Biotic components of dung beetles (Insecta: Coleoptera: Scarabaeidae: Scarabaeinae) from Pantanal – Cerrado Border and its implications for Chaco regionalization

Gimo Mazembe Daniel\textsuperscript{a,b} and Fernando Z. Vaz-de-Mello\textsuperscript{c,d}

\textsuperscript{a}\textsuperscript{b}Pós-graduação em Entomologia e Conservação da Biodiversidade, Universidade Federal da Grande Dourados, Dourados, Brasil; \textsuperscript{b}Curso de Biologia, Departamento de Ciências Naturais, Universidade Pedagógica de Moçambique, Nampula, Moçambique; \textsuperscript{c}Departamento de Biologia e Zoologia, Universidade Federal de Mato Grosso, Instituto de Biociências, Cuiabá, Brasil; \textsuperscript{d}Fellow of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq)

\textbf{ABSTRACT}

We use a panbiogeographical approach to determine the distribution pattern of dung beetles from a border region between Cerrado and Rondônia biogeographical provinces in Brazil. We constructed 54 individual tracks and 12 generalized tracks. The generalized tracks infer historical events that have happened in the past, highlighting the significant role of vicariant processes and their influence on the current distribution pattern of dung beetles from the Pantanal–Cerrado Border. The study region is a biogeographical node, including representatives from different biogeographic origins. Contrary to previous suggestions, the Scarabaeinae fauna of southern Rondônia province is not related to Amazonian fauna. Rather, it shows stronger connections with Chaco. Hence we suggest the inclusion of the southern part of the province of Rondônia, representing the Pantanal depression itself, as a new biogeographical district within Chaco province.

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\textbf{Introduction}

Biodiversity is not evenly distributed on the earth. The distribution patterns of species are strongly influenced by historical processes (Halfter 1991). Two approaches have dominated studies of the historical biogeography of continental biotas. The first concerns intercontinental waves: dispersal followed by adaptive radiation into the non-colonized niches of the continent (Mayr 1944; Darlington 1957; Simpson 1965; Cracraft 1972, 1973). The second dominant theme concerns the role played by refuges in the distribution and diversification of continental biotas (Haffer 1982, 2008; Prance 1982). Proponents of the refuge theory have claimed that during the drier conditions of the ice ages, the rainforests of Amazon were fragmented by the spread of vegetation adapted to drier conditions (Haffer 1969; Prance 1982). This vicariant process may have driven
speciation in disjunct patches of rainforest, which were continuously present in areas of higher rainfall (Haffer 1982).

It is noticeable that the effects of climatic fluctuations of the late Quaternary on the open formations in Central Brazil were not restricted to expansion and contraction among savannahs and forests, but also included complex changes even within the dry diagonal formations (Oliveira and Marquis 2002; Portillo-Quintero and Sánchez-Azofeifa 2010). Several kinds of vegetation (e.g. savannahs, seasonal forests, wet forests and Araucaria forests) were established at least in certain areas and times in the present Cerrado province (Pennington et al. 2000; Portillo-Quintero and Sánchez-Azofeifa 2010). In addition to the climatic fluctuations, other factors such as soils, biological pressure and disturbance could have had a strong palaeoenvironmental effect (Ratter et al. 1988; Prado and Gibbs 1993). These processes probably led to vicariance, resulting in the taxonomic differentiation of biotic components for any group of fauna that are restricted to Cerrado (Portillo-Quintero and Sánchez-Azofeifa 2010).

Geologically, the study region is the border between the Chacoan Depression (at the Cuiabá lowland) and the Brazilian Shield (Ab’Saber 1988). Biogeographically speaking, it is a border between southern Rondônia (within which is the Pantanal depression wetland) and the Cerrado provinces (sensu Morrone 2014, the former is not equivalent to the Brazilian state Rondônia). The region is characterized by an abrupt change of altitude and a complex mosaic of native vegetation, including savannah and forest formations (Oliveira and Marquis 2002).

In the Rondônia and Cerrado provinces, dung beetle studies have focused on ecology (Louzada et al. 2007; Da Silva et al. 2010; Correa et al. 2013; Puker et al. 2013; Rodrigues et al. 2013), natural history (Puker et al. 2014) and inventories (Nunes et al. 2012; Daniel et al. 2014). However, there are no studies concerning distribution patterns of these scarabs based on the history of the regions. In this paper, we aim to use a panbiogeographical approach to determine the distribution pattern of dung beetles from the border between the provinces of Rondônia and Cerrado in Brazil.

Material and methods

We studied dung beetles from the border region between Pantanal and Cerrado, Chapada dos Guimarães, State of Mato Grosso, Central Brazil (between 15°12’S and 15°30’S; 56°45’W and 56°50’W), (Figure 1). The procedures of dung beetle collection were described by Daniel et al. (2014).

Dung beetle identification

At the generic level, we used the identification key provided by Vaz-de-Mello et al. (2011), and at the species level, beetles were identified by the second author. Collected specimens are housed at Seção de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá, Brazil (CEMT). Distribution data of dung beetle species from other localities in the Neotropical region were obtained by consulting the literature and database at CEMT (Table 1).
Table 1. Checklist of the dung beetles species used in panbiogeographical analysis, and the respective source of distribution localities, which was based on the CEMT-UFMT = Coleção entomológica de Mato Grosso, Universidade Federal de Mato Grosso and literature.

| Species                        | CEMT-UFMT | Literature                                      |
|--------------------------------|-----------|-------------------------------------------------|
| *Ateuchus striatulus* (Preudhomme de Borre, 1886) | X         | Daniel et al. (2014)                            |
| Besourena amarinii (Aguilar-Julio)       | X         | Daniel et al. (2014)                            |
| Deltorhinum armatum Génier, 2010       | X         | Génier (2010), Daniel et al. (2014)             |
| Gentidium bidens (Balthasar)           | X         | Vaz-de-Mello and Génier (2005), Daniel et al. (2014) |
| Genieridium cryptops (Arrow)           | X         | Vaz-de-Mello and Génier (2005), Daniel et al. (2014) |
| Trichillum adjunctum Martinez          | X         | Vaz-de-Mello and Génier (2005), Daniel et al. (2014) |
| Trichillum externepunctatum Preudhomme de Borre | X         | Vaz-de-Mello and Génier (2005), Daniel et al. (2014) |
| Corpini                                |           |                                                 |
| Canthidium multipunctatum Balthasar    | X         | Daniel et al. (2014)                            |
| Canthidium kelleri (Martinez, Halfter & Pereira) | X         | Daniel et al. (2014)                            |
| Canthidium sladeni Arrow 1903          | X         | Gahan and Arrow (1903)                          |
| Dichotomius sexadentatus Luderwaldt    | X         | Gahan and Arrow (1903), Daniel et al. (2014)    |

(Continued)
Track analysis

We analysed distributional data of 54 species of dung beetles (Figure 2). The panbiogeographic method was applied, which comprises plotting distributions of species on maps and connecting their localities together via minimum distance lines to obtain individual tracks (Croizat 1958, 1964). Individual tracks that were not in complete congruence were regarded as partial overlap. The overlap of individual tracks of two
Figure 2. Individual tracks of the dung beetles species for panbiogeographical analysis.
Figure 2. Continued.
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or more species produces generalized tracks (Figure 3), which indicate the pre-existence of ancestral biotic components (Croizat 1958, 1964; Craw et al. 1999; Morrone 2004, 2009).

The following species were not included in the generalized tracks because of their widespread distribution, such distribution patterns would probably not reflect the history of their origins accurately: *Eurysternus caribaeus* (Herbst, 1789), *Canthon histrio* (Lepeletier de Saint-Fargeau & Audinet-Serville), *Trichillum externepunctatum* Preudhomme de Borre, *Diabroctis mimas* (Linnaeus, 1758), *Dichotomius nisus* (Olivier, 1789) and *Dichotomius lycas* (Felsche). We did not include *Canthidium sladeni* Arrow, 1903, *Dichotomius ingens* (Luderwalt) and *Deltorhinum armatum* Génier, 2010, because these species are endemic to the region (Daniel et al. 2014) and, due to their restricted occurrence, they would not show correlations between the two biogeographic provinces (Rondônia and Cerrado).

**Results**

We found two main distributional patterns for the species analysed, which seems to correlate with host vegetation type: open formations of the Chacoan dominion and forest formations of the South Brazilian, Parana, Boreal Brazilian and Southeastern Amazonian dominions (sensu Morrone 2014).
Figure 3. Generalized tracks (GT A–L) of dung beetles, different biotic components observed in the Pantanal–Cerrado Border.
Generalized tracks

Generalized track A. Cerrado based on *Canthon planus* Lucas, *Canthon fortemarginatus* Balthasar, *Canthon muticus* Harold, *Canthidium multipunctatum* Balthasar, *Isocopris hypocrita* (Lucas) and *Ontherus virescens* (Lucas).

Generalized track B. Chaco based on *Coprophanaeus bonariensis* (Gory), *Deltochillum cupreicolle* (Blanchard) and *Dichotomius cuprinus* (Felsche).

Generalized track C. Cerrado + Parana based on *Anomiopus mourai* Canhedo, 2006, *Ateuchus striatulus* (Preudhomme de Borre, 1886), *Besourenga amarillai* (Aguilar-Julio), *Diabroctis mirabilis* (Harold), *Dendropaemon viridipennis* (Laporte), *Isocopris foveolatus* (Luederwaldt), *Ontherus dentatus* Luederwaldt, and *Oxysternon palemo* Castelnau.

Generalized track D. Cerrado + Chaco + Parana based on *Canthidium kelleri* (Martinez, Halfter & Pereira), *Canthon edentulus* Harold, *Canthon maldonadoi* Martinez, *Dichotomius sexdentatus* Luederwaldt, *Malagoniella astyanax* (Oliver, 1789) and *Phanaeus kirbyi* (Vigors).

Generalized track E. Cerrado + Parana + *Araucaria* based on *Ontherus carinicollis* Luederwaldt, and *Trichillum adjuctum* Martinez.

Generalized track F. Cerrado + Chaco + Parana + Atlantic based on *Coprophanaeus ensifer* (Germar), *Eurysternus jessopi* Martinez, *Deltochillum pseudoicarus* Balthasar, and *Phanaeus palaeo* Blanchard.

Generalized track G. Cerrado + Chaco + Parana + Atlantic + *Araucaria* Forest + Pampean based on *Canthon virens* (Mannerheim), *Canthon chalibaeus* Blanchard, and *Gromphas inermis* Harold.

Generalized track H. Cerrado + Chaco + Parana + Atlantic + Caatinga based on *Eurysternus nigrovirens* Génier, 2009 and *Generidium cryptops* (Arrow).

Generalized track I. Cerrado + Parana + Atlantic + *Araucaria* Forest + Caatinga based on *Generidium bidens* (Balthasar), *Ontherus podiceps* Génier, and *Ontherus ulcopygus* Harold.

Generalized track J. Cerrado + Tapajós – Xingu based on *Phanaeus melibaeus* Blanchard, and *Oxysternon spiniferum curvispinum* d’Olsoufieff.

Generalized track K. Cerrado + Tapajós – Xingu + Parana based on *Deltochillum enceladus* Kolbe, *Dichotomius longiceps* (Taschenberg) and *Sulcophanaeus faunus* (Fabricius, 1775).

Generalized track L. Cerrado + Western Ecuador + Tapajós – Xingu + Madeira + Imeri + Guianian Lowlands + Desert based on *Coprophanaeus telamon* (Erichson), *Oxysternon conspicillatum* (Weber) and *Oxysternon silenus* Castelnau.

Discussion

The biotic components of dung beetles from Cerrado, which are observed in the upland savannah formations in the region of the Pantanal–Cerrado Border, can be interpreted as a result of a long process of New World savannah formation. The savannahs are believed to have expanded and retracted their ranges within Quaternary climatic cycles. During the cold, dry periods, savannahs expanded in Amazonia while the humid forests retracted to peripheral ecological refuges. During moist and warm periods, humid
forests spread again while the savannahs retracted to areas approximating their present
day ranges (Mayle et al. 2000; Pennington et al. 2000).

In the Chaco province, we observed biotic components of dung beetles, which occur
in dry and lowland savannah formations in the Pantanal–Cerrado Border. The lowland
savannah in this region was formed as a consequence of the subsidence of Chaco, a
phenomenon related with Pantanal’s formation and Andes uplift (Silva 1995; Zanella
2002). This could be interpreted as due to a cumulative strain since the late Oligocene,
when the Brazilian Shield started its westward migration, together with compression
and uplift of the Central Andes. The main phase of the wetland subsidence is very likely
related to the last compressional pulse in the Andes, during the upper Pliocene–lower
Pleistocene (~2.5 Ma) (Ussami et al. 1999).

Since the Chaco vegetation pre-dated this event, flora and fauna typical of the Chaco
province are found in the lowland of the Pantanal–Cerrado Border as a relic of their past
distribution. Here we found biotic components of dung beetles recorded from the
province of Chaco, which are commonly observed in the southern region of Rondônia
province. Diagnosis of biogeographical areas proposed by Morrone (2014) for the region
of Pantanal (currently this name is a synonym of Rondônia, Morrone 2006:481), should
have a relationship with biotic components from southwest of the Amazon, but in this
paper we have not found any biotic component spanning both regions. Amazonian
dung beetle fauna was only common in the north of Rondônia province. Therefore, it
seems that the biota of the northern and southern regions of Rondônia province have
different origins. We propose that the Pantanal should be included as a new biogeog-
raphical district within Chaco province as opposed to the Rondônia province
(Figure 3A; GT B).

In the region of the Pantanal–Cerrado Border, forest formations represent floristic
intrusions of the Amazonian and Brazilian Atlantic forests into the savannah formations
(Oliveira and Ratter 1986). Considerable numbers of dung beetle species are observed
with disjunct distribution patterns occurring concomitantly in the Amazonian and
Brazilian Atlantic forests. This pattern suggests that those intrusions are remnants of a
palaeoforest that was fragmented during the climatic fluctuations in the Quaternary.
Therefore, forest formations in the Cerrado form a true connecting network among
Amazonian and Parana subregions (Veloso 1966; Cabrera and Willink 1973; Daly and
Prance 1989). Hence, we suggest that the connections between the two biomes,
through patches of wet forest and gallery forests in the region of the Pantanal–
Cerrado Border, enable the survival of dung beetles from the Amazonian and Brazilian
Atlantic forests.

Conclusions

We have found several biotic components of dung beetle fauna from the Pantanal–
Cerrado Border. The distributions of those components seem to be well explained by
historical events, with a prominent role of Quaternary climatic fluctuations generating
vicariant events.

The region of the Pantanal–Cerrado Border is a biogeographical node, including
representatives from different biogeographic origins. However, the region is not homo-
genous and the fauna of southern Rondônia province (Pantanal Depression) clearly has
strong links with the Chaco province and none with the Amazonian fauna. According to the International code of area nomenclature (Ebach et al. 2008) we propose to formalize the Pantanal area as a biogeographical district within Chaco province (Pantanal district, stat. nov).

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Disclosure statement

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