

How Does Dung Beetle (Coleoptera: Scarabaeidae) Diversity Vary Along a Rainy Season in a Tropical Dry Forest?

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Abstract

Dung beetle community dynamics are determined by regional rainfall patterns. However, little is known about the temporal dynamics of these communities in tropical dry forests (TDFs). This study was designed to test the following predictions: 1) Peak diversity of dung beetle species occurs early in the wet season, with a decrease in diversity (α and β) and abundance throughout the season; 2) Nestedness is the primary process determining β -diversity, with species sampled in the middle and the end of the wet season representing subsets of the early wet season community. Dung beetles were collected in a TDF in the northern Minas Gerais state, Brazil over three sampling events (December 2009, February and April 2010). We sampled 2,018 dung beetles belonging to 39 species and distributed among 15 genera. Scarabaeinae α -diversity and abundance were highest in December and equivalent between February and April, while β -diversity among plots increased along the wet season. The importance of nestedness and species turnover varies between pairs of sample periods as the main process of temporal β -diversity. Most species collected in the middle and end of the wet season were found in greater abundance in early wet season. Thus, the dung beetle community becomes more homogeneous at the beginning of the wet season, and as the season advances, higher resource scarcity limits population size, which likely results in a smaller foraging range, increasing β -diversity. Our results demonstrate high synchronism between the dung beetle life cycle and seasonality of environmental conditions throughout the wet season in a TDF, where the onset of rains determines adult emergence for most species.

Key words: seasonality, temporal distribution, Scarabaeinae, nestedness, β -diversity

Tropical insect community structure varies over time due to changes in climatic conditions and the availability of food resources (Wolda 1978). Rainfall seasonality is a particularly important factor for dung beetle community structure because it determines the abundance and quality of their primary resources (i.e., manure and carcasses) (Cambefort 2014a). The bulk of these resources arises from mammals, whose abundance decreases during periods of lower rainfall due to death or migration to areas with greater availability of water (see Cambefort 2014a). Moreover, dung beetles depend on the nutrients present in the water component of manure; lack of water in the dry season reduces the amount of water in manure as well as the amount of time that it remains a high-quality resource (Cambefort 2014b).

Dung beetle communities respond to rainfall variation, exhibiting synchronized or maximal activity when rains arrive (Hanski and Cambefort 2014). Even in environments with limited seasonality

such as tropical rainforests, species diversity is greater in periods of higher precipitation (Peck and Forsyth 1982, Hill 1993, Andersen 2002). This seasonal pattern becomes more evident when beetle diversity is compared between the dry and wet seasons of highly seasonal environments, such as tropical dry forests (TDFs) (Andersen 2005, Neves et al. 2010, Liberal et al. 2011, but see Medina and Lopes 2014).

Despite the low number of studies in TDFs, the seasonal patterns in dung beetle communities are evident. Of 38 species (total of 2,748 collected individuals) recorded during the wet season in a TDF (same study area as in present work) in southeastern Brazil only one species (with four individuals) was also found in the dry season (Neves et al. 2010). However, little is known about the temporal dynamics of beetle community structure and composition throughout the wet season in TDFs.

In seasonal habitats, the first rains at the end of the dry season mark the beginning of the wet season, which increases humidity and causes rapid budding of new leaves (Pezzini et al. 2014). Most insect activity synchronously declines in the dry season, then increases again with the arrival of the rains due to better environmental conditions and higher availability of food resources (Silva et al. 2011; Novais et al. 2016). However, this pattern can vary among insect guilds. Ambrosia beetles, e.g., show increased activity at the end of the dry and wet seasons, when the presence of the air moisture in the beginning or end of the rains in association with the water stress on plants favors adult ambrosia beetle emergence to colonize a new host (Macedo-Reis et al. 2016).

In addition to having a paucity of studies in TDFs in general, most studies of dung beetles have evaluated spatial variation in β -diversity at the expense of studying temporal variation (Viljanen et al. 2010, Costa et al. 2014, Silva and Hernández 2014). β -diversity can be decomposed into two processes, turnover and nestedness. For temporal β -diversity turnover describes the replacement of species by other distinct species during a sampling period; nestedness describes the condition of the loss (or gain) of species such that the group with lower α -diversity is actually a subset of the species found in the period with greater α -diversity (Baselga 2010).

The objective of this study was to evaluate temporal patterns of beetle community structure along the wet season in a Brazilian TDF. We tested the following predictions: 1) dung beetle diversity will peak early in the wet season, with a decrease in α - and β -diversity and abundance as the season progresses; and 2) β -diversity is mainly shaped by nestedness, with species sampled in the middle and the end of the wet season representing subsets of the early wet season community.

Material and Methods

Study Area

The study was conducted at the Mata Seca State Park (MSSP), located in the Middle São Francisco valley in the Manga municipality, northern Minas Gerais state, Brazil (14°48'36"–14°56'59" S and 43°55'12"–44°04'12" W; Fig. 1). The MSSP was created in 2000 and has a total area of 15,466.44 ha consisting predominantly of deciduous forest (Madeira et al. 2009). Climate in this region is classified as semi-arid according to the Köppen system, with an average temperature of 24.4°C and average annual rainfall between 242 and 848 mm. The dry season extends from May to October, in which ~90–95% of tree species shed their leaves (Pezzini et al. 2014).

Dung beetles were collected in the beginning, middle, and end of the wet season in December, February, and April of 2009–2010 (Fig. 2). Despite the consistent rains start in October, we consider our first sampling (December) as the beginning of the rainy season. We believe that the biotic and abiotic conditions are maintained in the first months of the rainy season due to abundant rainfall during this period (Pezzini et al. 2014). Ten pre-existing 50 × 20 m plots (Madeira et al. 2009, Macedo-Reis et al. 2016) presenting vegetation in advanced stages of secondary succession (over 20 years) were selected, with plots located at least 0.2 km apart (Fig. 1). To ensure the absence of vegetation structure effects on dung beetle communities we used the database from a prior study to calculate the richness and abundance of plants per plot (Madeira et al. 2009). In each sample period, four traps were placed at the extremes of each plot.

Dung Beetle Sampling

Dung beetles were collected using pitfall-type traps consisting of plastic containers (14 cm in diameter × 11 cm in deep) buried with

openings flush with the ground. Traps were covered with rain shields. For use as bait, 50 g of human feces was hung from a wire above the trap opening. Traps contained 250 ml of liquid detergent, water and salt solution to kill and preserve the beetles. The pitfalls remained in the field for 48 h. Subsequently the beetles were collected, sorted, and identified to the lowest taxonomic level using keys (Vaz de Melo et al. 2011) and with the help of the taxonomist Fernando Vaz-de-Melo. The species were deposited in the collection of Fernando Vaz-de-Melo at the Federal University of Mato Grosso, Mato Grosso state, Brazil.

Data Analysis

Each plot was considered a sample unit for the calculation of α -diversity (richness of species in a plot) and dung beetle abundance. β -diversity among plots was calculated by $\beta = \alpha_{\text{period}} / \alpha_{\text{plot}}$ (Whittaker 1972), where α_{period} is the total number of species per sample period (December, February, April), and α_{plot} is the average species richness of the four sampling points (pitfall traps) within a plot. Only for β -diversity calculation, the α -diversity was considered as the average of species richness between traps within a plot. Using this approach, mathematically independent values of α and β allow comparisons of β values between sample periods with different values of α -diversity (Chao et al. 2012).

We used Generalized Mixed Linear Models (GLMERs; lme4 package in R) to test whether dung beetle α -diversity and abundance were affected by sample period, assuming temporal pseudoreplication. We used Linear Mixed Models (LMER) for analysis of β -diversity among sample periods. Plant richness and abundance were added to the models to test for effects of vegetation structure on dung beetles. In this approach, collection period, plant richness and abundance were used as explanatory variables, all nested within plot (random effect), which were sampled temporally (Bates et al. 2014).

Significance was estimated with an ANOVA between the complete (H1) and the null model (H0). The Akaike Information Criterion (AIC) was used to rank the models, since it represents the uncertainty of the model, a lower value of the AIC represents the more parsimonious model. When significant differences were observed between sample periods, the data were submitted to contrast analysis by aggregating levels (Crawley, 2013). If the level of aggregation was not significant and did not alter the deviance explained by the null model, the levels were pooled together (contrast analyses). All analyses were performed using R software (R Development Core Team 2015).

We decomposed β -diversity (β_{temporal}) to determine the primary processes shaping community structure. The decomposition of β was performed using the Sørensen (β_{SOR}) and Simpson (β_{SIM}) dissimilarity indices (Baselga 2010). β_{SOR} represents the total β -diversity and incorporates both species turnover and the nestedness. β_{SIM} shows only species replacement, or turnover, and does not consider variation in species richness. The difference between these indices indicates the total loss of species due to nestedness (β_{NES}), such that ($\beta_{\text{NES}} = \beta_{\text{SOR}} - \beta_{\text{SIM}}$).

Results

We collected a total of 2,018 dung beetles across 39 species, distributed among 15 genera. The December collection had the highest species richness, with 34 species (1,706 individuals). February and April collections yielded 15 and 16 species (143 and 169 individuals, respectively). Six species were shared among all sample periods, and no species was sampled only in February. Three species were found

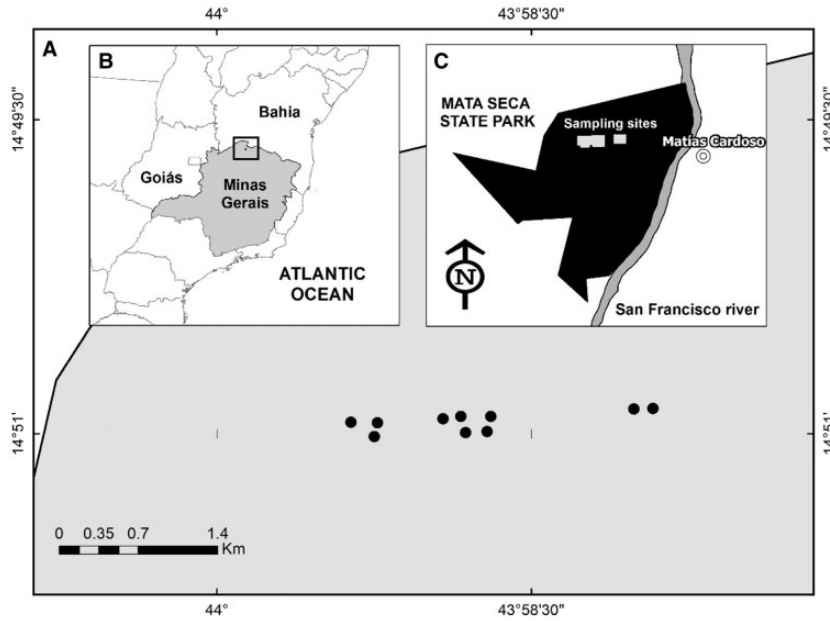


Fig. 1. Sampling sites at Mata Seca State Park, southeastern Brazil. Maps indicating (A) plot distribution, (B) location of the study area in Brazil and (C) shape of the Mata Seca State Park.

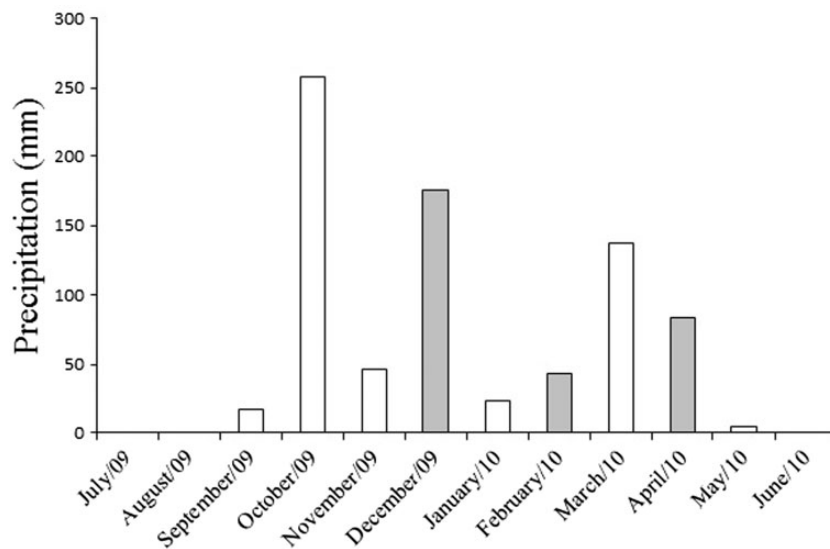


Fig. 2. Precipitation (mm) during July/2009 to June/2010, data from Mocaminho Meteorological Station, 15 km from Mata Seca State Park; and sampling periods (December 2009, February 2010, and April 2010) indicated by gray bars.

only in April (Table 1). *Canthon histrio*, *Onthophagus* aff. *Hirculus*, and *Deltochilum verruciferum* were the most abundant species, representing together >61% of the samples.

We found no effects of plant species richness and abundance on the dung beetle community (α - and β -diversity, and abundance) (Table 2). Scarabaeinae α -diversity and abundance were higher in December, and did not differ between February and April (Tables 2, Fig. 3A and B), while β -diversity among plots was lowest in December (Table 2; Fig. 3C).

The decomposition of β -diversity revealed that the relative importance of nestedness and species turnover varies between pairs of sample periods. Nestedness was the main process between December and February, while turnover was more important between February and April (Table 3). Between December and April,

the two processes were equally important for structuring dung beetle communities (Table 3).

Discussion

Dung beetle communities changed dramatically throughout the wet season, and the importance of nestedness and species turnover varies between pairs of sample periods as the main process of temporal β -diversity. Individuals sampled at the beginning of the wet season accounted for nearly 85% of the total number collected. Species richness showed a similar pattern; out of 39 species, >90% were sampled in the beginning of the wet season. Andersen (2005) found similar results for dung beetle abundance in a TDF in Mexico, with

Table 1. Abundances of Scarabaeinae species sampled in the beginning, middle and end of the wet season (December 2009, February, and April 2010) in a TDF at the Mata Seca State Park, Minas Gerais, Brazil

Taxon		December	February	April
<i>Agamopus unguicularis</i>	Harold, 1883	22	0	0
<i>Atheucus</i> aff. <i>histrion</i>	Balthasar, 1939	6	0	1
<i>Atheucus</i> sp1		1	0	0
<i>Canthidium</i> aff. <i>ardens</i>	Bates, 1887	14	0	1
<i>Canthidium</i> aff. <i>barbacenicum</i>	Borre, 1886	4	0	5
<i>Canthidium manni</i>	Arrow, 1913	109	0	0
<i>Canthon</i> aff. <i>piluliformes</i>		52	1	2
<i>Canthon callybaeus</i>	Blachard, 1846	7	1	0
<i>Canthon carbonarius</i>	Harold, 1868	3	0	0
<i>Canthon histrion</i>	Serville, 1828	468	24	53
<i>Canthon lituratus</i>	Germer, 1813	8	1	0
<i>Canthon obscurielus</i>	Schmidt, 1922	5	0	0
<i>Canthon</i> sp1		0	1	2
<i>Canthon unicolor</i>	Blanchard, 1846	0	0	1
<i>Coproghanaeus pertyi</i>	Olsufieff, 1924	1	0	0
<i>Coproghanaeus cyanescens</i>	Olsufieff, 1924	21	1	3
<i>Deltochilum</i> aff. <i>calcaratum</i>	Bates, 1870	41	17	1
<i>Deltochilum enceladus</i>	Kolbe, 1893	30	2	0
<i>Deltochilum pseudoicarus</i>	Balthasar, 1939	1	1	0
<i>Deltochilum</i> sp1		37	26	0
<i>Deltochilum verruciferum</i>	Felshe, 1911	174	44	9
<i>Diabrotis mimas</i>	Linnaeus, 1758	9	0	0
<i>Dichotomius</i> aff. <i>cuprinus</i>	Felche, 1901	3	0	0
<i>Dichotomius bos</i>	Blanchard, 1846	15	0	0
<i>Dichotomius carbonarius</i>	Mannerheim, 1829	63	0	0
<i>Dichotomius geminatus</i>	Arrow, 1913	0	1	1
<i>Dichotomius glaucus</i>	Harold, 1869	14	0	0
<i>Dichotomius nisus</i>	Oliver, 1789	0	0	2
<i>Dichotomius puncticolis</i>	Luederwaldt, 1935	31	0	2
<i>Eurysternus caribaeus</i>	Herbst, 1789	6	0	0
<i>Genieridium cryptops</i>	Arrow, 1913	12	0	0
<i>Ontherus appendiculatus</i>	Mannerheim, 1829	11	3	0
<i>Ontherus azteca</i>	Harold, 1869	21	0	0
<i>Ontherus dentatus</i>	Luederwaldt, 1930	0	0	8
<i>Ontherus digitatus</i>	Harold, 1868	33	1	0
<i>Onthophagus</i> aff. <i>hirculus</i>	Mannerheim, 1829	385	19	68
<i>Trichillum externepunctatum</i>	Borre, 1880	5	0	0
<i>Uroxix bahianus</i>	Boucomont, 1927	66	0	10
<i>Zoonocropi smachadoi</i>	Vaz-de-Melo, 2007	28	0	0
Total		1706	143	169

Table 2. Results of the models (GLMER and LMER), showing temporal variation in α -diversity, abundance and β -diversity of dung beetles in a TDF

Response variables	Explanatory variables	AIC (H1)	AIC (H0)	P
Dung beetle α -diversity	Plant richness	135.68	133.99	0.579
	Plant abundance	134.0	131.99	0.981
	Month	131.99	268.75	<0.001
Dung beetle abundance	Plant richness	299.64	299.59	0.163
	Plant abundance	299.59	297.69	0.754
	Month	297.69	2459.84	<0.001
Dung beetle β -diversity	Plant richness	172.82	171.48	0.417
	Plant abundance	171.48	169.48	0.966
	Month	169.48	180.20	<0.001

Significance was estimated with an ANOVA between the complete (H1) and the null model (H0). The AIC represents the uncertainty of the model, thus a low value of the AIC represents the more parsimonious model.

more than twice as many individuals found at the beginning of the wet season compared with the middle.

Of the 34 species sampled at the beginning of the wet season, 32 either had reduced abundances or were not sampled in later periods. These results indicate a peak adult emergence of the vast majority of species at the beginning of the wet season. Hence our study contradicts the hypothesis raised by Andersen (2008), which suggests that the dung beetles are likely to experience drastic fluctuations in abundance, with different peaks during different periods.

Lack of rainfall, high solar radiation, and low humidity are typical of TDFs for at least 3 months during the dry season (Murphy and Lugo 1986). These conditions affect the availability of resources and limit reproduction and survival of many animals, including dung beetles, which synchronize their life cycle to tolerate these adversities (Andersen 2005, Neves et al. 2010, Liberal et al. 2011, Cambefort 2014a). For example, the Guinean savannas in Africa have two wet seasons, so dung beetles have two peaks in emergence during the year (Cambefort 2014a). Many species weather

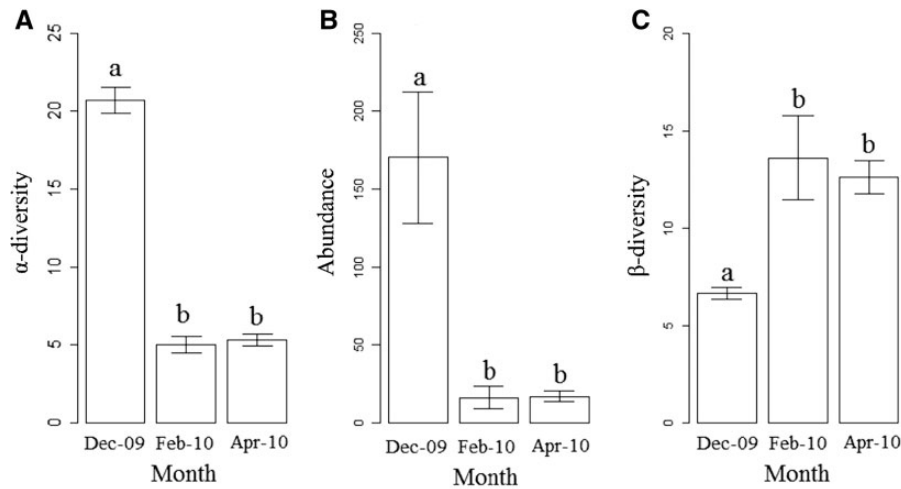


Fig. 3. Dung beetles α -diversity (A), abundance (B), and β -diversity (C) (mean \pm SE) along a rainy season at the Mata Seca State Park, southeastern Brazil.

Table 3. Results from decomposition of dung beetle β -diversity in the beginning, middle and end of wet season (December 2009, February, and April 2010) in a TDF at the Mata Seca State Park, Minas Gerais, Brazil

Parameter	Period	β_{SIM}	β_{NES}	β_{SOR}
Species presence	December \times February	0.133 (28.4%)	0.336 (71.6%)	0.469
	December \times April	0.312 (55.9%)	0.248 (44.3%)	0.56
	February \times April	0.466 (96.5%)	0.017 (3.5%)	0.483

unfavorable environmental conditions (i.e., during droughts) in diapause (hibernation) or in larval stages in the soil (Doube 2014). The adults emerge with the onset of the rains, and immediately concentrate efforts on accumulation of resources for making nests, reproduction, and subsequent oviposition (Cambefort 2014a).

We found the greatest within-plot β -diversity in the middle and end of the wet season. In the middle and end of the wet season only 13–47% of the collected species were present in individual plots, compared with 47–74% of species per plot at the beginning of the wet season. With the emergence of most species of dung beetles due to improved abiotic conditions and the increased availability of resources the community becomes more homogeneous at the beginning of the wet season. As the season advances, higher resource scarcity limits population size, which likely results in a smaller foraging range, increasing β -diversity.

Decomposition of β -diversity demonstrated that the dung beetle community sampled in the middle of the wet season is indeed a subset of the species present at the beginning of the wet season. At the end of wet season turnover and nestedness were equally important, due to some species that were exclusively found in this period. These results reinforce the pattern of peak adult emergence found in most dung beetle species at the start of the wet season, since the community changes little (i.e., in terms of species composition) throughout the season. The high turnover value between the beginning and end of the wet season was due to only five species not sampled at the beginning, which only represented 8% of the total individuals at the end of the wet season.

Conclusions

Our results demonstrate a peak in adult emergence for most dung beetle species at the beginning of the wet season. Additionally, most species present in the middle and end of the wet season were also

sampled at the beginning, whereas only a few species with few individuals were absent in the beginning. These results suggest strong synchronism between the life cycle of these organisms and the seasonality of environmental conditions throughout the year, where the onset of the rains determines adult emergence in most species in the TDF studied.

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