



Rainfall seasonality drives the spatiotemporal patterns of dung beetles in Amazonian forests in the arc of deforestation

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Abstract

The Amazon Rainforest is facing high rates of deforestation, leaving anthropogenically dominated landscapes across the Amazon. Understanding the biodiversity response to the effects of rainfall seasonality can provide important examples of how species may respond to drastic climate conditions in anthropogenic landscapes. Here, we sampled dung beetles across the same Amazon forest sites during the rainy and dry seasons to evaluate the effect of seasonality on biodiversity patterns. We found a significant space–time interaction for the whole set of forest sites indicating that the spatial structure of the species abundance data has changed significantly between seasons. Dung beetle abundance and species richness was higher in the rainy season when evaluating all species and separately for nesting behavior group. For presence-absence and abundance data of the whole assemblage, the mean differences between losses and gains over all forest sites was negative, indicating dominance of species and individuals-per-species losses across all forest sites. Eleven species (5 tunnellers, 4 rollers, and 2 dwellers) had significant decreases in abundances in the forest sites from the rainy to the dry season, whereas one roller species increased in abundance from the rainy to the dry season. Rainfall seasonality drives the temporal patterns of dung beetle diversity in the Amazonian forests in the study region in the arc of deforestation.

Implications for insect conservation Understanding species vulnerability to changes in climatic conditions could help to predict species distributions in an increased scenario of higher temperatures and longer drought periods during dry seasons in the near future.

Keywords Beta diversity · Biodiversity conservation · Scarabaeinae · Temporal patterns · Tropical forest

Introduction

The Amazon rainforest is one of the richest and largest tropical forests, occurring in the northern South America and covering an area of *ca.* 6,000,000 km², mostly of it belonging to the Brazilian territory (comprising almost 50% of Brazil's total area). Over the last decades, deforestation in the Amazon has been a major issue in the environmental agenda, driven by concerns about deteriorating ecosystem services, biodiversity loss, and increasing carbon emissions (Davidson et al. 2012; Aragão et al. 2014; Barlow et al. 2016). The most deforestation hotspots are concentrated along the 'arc of deforestation' (Fine and Mamani 2020) extending across the southern rim of the Brazilian Amazon from Pará to Rondônia, with an especially large hotspot in Mato Grosso (Kalamandeen et al. 2018). Climate change is also acknowledged as a key driver of changes in the Amazon forest, increasing both dry season lengths and temperatures (Brando et al. 2019). Over the past century, the average temperature in

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the Amazon has increased by 1–1.5 °C (Nobre et al. 2016). Recent works also show that climate change is increasing the frequency and intensity of climate extremes such as severe drought and flood events in the Amazon (Marengo and Espinoza 2016; França et al. 2020a). Thus, the dry season has also expanded during the last decades, from four months to almost five (Marengo and Espinoza 2016). Jointly, these processes, coupled to an intensification of deforestation-related fires encouraged by Brazil's government, have resulted in a fire crisis in the Amazon (*see* Aragão et al. 2018; Barlow et al. 2020).

Rainfall is expected to be the most important environmental cue influencing the seasonal activities of tropical insect populations (Wolda 1978; Kishimoto-Yamada and Itioka 2015). Although the Amazon is predominantly a rainforest, there are some regions with high annual rainfall regimes that show dry winters (Alvares et al. 2014). Droughts in the Amazon are recurrent and have been increasing in intensity and frequency over the past few decades (Marengo and Espinoza 2016; França et al. 2020a). This interaction between climate and land-use practices in the Brazilian Amazon has drastic implications for conservation since we expect extended dry seasons and more frequent years of drought due to climate change (Aragão et al. 2007; Marengo and Espinoza 2016; Brando et al. 2019).

The seasonality of insect populations still lacks evidence for many species' groups in tropical forests, which may have seasonal or aseasonal patterns. Also, the mechanisms affecting seasonal patterns in abundance fluctuations and the evolution of tropical insect seasonality are not fully understood (Kishimoto-Yamada and Itioka 2015). This calls for more attention if one considers a scenario where different factors interact to determine the spatiotemporal dynamics of the biological communities, such as in the Brazilian Amazon (*see* Nobre et al. 2016; Barlow et al. 2018). Furthermore, understanding the biodiversity patterns between rainy and dry seasons can provide important examples of how species may respond to drastic climate conditions. This will be helpful to develop better conservation and management initiatives in an increased scenario of climate change (*i.e.*, higher temperatures, longer periods of drought during dry season).

Dung beetles (Coleoptera: Scarabaeinae) are a highly diverse group of insects that have been widely used to evaluate anthropogenic changes caused to natural environments across the world, but specially in the Amazon forest where they are highly cost-effective, responsive study models and biodiversity bioindicators (Braga et al. 2013; Franca et al. 2016; Beiroz et al. 2017). Furthermore, dung beetles are responsible for many ecological functions and services, which involve nutrient cycling, bioturbation, plant growth enhancement, secondary seed dispersal, biocontrol of dung-inhabiting parasites, and reduction of greenhouse gas emissions (Nichols et al. 2008; Slade et al. 2016). In

addition, dung beetles are stenotopic and sensitive to both broad- and fine-scale changes in the ecosystem (Nichols et al. 2007; Gardner et al. 2008; Audino et al. 2014; da Silva and Hernández 2016). Therefore, these beetles respond to changes in habitat attributes (Pinto Leite et al. 2018; da Silva et al. 2019; Storck-Tonon et al. 2020) but also to changes in climate (Andresen 2005; Hernández and Vaz-de-Mello 2009; Neves et al. 2010; da Silva et al. 2013; Medina and Lopes 2014; Correa et al. 2018). However, there is little information on how seasonality affects dung beetle diversity patterns in the Amazon (*see* Gardner et al. 2008; Andrade et al. 2011; Cajaiba et al. 2017). For example, Gardner et al. (2008) did not find effects of seasonality on patterns of dung beetle assemblages (*e.g.* richness and abundance) in Amazonian forests located in the state of Pará in north-eastern Brazilian Amazon. In contrast, Cajaiba et al. (2017) found higher abundance and richness of dung beetles in the rainy season when compared to dry season in Amazonian forests of Uruará, state of Pará. Evaluating seasonal patterns can be decisive for the development of more efficient management and conservation strategies.

Here, we evaluated how rainfall seasonality influences the composition and structure of dung beetle assemblages in the arc of deforestation in the Amazon forest. Therefore, we sampled dung beetles using standardized protocols of sampling over dry and rainy seasons across Amazon forest sites in an anthropized landscape situated in a large deforestation hotspot in South America (Kalamandeen et al. 2018). Specifically, we aimed to address the following questions: (i) Are there changes in composition and structure of dung beetle assemblages between rainy and dry seasons? (ii) Are the compositional changes characterized by species and abundances-per-species losses or gains?

Material and methods

Study area

We carried out the study in Juína, Mato Grosso, midwestern Brazil (11°26'55" S; 58°43'24" W; 320 m above sea level), within the vegetation domain of the Brazilian Amazon rainforest (*terra firme*). The climate of the region is a transition between *Am* and *Aw*, with two well-defined seasons, the dry season from May to September and the rainy season from October to April (Peel et al. 2007; Alvares et al. 2014). The average temperature is 24 °C (ranging from 20 to 40 °C) and the average annual precipitation is approximately 2000 mm (Batistão et al. 2013), while in the dry season the rainfall is below 100 mm per month (Aragão et al. 2007). The vegetation is formed by tree species typical of Amazonian vegetation, such as *Bertholletia excelsa* (Castanha-do-Brasil) (Lecythidaceae), *Cedrela fissilis* (Cedro) (Meliaceae), *Ceiba*

pentandra (Sumaúma) (Malvaceae), *Copaifera glycyarpa* (Copaíba) (Fabaceae), *Enterolobium contortisiliquum* (Tamburil) (Fabaceae), *Handroanthus serratifolius* (Ipê amarelo da mata) (Bignoniaceae), *Hymenaea courbaril* (Jatobá) (Fabaceae), and *Inga edulis* (Ingá cipó) (Fabaceae).

Historically, the occupation and land use of the study region was based on the exploitation of wood typical of Amazonian vegetation and on mining activities for the extraction of gold and diamonds. Currently, livestock, subsistence agriculture and the planting of agroforestry systems (e.g., pupunha and teak) predominate, while fragments of native vegetation (Amazonian forest) of varying sizes and degrees of conservation still remaining. The forest fragments are relatively conserved but humans often enter the fragments aiming to extract firewood, timber, and medicinal herbs from the forest and/or hunt since the main economic activity in the region is characterized as extractivism and agribusiness industrial exploitation.

Dung beetle sampling

We sampled dung beetles in July 2018 (dry season) and March 2019 (rainy season) in 10 Amazon forest sites separated by at least 0.5 km. The dry season 2018 is inside the rainfall patterns found in the last ten years (until 2008) before our samples (CHIRPS 2021). The distance used among sites sampled was used to ensure independence of the samples (da Silva and Hernández 2015). In addition, we performed a Mantel test to investigate a possible spatial autocorrelation between sample sites and dung beetle assemblage using the “vegan” package in the R software (R Core Team 2020). We did not find spatial autocorrelation ($r=0.11$; $p=0.29$) ensuring a sampling independence in our study design.

In each site, we installed a set of three baited pitfall traps separated from each other by 3 m in a triangular shape approximately 100 m from the edge (Correa et al. 2018). The traps of each set were baited with approximately 40 g of fresh swill pig dung, 40 g of grain pig dung, and 40 g of human feces. Swill pig dung was obtained from pigs raised by family farmers in the study region. Grain pig dung was obtained from Landrace industrial pigs, which are raised by large producers in intensive production systems. These feces were chosen due to the high attractivity of omnivorous feces to dung beetles (Larsen et al. 2006; Marsh et al. 2013; Ferreira et al. 2020). The evaluation of different baits in attracting dung beetles will not be considered in this study. Therefore, the data from traps belonging to the same set were pooled.

Each trap consisted of a plastic container (15 cm diameter, 9 cm depth), installed at ground level, covered with a plastic lid (15 cm diameter) supported with three wooden sticks (25 cm) to reduce desiccation of the bait and to protect

against rain and fall of leaves and branches. Within each trap, we added a 250 ml saline solution + neutral detergent (1.5%). The baits were placed in plastic containers (50 mL) at the center of each trap using a wire as bait holder. The total sampling effort was 60 traps (i.e., 30 traps per season). The traps remained active for 48 h in each forest site, after which time the specimens were removed and packed in plastic bags containing 70% alcohol for further sorting and taxonomic identification.

Dung beetles were first identified at genus level (Vaz-de-Mello et al. 2011) and then sent to the Universidade Federal de Mato Grosso (UFMT; Cuiabá, Mato Grosso, Brazil) to be identified at species level by an expert, Dr. Fernando Z. Vaz-de-Mello. Voucher specimens are deposited in the Entomology Section (CEMT), Zoological Collection at the UFMT, and in the Entomological Collection at the Instituto Federal de Educação, Ciência e Tecnologia de Mato Grosso (IFMT; Juína, Mato Grosso, Brazil). We grouped species into three nesting behavior relative to food source: dwellers, rollers, and tunnellers (Halffter and Edmonds 1982; Hanski and Cambefort 1991) to search for different response patterns among those groups.

Data analysis

First, we tested for the interaction between space (S) and time (T), which is an adequate approach for repeated samplings through time. A significant interaction can indicate that the spatial structure of the response data (e.g., community composition) has changed through time, and conversely, that the temporal variations differed significantly among the forest sites (Legendre and Condit 2019). The space–time interaction (STI) was tested on multivariate data using the method proposed by Legendre et al. (2010). This method was implemented using the function *stimodels* of the R package *adespatial* (Dray et al. 2020). The community data were Hellinger-transformed before the analysis (Legendre and Gallagher 2001).

Thereafter, the dissimilarity in community composition was measured for each forest site between the rainy (T1) and dry seasons (T2), according to the sequence of samplings. The analysis was repeated for each nesting behavior group of dung beetles and separately for presence-absence and abundance data. We used the Sørensen index for presence-absence data and the percentage difference (% difference) or Bray–Curtis index for abundance data when calculating the dissimilarity of community composition data (Legendre 2019). The Sørensen index is the binary form of the percentage difference index (Legendre and Legendre 2012). In the context of a comparison through time, these indices are called *Temporal Beta Indices* (TBI) (Legendre 2019). These indices allow the calculation of both individuals-per-species and species loss and gain components of these

dissimilarities. Furthermore, they can be tested for significance, as shown in Legendre (2019). Each index, which compares data from a forest site at T1 and T2, is composed of two parts: B = species (Sørensen) or abundances-per-species (Bray–Curtis) losses and C = species or abundances-per-species gains (Legendre and Condit 2019). The B and C statistics will be used to produce B – C plots, with B (losses per forest site) in the abscissa and C (gains per forest site) in the ordinate, as described in Legendre (2019). B – C plots display visually the relative importance of the species and abundance-per-species loss and gain processes in a study area, informing about details of the key processes of biodiversity losses and gains across the forest sites, through time, in space–time surveys (Legendre and Condit 2019). B – C plots will be shown for the whole dataset and for separate dung beetle groups according to their nesting behavior.

The mean of the differences between the B and C statistics is also computed across all forest sites. A positive value of $(C - B)$ indicates that the study area was dominated by gains, whereas a negative value indicates overall losses of species or abundances-per-species (Legendre 2019). The $(C - B)$ difference across all forest sites was tested for significance using a paired t -test computed for the C and B statistics from all forest sites. The calculations were implemented in the TBI and $plot.TBI$ functions, available in the R package *adespatial* (Dray et al. 2020). We also evaluated the demographic changes in forest sites between rainy and dry seasons using paired t -tests (Legendre and Condit 2019). The tests were carried out with 9999 random permutations of the values, in each forest site, between rainy and dry seasons. A Holm correction for multiple testing (n = number of sampled species) was applied to the computed p -values. The calculations were implemented using the function *tpaired.krandtest* of the R package *adespatial* (Dray et al. 2020).

We also used Generalized Linear Models (GLMs) to test for differences in species richness and number of individuals (response variables) of dung beetles between seasons (dry and rainy; explanatory variables). We used the Poisson error distribution corrected for overdispersion (quasi-Poisson) for abundance and species richness. We checked the error distribution for each model to find the best one (Crawley 2013). These analyses were done using all species and separately for each group of dung beetle species related to nesting behavior. All analyses were carried out in R (R Core Team 2020).

Results

In both seasons a total of 2085 dung beetles belonging to 17 genera and 51 species were collected. In the rainy season, we captured 40 (78.4%) species and 1651 (79.2%) individuals [mean \pm standard deviation; $S = 15.9 \pm 3.0$,

$n = 165.1 \pm 97.9$], while in the dry season we found only 25 (49.0%) species and 434 (20.8%) individuals [$S = 6.2 \pm 2.9$, $n = 43.4 \pm 42.6$]. Only 14 (27.4%) species occurred in both seasons, 11 (21.6%) species were sampled only in the dry season, while 26 (51.0%) species occurred only in the rainy season. Almost half of sampled species are grouped as tunnellers (25 species, 49%), 19 species as rollers (37%), five species as dwellers (10%), and two not grouped (4%) (Table S1).

We found a significant space–time interaction for the whole set of forest sites ($R^2 = 0.229$; $F = 1.897$; p -value = 0.014). This significant interaction means that the spatial structure of the multivariate data (species abundance data) has changed significantly between the seasons.

Temporal beta diversity analysis

For presence-absence data, TBI values ranged between 0.636 and 0.900 among all forest sites taking into account all species. The mean of the differences between losses (B) and gains (C) over all forest sites was negative, indicating dominance of species losses across all forest sites (Paired t -test = -9.450 , p -value = 0.002, $mean_{(C-B)} = -0.461$). Individually, no forest site had significant TBI values. In the B – C plot, the green line ($B = C$) is above the red line (centroid of points), indicating the losses of species dominated the changes in the entire forest from the rainy to the dry season (Fig. 1, top left panel).

For roller species, TBI values ranged between 0.429 and 1.000, while for tunneller species TBI ranged between 0.333 and 1.000 among all forest sites. The mean of the differences between losses and gains over all forest sites was also negative for both groups (roller species: Paired t -test = -6.354 , p -value = 0.002, $mean_{(C-B)} = -0.354$; tunneller species: Paired t -test = -5.427 , p -value = 0.004, $mean_{(C-B)} = -0.504$). Individually, no forest site had significant TBI values for both groups. In the B – C plot, the green lines are above the red lines, indicating the losses of species dominated the seasonal changes for both groups (Fig. 1, top central and right panels). TBI values based on presence-absence could not be computed for dweller species because only three sites contained species during the dry season. However, this in general shows a loss of dweller species from the rainy to the dry season.

For abundance data, TBI values ranged between 0.794 and 0.986 among all forest sites taking into account all species. The mean of the differences between losses (B) and gains (C) over all forest sites was negative, indicating dominance of individuals-per-species losses across all forest sites (Paired t -test = -4.774 , p -value = 0.008, $mean_{(C-B)} = -0.580$). Individually, no forest site had significant TBI values, although one site had more gains than losses. In the B – C plot, the green line is below the red line

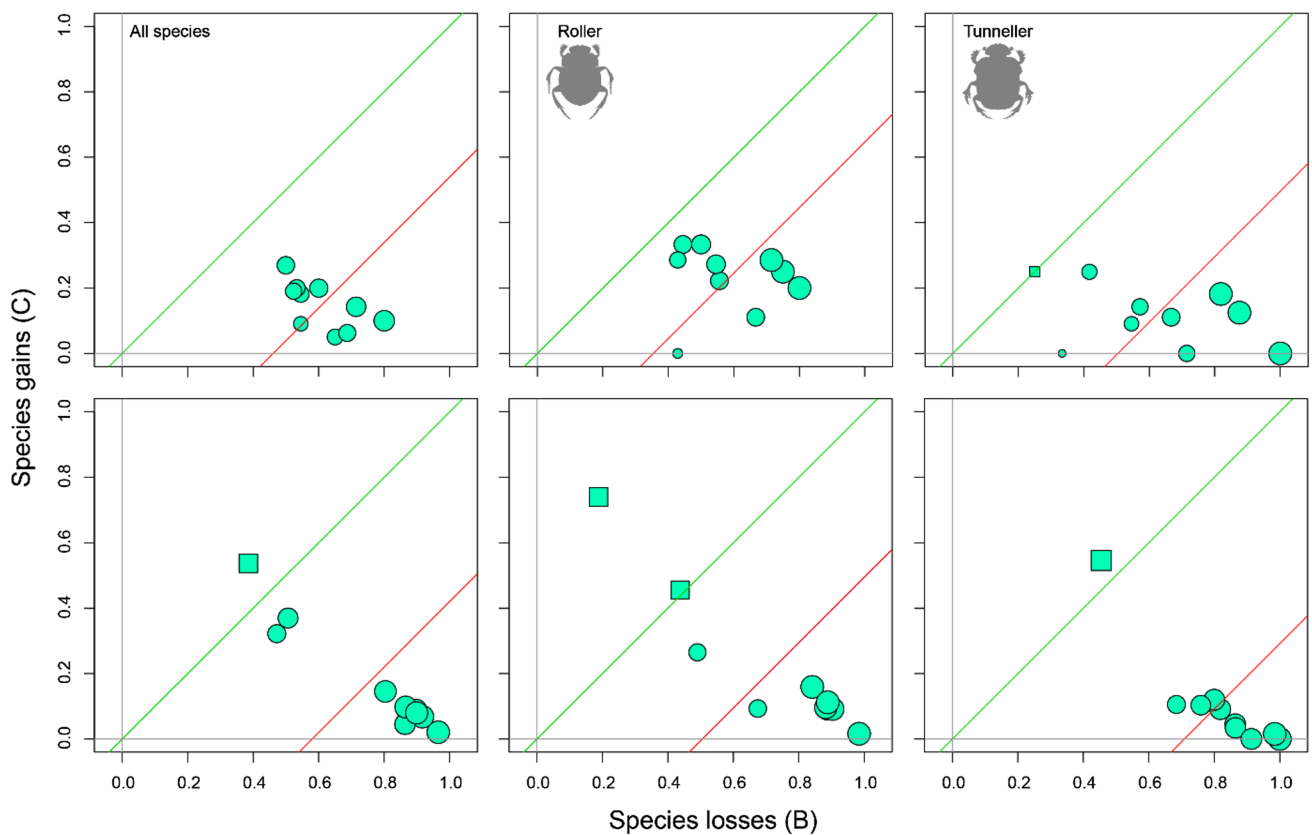


Fig. 1 $B-C$ plots comparing the samplings of rainy and dry seasons where the 10 Amazon forest sites are plotted using the losses (B) and gains (C) computed from the dung beetle species presence-absence (upper panels) and abundance (lower panels) data for all species (left panels), roller species (central panels), and tunneller species (right panels). Green line with slope of 1: line where gains equal losses.

The red line was drawn parallel to the green line (*i.e.*, with slope = 1) and passing through the centroid of the points. Its position below the green line indicates that, on average, species losses dominated gains from rainy and dry seasons. Circles indicate dominance of losses, while squares indicate dominance of gains or equal contribution (smaller squares). Circle and square sizes are scaled to their values

(centroid of points), indicating the losses of abundances-per-species dominated the changes in the entire forest from the rainy to the dry season (Fig. 1, bottom left panel).

For roller species, abundance-based TBI values ranged between 0.755 and 1.000, and between 0.789 and 1.000 for tunneller species. The mean of the differences between losses and gains over all forest sites was negative for both groups, indicating dominance of individuals-per-species losses across all forest sites (roller species: Paired t -test = -3.349 , p -value = 0.012, $\text{mean}_{(C-B)} = -0.505$; tunneller species: Paired t -test = -7.155 , p -value = 0.004, $\text{mean}_{(C-B)} = -0.708$). Only two sites had more gains than losses for roller species, while one site had more gains than losses for tunneller species. However, no forest site had significant TBI values for both groups. In the $B-C$ plot, the green line ($B = C$) is below the red line (centroid of points), indicating the losses of abundances-per-species dominated the changes in the entire forest from the rainy to the dry season (Fig. 1, bottom central and right panel). TBI values based on abundance data could not be computed for

dweller species because only three sites contained dwellers during the dry season. However, based on the abundance of those dweller species found in both seasons there was a loss of abundance-per-species from the rainy to the dry season as well.

Paired t -tests computed separately for the 51 species showed that 11 species (5 tunnellers, 4 rollers, and 2 dwellers) had significant decreases in abundances in the forest sites from the rainy to the dry season. These species included the dwellers *Eurysternus atrosericus* and *Eurysternus caribaeus*, the rollers *Canthon histrio*, *Canthon nitidicollis*, *Sylvicanthon monnei* and *Sylvicanthon proseni*, and also the tunnellers *Ateuchus pygidialis*, *Canthidium* sp. 1, *Canthidium* sp. 3, *Dichotomius* aff. *lucasi*, and *Onthophagus rubrescens* (Table 1). On the other hand, the roller *Canthon triangularis*, increased in abundance (Table S1). This species also increased in occurrences (from no occurrence in the rainy season to occur in 9 of the 10 forest sites in dry season; $n = 104$) (Table 1).

Table 1 Paired *t*-tests computed for all dung beetle species sampled in 10 Amazon forest sites during the rainy (T1) and dry (T2) seasons

| Species | Mean(T1–T2) | <i>t</i> -test | p-value | Status | Functional group |
|---|-------------|----------------|---------|----------|------------------|
| <i>Ateuchus pygidialis</i> (Harold) | 4.4 | 2.152 | 0.004 | Decrease | Tunneller |
| <i>Canthidium</i> sp.1 | 8.6 | 2.305 | 0.002 | Decrease | Tunneller |
| <i>Canthidium</i> sp.3 | 0.9 | 2.212 | 0.043 | Decrease | Tunneller |
| <i>Canthon histrio</i> (Lepelletier and Serville) | 15.3 | 1.963 | 0.003 | Decrease | Roller |
| <i>Canthon nitidicollis</i> Lucas | 34.7 | 3.202 | 0.004 | Decrease | Roller |
| <i>Canthon triangularis</i> (Drury) | – 10.4 | – 2.637 | 0.002 | Increase | Roller |
| <i>Dichotomius</i> aff. <i>lucasi</i> (Harold) | 0.9 | 1.868 | 0.030 | Decrease | Tunneller |
| <i>Eurysternus atrosericus</i> Génier | 3.5 | 2.206 | 0.015 | Decrease | Dweller |
| <i>Eurysternus caribaeus</i> (Jablonsky and Herbst) | 3.8 | 4.321 | 0.002 | Decrease | Dweller |
| <i>Onthophagus rubescens</i> Blanchard | 6.5 | 3.434 | 0.012 | Decrease | Tunneller |
| <i>Sylvicanthon monnei</i> Cupello and Vaz-de-Mello | 35.6 | 2.117 | 0.002 | Decrease | Roller |
| <i>Sylvicanthon proseni</i> (Martínez) | 1.6 | 2.278 | 0.030 | Decrease | Roller |

Significance was computed comparing abundance in both seasons per species via 9999 permutations to account for multiple testing. Status means increase or decrease in abundance from rainy to dry seasons. Results were shown only for those species with p-values < 0.05

Effect of seasonality on dung beetle assemblage

We found that seasons determined the temporal distribution of both abundance of species richness of dung beetles when evaluating all species and separately for nesting behavior group (Table 2). Higher values of dung beetle abundance and species richness were always found in the rainy season (Fig. 2).

Discussion

Our results clearly evidenced that rainfall seasonality drives the temporal patterns of dung beetle diversity in Amazonian forests in the study region in the arc of deforestation, with a strong species and abundances-per-species losses from the rainy to the dry season. Therefore, the rainfall seasonality is determinant to host higher abundance and species richness in the rainy season.

Table 2 Results of generalized linear models to test the effect of season on dung beetle abundance and species richness sampled in Amazon forest sites in the rainy and dry seasons

| Group | Response variable | Model | Df | Deviance | Resid.Df | Resid.Deviance | F-test | p-value |
|-------------|-------------------|--------|----|----------|----------|----------------|--------|---------|
| All species | Richness | Null | | | 19 | 61.406 | | |
| | | Season | 1 | 44.059 | 18 | 17.346 | 46.764 | <0.001 |
| | Abundance | Null | | | 19 | 1556.69 | | |
| | | Season | 1 | 757.47 | 18 | 799.22 | 15.171 | 0.001 |
| Dwellers | Richness | Null | | | 19 | 32.342 | | |
| | | Season | 1 | 14.778 | 18 | 17.564 | 16.358 | <0.001 |
| | Abundance | Null | | | 19 | 156.66 | | |
| | | Season | 1 | 81.894 | 18 | 74.770 | 20.142 | <0.001 |
| Rollers | Richness | Null | | | 19 | 19.080 | | |
| | | Season | 1 | 9.405 | 18 | 9.675 | 17.416 | <0.001 |
| | Abundance | Null | | | 19 | 1288.73 | | |
| | | Season | 1 | 469.58 | 18 | 819.14 | 9.2215 | 0.007 |
| Tunnellers | Richness | Null | | | 19 | 39.349 | | |
| | | Season | 1 | 24.018 | 18 | 15.331 | 34.090 | <0.001 |
| | Abundance | Null | | | 19 | 455.55 | | |
| | | Season | 1 | 229.26 | 18 | 226.29 | 14.045 | 0.001 |

We tested all species together and separately for each nesting behavior group. *Df* degrees of freedom, *Resid.* Residual

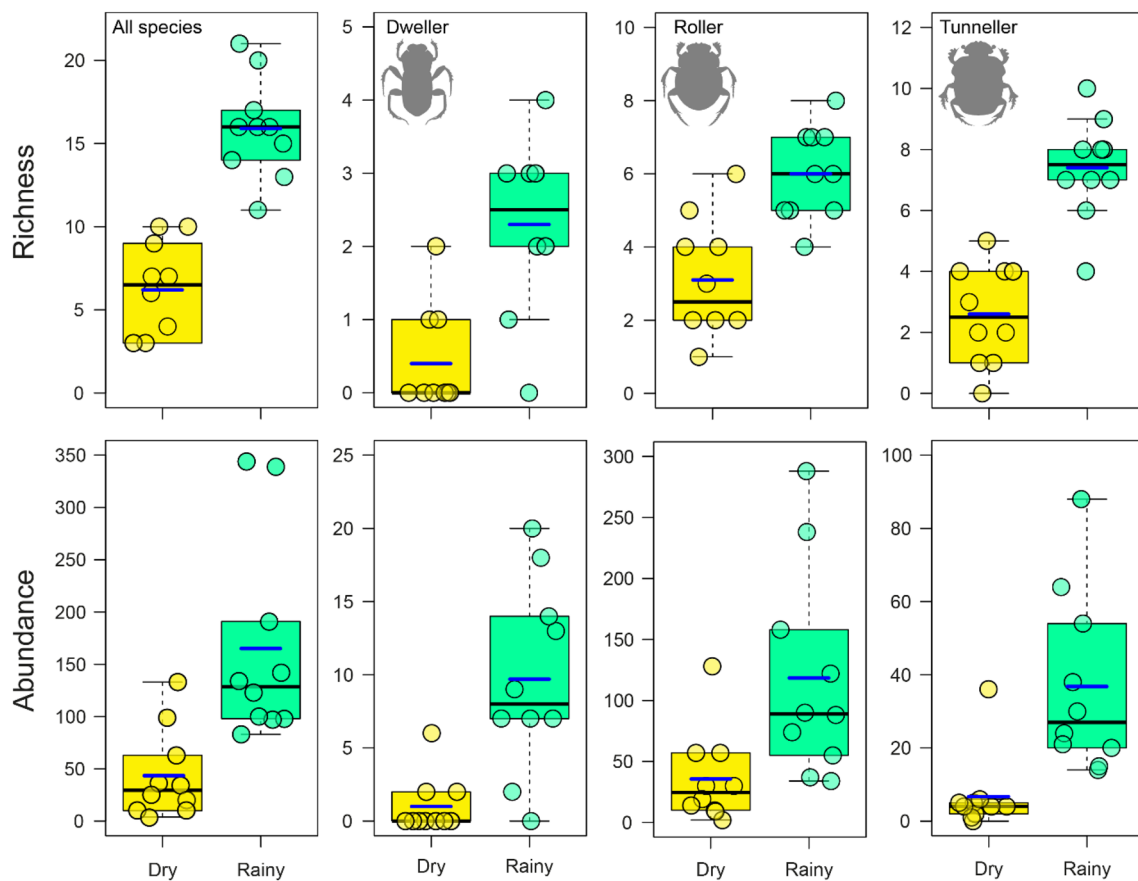


Fig. 2 Boxplots of dung beetle species richness (upper panels) and abundance (lower panels) of dung beetles sampled in dry (yellow) and rainy (green) seasons in 10 Amazon forest sites. We show results for all species and separately for each nesting behavior group (dwell-

ers, rollers, and tunnellers). All plots show statistical differences between the dry and rainy seasons. Blue lines indicate average values. Circles indicate observed values

Effects of rainfall seasonality on patterns of abundance, species richness, and species composition

We found that spatial structure of the species abundance data has changed significantly between seasons, with higher dung beetle abundance and species richness in the rainy season when evaluating all species and separately for nesting behavior group. This strong seasonal pattern found in our study region is similar that found by Cajaíba et al. (2017), in Pará state. However, Gardner et al. (2008) did not observe any seasonality among dung beetles in Amazonian rainforests from other region in the Pará state. Thus, our results suggest that the effects of seasonality on dung beetle patterns may vary across Amazonian regions. Silva et al. (2010) suggested two hypotheses that may explain the lower abundance and richness of dung beetles in the dry season in Neotropical rainforests: (i) adult beetles are sensitive to the effects of drought and remain underground during this period; or (ii) the adults die in the dry season and only

the immature beetles survive in brood chambers, reaching the adult stage at the beginning of the rainy season. To our knowledge, both hypotheses can be true for those species that are drought-intolerant, which may show species-specific responses depending on, *e.g.*, body size and voltinism (Kishimoto-Yamada and Itioka 2015). Besides, during the dry season, active populations may decline to small “population pockets” concentrated in humid microhabitats (Leather et al. 2008), such as forest sites within an anthropogenically-changed landscape like the arc of deforestation in South America (Kalamandeen et al. 2018).

Variability in rainfall appears to be the prime factor influencing seasonality in tropical organisms (Wolda 1978; Kishimoto-Yamada and Itioka 2015), and this is also true for many dung beetle species (Gill 1991; Andresen 2005). Large-bodied dung beetles are the most sensitive to dry conditions; they appear during the rainy conditions and disappear during the dry season in tropical forests, in general leaving small-bodied species (Janzen 1983). In our case, most *Dichotomius* spp., all *Coprophanaeus* spp., all *Phanaeus*

spp., (tunnelers) and all *Deltochilum* spp., (rollers), which comprise large-bodied dung beetles, were sampled only in the rainy season. Of course, there are few large-bodied species, such as *Oxysternon conspicillatum*, being sampled in both seasons. However, this species is commonly found in tropical lowland forests of western Amazon basin, being an aggressive diurnal competitor on feces collected throughout the year (Peck and Forsyth 1982; Edmonds and Zidek 2004).

Dweller dung beetles (which nest within the food resource) generally compose the smaller fraction of dung beetle assemblages across the Neotropics when compared to rollers and tunnellers. Due to their nesting behavior, dwellers are expected to be more susceptible to environmental and climate changes than other groups. This occurs because some species can spend much time (*e.g.*, 200 days for some species of *Eurysternus*) feeding and preparing the nest in the food source (Halffter et al. 1980). This implies greater exposure to stochastic events (*e.g.*, fires, floods) that can affect their reproductive success. Among the dwellers, three species were found only in the rainy season: *Eurysternus hamaticollis*, *Eurysternus wittmerorum*, and *T. externepunctatum*. The first two species are large-bodied dwellers (> 1 cm) that inhabit primary and secondary forests in the Amazon (Génier 2009). On the other hand, *T. externepunctatum* (<0.5 cm) is a small dweller considered of high importance for pastures (Tissiani et al. 2017). It frequents non-forested vegetation and anthropized environments from the south of the Amazon to the south of Uruguay (Tissiani et al. 2017). The other dweller species (two species of *Eurysternus*) were also more abundant in the rainy season. The occurrence of *T. externepunctatum* in forest sites only in the rainy season suggests a spatial displacement from open areas with high population density into forested areas to exploit new resources.

Eleven species were sampled only in the dry season, 26 species were sampled only in the rainy season, while only 14 occurred in both seasons. The high number of restricted species sampled only in the rainy season was also found in other studies in the Amazon (*e.g.*, Andrade et al. 2011; Cajaiba et al. 2017). Even though some species were restricted to the dry season, these species were mostly represented by few individuals. In terms of functional groups, 5 tunnellers, 4 rollers, and 2 dweller species had significant decreases in abundance in the forest sites from the rainy to the dry season. Rollers, especially large rollers together with large tunnelers, constitute the most important functional groups in regards to ecosystem service provisioning (Slade et al. 2007; Batilani-Filho and Hernández 2017; Frank et al. 2017), such as dung removal and/or seed dispersal (Nichols et al. 2008; Braga et al. 2013). Indeed, in the absence of large beetles, mainly large tunnelers, there is an approximate 75% reduction in dung removal (Slade et al. 2007), largely affecting the functional role of the assemblage. Thus, the seasonal decreasing of tunneler and roller dung beetles can considerably affect

the removal and incorporation of feces into the soil during the dry season. This scenario is also exacerbated due to the increasing the frequency and intensity of severe drought in Amazon rainforest (Marengo and Espinoza 2016; França et al. 2020a).

The small-bodied roller *Canthon triangularis* increased in abundance from the rainy to the dry season. This species has been found in small forest fragments of 1.0–10 ha, but also in continuous forests (Klein 1989; Andresen 2003; Silva et al. 2015) and pastures within the Amazon forest (Korasaki et al. 2012). This coprophagous species is widely distributed across the Amazon, inhabiting both dry and wet forests associated with floodplains and river border habitats (Vaz-de-Mello et al. 2014). The high occurrence of this species in the dry season within almost all forest sites seems to be associated to low competition. On the contrary, its absence within the forest could be associated with a highly competitive demand, with more species and individuals found in the rainy season. We hypothesized that this species can supply its trophic and sexual requirements both outside and inside the forest, depending on the season. For instance, da Silva et al. (2019) found a positive relationship between both matrix-tolerance dung beetle species' abundance and richness and canopy cover during winter and a negative relationship in summer. These authors stated that matrix-tolerance species may use forest islands as refuges during harsh climatic conditions and times of low resource availability in the open matrix. In our case, it seems that *C. triangularis*, a matrix-tolerant species, is able to inhabit forest fragments during the dry season due to low competition and is excluded from these fragments due to high competition in the rainy season, being able to occur in the open matrix.

We found that seasonality is quite important for dung beetles as a whole, and rainfall seasonality drives the temporal patterns of dung beetle diversity in the Amazonian forests in the study region in the arc of deforestation. The strong species and abundances-per-species losses from the rainy to the dry season has clear implications for the ecosystem services provided by dung beetles, such as dung burial and secondary seed dispersal (Andresen 2002; Nichols et al. 2008). Changes in the duration and severity of the dry season coupled with changes in land use can alter the animal cycles and occur both changes in abundance (decreased ecological functions) and species loss locally (Barlow et al. 2018; França et al. 2020b). Such changes can also contribute to more generalized species to become dominant and the relative importance of species associated exclusively with forest to decrease in terms of functions (da Silva et al. 2019). Given the current and future scenarios of increased dry seasons, droughts, and fires in the Amazon (Marengo and Espinoza 2016; Aragão et al. 2018; Barlow et al. 2020; Brando et al. 2019; França et al. 2020a,b), the effects on dung beetle functions could be severe.

Understanding species vulnerability to changes in climatic conditions could help to predict species distributions in the future. Thus, we used dung beetle response to seasonality aiming to provide examples of how species may respond to drastic climate conditions. This approach can be helpful to develop better conservation and management initiatives in an increased scenario of higher temperatures and longer drought periods during dry seasons in the near future. Finally, due to the temporal limitation of our study, we stress the need for further studies to better understand the dung beetle responses and better predict their response to the climate change scenario, especially in the Amazon (Marengo et al. 2018).

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