x
- Salomao RP, Gonzalez-Tokman D, Dattilo W, Lopez-Acosta JC, Favila ME (2018) Landscape structure and composition define the body condition of dung beetles (Coleoptera: Scarabaeinae) in a fragmented tropical rainforest. Ecological Indicators 88: 144-151. https://doi.org/10.1016/j.ecolind.2018.01.033
- Santana EC, Pacheco TL, Vaz-de-Mello FZ (2019) Taxonomic revision of the *Canthidium* Erichson, 1847 species of the *gigas* group (Coleoptera, Scarabaeidae, Scarabaeinae). European Journal of Taxonomy 530 https://doi.org/10.5852/ejt.2019.530
- Schoolmeesters P (2022) Scarabs: World Scarabaeidae Database Species 2000 & ITIS Catalogue of Life. In: Roskov Y, Abucay L, Orrell T, Nicolson D, Flann C, Bailly N, Kirk P, Bourgoin T, DeWalt RE, Decock W, De Wever A (Eds) Annual checklist digital resource at: http://www.catalogueoflife.org/annual-checklist/2019/. Species 2000: Naturalis.
- Silva F, Génier F (2019) A new Peruvian species of *Scybalocanthon* Martínez, 1948 (Coleoptera, Scarabaeidae, Scarabaeinae, Deltochilini) and some remarkable intrapopulational variation in the endophallus of *S. pinopterus* (Kirsch, 1873). ZooKeys 884: 69-80. https://doi.org/10.3897/zookeys.884.39322
- Silva FA, Valois M (2019) A taxonomic revision of the genus *Scybalocanthon* Martínez, 1948 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini). Zootaxa 4629 (3): 301-341. https://doi.org/10.11646/zootaxa.4629.3.1
- Silva JMCd, Dias TCAdC, Cunha ACd, Cunha HFA (2021) Funding deficits of protected areas in Brazil. Land Use Policy 100 https://doi.org/10.1016/j.landusepol.2020.104926
- Silva PG, Audino LD (2011) Escarabeíneos (Coleoptera: Scarabaeidae: Scarabaeinae) atraídos a diferentes iscas em campo nativo de Bagé, Rio Grande do Sul Brasil. Revista Brasileira de Zoociências 13: 1-3.
- Silva RJ, Coletti F, Costa DA, Vaz-de-Mello FZ (2014) Rola-bostas (Coleoptera: Scarabaeidae: Scarabaeinae) de florestas e pastagens no sudoeste da Amazônia brasileira: Levantamento de espécies e guildas alimentares. Acta Amazonica 3: 345-352. https://doi.org/10.1590/1809-4392201304472

- Soares-Filho B, Moutinho P, Neptad D, Anderson A, Rodrigues H, Garcia R (2010) Role of Brazilian Amazon protected areas in climate change mitigation. Proceedings of the National Academy of Sciences 107 (24): 10821-10826. https://doi.org/10.1073/pnas.0913048107
- Sobral-Souza T, Lima-Ribeiro M (2017) De volta ao passado: revisitando a história biogeográfica das florestas neotropicais úmidas. Oecologia Australis 21 (2): 93-107. https://doi.org/10.4257/oeco.2017.2102.01
- Solis A, Kohlmann B (2004) El género *Canthidium* (Coleoptera: Scarabaeidae) en Costa Rica. Giornale Italiano di Entomologia 11: 1-73.
- Sollmann R, Torres NM, Silveira L (2008) Jaguar conservation in Brazil: the role of protected areas. Cat News 4: 15-20.
- Spector S (2006) Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. The Coleopterists Bulletin 60: 71-83. https://doi.org/10.1649/0010-065X(2006)60
- Spinola NJ, Silva SM, Silva AJ, Barlow J, Ferreira J (2020) A shared perspective on managing Amazonian sustainable-use reserves in an era of megafires. Journal of Applied Ecology https://doi.org/10.1111/1365-2664.13690
- Tarasov SI, Kabakov ON (2010) Two new species of *Onthophagus* (Coleoptera: Scarabaeidae) from Indochina, with a discussion of some problems with the classification of Serrophorus and similar subgenera. Zootaxa 2344 (1): 17-28. https://doi.org/10.11646/zootaxa.2344.1.2
- Valois M, Vaz-De-Mello FZ, Silva FA (2015) A taxonomic review of the Neotropical genus *Hansreia* Halffter & Martínez, 1977 (Coleoptera: Scarabaeidae: Scarabaeinae). Zootaxa 4027 (2): 205-226. https://doi.org/10.11646/zootaxa.4027.2.2
- Valois MC, Vaz-De-Mello FZ, Silva FA (2017) Taxonomic revision of the *Dichotomius* sericeus (Harold, 1867) species group (Coleoptera: Scarabaeidae: Scarabaeinae). Zootaxa 4277 (4): 503-530. https://doi.org/10.11646/zootaxa.4277.4.3
- Vaz-de-Mello FZ, Louzada JN, Schoereder JH (1998) New data and comments on Scarabaeidae (Coleoptera: Scarabaeoidea) associated with Attini (Hymenoptera: Formicidae). The Coleopterists' Bulletin 52 (3): 209-216.
- Vaz-de-Mello FZ (1999) Scarabaeidae s. str. (Coleoptera: Scarabaeoidea) de um fragmento de Floresta Amazônica no estado do Acre, Brasil. 1. Taxocenose. Anais da Sociedade Entomológica do Brasil 28 (3): 439-446. https://doi.org/10.1590/S0301-80591999000300009
- Vaz-De-Mello FZ (2008) Synopsis of the new subtribe Scatimina (Coleoptera: Scarabaeidae: Scarabaeinae: Ateuchini), with descriptions of twelve new genera and review of *Genieridium*, new genus. Zootaxa 1955: 1-75. https://doi.org/10.11646/zootaxa.1955.1.1
- Villalobos FJ, Diaz A, Favila ME (1988) Two species of *Canthon* Hoffmannsegg (Coleoptera: Scarabaeidae) feed on dead and live invertebrates. The Coleopterists' Bulletin 52 (2): 101-104.
- Walker R, Moore NJ, Arima E, Perz S, Simmons C, Caldas M, Bohrer C (2009) Protecting the Amazon with protected areas. Proceedings of the National Academy of Sciences 106 (26): 10582-10586. https://doi.org/10.1073/pnas.0806059106
- Walker WS, Gorelik SR, Baccini A, Aragon-Osejo J, Josse A, Meyer C (2020) The role of forest conversion, degradation, and disturbance in the carbon dynamics of Amazon

indigenous territories and protected areas. Proceedings of the National Academy of Sciences 117 (6): 3015-3025. https://doi.org/10.1073/pnas.1913321117
- Xu X, Huang A, Belle E, De Frenne P, Jia G (2022) Protected areas provide thermal buffer against climate change. Science Advances 8 (44). https://doi.org/10.1126/sciadv.abo0119
- Zhang ZQ (2011) Animal biodiversity: an introduction to higher-level classification and taxonomic richness. Zootaxa 3148 (1): 7-12. https://doi.org/10.11646/zootaxa.3148.1.3