Title

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soil biodiversity and ecosystem function in a Neotropical savanna

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Abstract

Conserving the remaining savanna ecosystems in the Brazilian savanna (Cerrado) — a global biodiversity hotspot that stores carbon and provides water to a large portion of South America — requires understanding the ecological processes maintaining their function. Nutrient cycling supports savanna function via plant litter production and decomposition by soil fauna, releasing nutrients for plant and soil organism uptake. Soil biodiversity and biogeochemistry linkages with litter dynamics in Neotropical savannas under a changing climate are poorly understood. Here, we combined two years of rainfall seasonality, leaf and wood litter production and decomposition with soil epigeic fauna abundance — the number of ground-surface dwelling invertebrates collected through pitfall traps — taxa richness, Shannon's diversity and Pielou's evenness, and 16 soil biogeochemical variables measured in 12 plots of preserved savanna. Rainfall seasonality modulated the mean soil epigeic fauna diversity and evenness across all plots, which were highest in the rainy season, in contrast to litterfall rates, which peaked in the dry season. In the dry season (April to September), the Formicidae family was the most abundant with 50% of all individuals, while in the rainy season (October to March), the Isoptera order was the most abundant with approximately 39% of individuals. Wood litter decomposition grouped with annual Hemiptera abundance, co-varying with soil epigeic fauna diversity and evenness per plot and against soil fertility variables. Leaf litter decomposition co-varied with the total epigeic fauna abundance and soil pH. We speculate that the specific need to decompose wood litter may be associated with a greater need for diversity than an abundance of soil epigeic fauna. Our work highlights the role of rainfall seasonality on soil biodiversity and physicochemistry, which is also tightly linked with litter production and decomposition. This study advances our understanding of the mechanisms governing nutrient cycling in savanna ecosystems on nutrient-impoverished soils, with implications for achieving sustainable conservation and restoration goals.

Keywords: Biodiversity; Community ecology; Epigeic fauna; Nutrient cycling; Soil carbon; Soil ecology; Cerrado.

1. Introduction

The Brazilian savanna (Cerrado) is the second-largest biome in South America, covering nearly 21% (approximately 1.8 million km²) of Brazil's territory. As one of the world's hotspots for biodiversity conservation, the Cerrado has high species endemism, heterogeneity of landscapes, and faces rampant human threat (Morandi et al., 2018; Myers et al., 2000; Strassburg et al., 2020); between 2008 and 2012, annual deforestation rates were twice as those in the Brazilian Amazon (Lambin et al., 2013). Also, less than half of the original land covered by Cerrado ecosystems is still conserved (Zuin, 2020), which jeopardizes their role in the water and carbon cycles (Arantes et al., 2016; Brasil, 2018). Reducing greenhouse gas emissions by avoiding deforestation can provide a monetary incentive through REDD+ initiatives in Cerrado areas (Gallo and Albrecht, 2019).

Conserving, sustainably managing, and actively restoring native Cerrado ecosystems depend on understanding the ecological processes that maintain their function and ecosystem service provision

(Buisson et al., 2021; Morandi et al., 2018). A critical ecosystem process is litterfall, which is the main conduit for nutrient recycling in systems on highly-weathered, nutrient-poor soils covering 46% of the Cerrado (Djukic et al., 2018). For instance, litter production and decomposition explain over 3.6 tons of carbon uptake per hectare in Cerrado savanna ecosystems (*e.g.*, cerrado *sensu stricto*) (Park et al., 2020; Pompeo et al., 2016). Litterfall is highly seasonal in savanna ecosystems in the Cerrado, with the highest rates occurring at the end of the four-to-seven-month dry season (Bustamante et al., 2012). Nevertheless, several biotic and abiotic factors control litter dynamics, especially those related to ecosystem structure and composition, soil fertility, and climate variables such as rainfall, wind speed, and relative humidity (Ferreira and Uchiyama, 2015; Giweta, 2020). Thus, understanding the patterns of and controls on litterfall and its role in nutrient cycling in savanna ecosystems in the Cerrado is essential to restore and conserve those ecosystems in a changing climate.

Soil organisms are critical decomposers of senesced plant materials, converting litter nutrients into mineral nutrients incorporated into the soil solution and taken up by plants for growth and development (Garlet et al., 2019; Lavelle and Pashanasi, 1989; Pritchett, 1979). The edaphic organisms are composed of individuals that remain at least part of their life cycle in the soil (Swift et al., 1979). However, some of these emerge after the larval phases and become exclusively epigeic. Therefore, soil organism classifications are essential for the various ecological compartments and provision of essential ecosystem services such as organic matter decomposition.

In general, the soil fauna (meso and macrofauna) explains about 7% of litter decomposition through fragmentation (Wall et al., 2008), contributing to biological balance through microorganism consumption and food provision for other fauna groups. It is essential to investigate the ecological role of soil fauna diversity and abundance, which is also a useful environmental quality indicator (Rosa et al., 2015; Zagatto et al., 2017). Because so many processes are conducted and affected by these organisms — nutrient cycling, waste decomposition, soil aggregation, climate regulation, pathogen resistance — understanding these communities is essential for ecosystem conservation practices (Guerra et al., 2021). Still, little is known about soil epigeic fauna communities and their links with litter decomposition and how climate drivers and soil properties can alter litter production and decomposition rates, in turn affecting those soil communities in savanna ecosystems.

Litter decomposition rates are generally empirically estimated through decomposition bags, where the leaf fraction is stored and left in the field to measure the decay rate (Olson, 1963). This method is limited by not considering the decomposition rate of all litter fractions separately. A recent systematic review on Cerrado litter decomposition Inkotte et al., (2019) indicated a lack of studies quantifying wood decay rates in Cerrado ecosystems. However, fractions other than leaves, especially fine wood, can make up to 30–40% of the total plant material deposited on the soil (Correia and Andrade, 2008). This knowledge gap is concerning because quantifying fine wood decomposition rate is necessary to fully comprehend nutrient recycling patterns in Cerrado ecosystems on nutrient-poor soils.

Our main objective in this study was to investigate biodiversity-ecosystem function relationships in a Neotropical savanna ecosystem. We related soil epigeic fauna community metrics to litter production, leaf and wood litter decomposition, 16 soil biogeochemical variables, and their relationships with rainfall in central Brazil. Specifically, we aimed at answering the following questions: i) How are litterfall and soil epigeic fauna diversity, richness, abundance, and evenness affected by rainfall seasonality?; ii) Do leaf and wood litter decomposition rates differ?; and iii) Do leaf and wood decay rates correlate with soil epigeic fauna metrics and biogeochemistry? We hypothesized that: (H_1) Litterfall and soil epigeic fauna diversity and abundance vary seasonally, increasing during the rainy season; (H_2) Wood decomposition is slower than leaf decomposition; and that (H_3) Leaf litter decomposition correlates positively with soil epigeic fauna abundance, diversity, and soil fertility.

2. Methods

2.1 Study area

This study was conducted at the University of Brasilia's research station (Fazenda Água Limpa; 15°56'–15°59' S and 47°55'–47°58' W), which covers over 4.3 thousand hectares of Brazilian savanna. Located within UNESCO’s Cerrado Biosphere Reserve, about 86% of the research station is preserved, and 45% is covered by native savanna vegetation (dense savanna woodland) known as cerrado *sensu stricto* (Felfili et al., 2000). The region's climate is classified as AW, according to Köppen's classification (Köppen and Geiger, 1928), with well-defined dry (May to October) and rainy (November to April) seasons. The mean annual precipitation is 1,486 mm ± 146.8 mm, with monthly means ranging from 9 mm in June to 466 mm in December. Monthly mean temperatures range from 19ºC in June to 21.4ºC in December (Campos and Chaves, 2020). Soils at the research station are mainly deep Oxisols (Soil Survey Staff, 2010), Red Latosols (EMBRAPA classification system; Santos et al., 2018) or Rhodic Ferralsols (World Reference Base; Gardi et al., 2015) on flat terrain, characterized by high acidity and low nutrient (*e.g.*, phosphorus-P) availability (Haridasan, 2008).

Within approximately 1.929 ha of preserved cerrado *sensu stricto*, we randomly selected 12 20 m × 50 m plots following previously established protocols (Felfili et al., 2000), in a total of 1.2 hectares (Supplementary Fig. S1). In each plot, litterfall and soil samples were collected, soil epigeic fauna abundance, diversity, richness (number of taxa), and evenness were quantified, and litter decomposition rates were measured for two years between 2018 and 2020. On average, each plot contained a woody basal area of 13.11 m^2 ha^{-1}, approximately 156 woody individuals, and 36 woody species (Mota, 2017). To the best of our knowledge, only an accidental fire occurred in 2011 within the studied area, a typical disturbance in savanna ecosystems in the Cerrado.

2.2 Soil epigeic fauna sampling and biogeochemical measurements

We assessed soil epigeic fauna abundance and composition during the dry (September 2018) and rainy (January 2020) seasons. A total of sixty (five per plot) plastic pitfall traps containing approximately 200 ml of water and 10 ml of colorless neutral detergent — sensu Baretta et al., (2007)— were deployed near the decomposition bags (15-cm diameter; described in 2.4). All traps were left in the field for 48 hours, then collected and taken to the laboratory for manual separation of organisms using a 0.125-mesh sieve. All organisms were transferred to flasks containing absolute ethyl alcohol for fixation. Soil epigeic fauna organisms were identified at the highest possible taxonomic level (genera, order, or family whenever possible) using a magnifying lens and taxonomic keys. Individuals in the larval phase were designated as 'others,' as their identification was not possible. Our choice of collection method, similar to other studies (*e.g.*, (Vanolli et al., 2021), was due to most epigeic fauna groups are found in the litter-soil interface.

We collected four soil samples at three depths (0–20, 20–40, and 40–60 cm) per plot to quantify key soil biogeochemical variables and combined them in one sample per depth per plot. After the sampling, soils were air-dried in the shade and then analyzed according to EMBRAPA, (1998): Exchangeable aluminum (Al^{3+}) and potential acidity (H + Al) by titration. Phosphorus (P_{av}) and potassium (K) by Mehlich-1 extractor, where remaining P (P_{rem}) was determined using molecular absorption spectrophotometer as well as calcium (Ca^{2+}) and magnesium (Mg^{2+}), and K by photometer of flame. Soil organic matter (SOM) was determined by (Walkley and Black, 1934). For all samples, we calculated the total cation exchange capacity (CECt), effective cation exchange capacity (CECe), the sum of bases (SB), base saturation (V), and aluminum saturation (m). The studied soils are the typical nutrient-poor Oxisols in central Brazil (Haridasan, 2008). The low levels of exchangeable cations, especially Ca^{2+} and Mg^{2+}, reflected the soil's acidic nature, which negatively affected SB, CEC, and V. See Supplementary Table S1 for additional information.

2.3 Soil physical measurements and SOC stock calculation

We randomly selected three plots to sample soils every four months in randomly selected points where trenches of 40 cm × 40 cm × 100 cm (160 L) were opened. Soil samples were collected and measured following EMBRAPA, (2011) at the 0-20 and 20-40 cm depths using a volumetric steel ring (88.60 cm^3). Then, samples were transported to the laboratory to determine their wet weight and were then oven-dried at 105°C until constant weight. Volumetric moisture (m^3 m^{-3}), soil density (g cm^{-3}), gravimetric moisture (g cm^{-3}) content, and total porosity (kg dm^{-3})

Soil organic carbon (SOC) was calculated as soil organic matter concentration in g kg^{-1} divided by 1.724 (Walkley and Black, 1934). Soil C stock was calculated in Mg C ha^{-1} following Usuga et al., (2010): SOC stock = (SOC × BD × d)/10, where SOC is the concentration of soil organic carbon at a given soil depth in g C kg^{-1}, BD is bulk density in g cm^{-3}, and d is soil layer depth in cm (Table 1).

2.4 Litter decomposition rates

Leaf and wood decomposition rates were measured following Olson, (1963). Briefly, 20 g of each freshly deposited leaf and fine wood (< 1 cm diameter) litter fraction were collected on the soil surface of each plot (SFB, 2020) . Both leaf and wood litter were confined in 20 cm × 20 cm litter decomposition bags made with 2-mm mesh nylon. The collections were carried out with one litterbag per plot at 30, 60, 120, 240, 365 days after litter bags were randomly placed on the ground (between May 2018 and April 2019). As a result, a total of 120 litterbags (2 types × 5 sampling dates × 12 replicates) were used. After each litter bag collection, the remaining leaf and wood material was taken to the research station's laboratory. Then, roots and soil were removed from the litter materials using a brush, and litter mass was determined by weighing before and after oven drying at 65ºC until constant weight. Leaf and wood decomposition rates (k) were calculated by decay rates: Remaining mass (%) = (final mass - initial mass) × 100.

The decomposition rate *k* indicates the annual mass loss, while the half-life proposed by Olson, (1963) indicates the time required for 50% of the initial mass stored in the bags to decay. The half-life was calculated as: $X_t = X_0 \times e^{-kt}$, where X_t is the dry weight of the remaining litter after t days and X_0 is the dry weight of litter material at t = 0, and $T_{1/2} = \ln (2)/k$, where $T_{1/2}$ is the number of days needed to decay 50% of the initial mass, ln is the natural logarithm and *k* is the decomposition rate.

2.5 Monthly litterfall sampling and climate data compilation

Litterfall was collected monthly for two years (from May 2018 to April 2020) from two replicated baskets (50 cm × 50 cm) (Scoriza et al., 2012) randomly placed inside each of the 12 plots. All senesced plant material deposited monthly in each basket was carefully collected and placed in paper bags in a total of 576 samples (12 plots × 2 replications × 24 sampling dates). Litterfall samples were oven-dried at 65ºC until constant weight and immediately sorted into the following fractions: leaves, reproductive parts (*i.e.*, fruits, flowers, and seeds), fine wood (diameter < 1cm), and miscellaneous (unidentifiable plant material). Each fraction was weighed, and the relative contribution to monthly total litterfall rates was estimated by extrapolating the results to Mg ha^{-1} $month^{-1}$.

Rainfall rates were obtained from manual and automatic stations controlled by Brazil's National Meteorological Institute (INMET, n.d.) through daily observations. Because this variable may influence litter production and decomposition, and soil epigeic fauna composition, the data obtained were used as a predictive variable in this study.

2.6 Statistical Analysis

Calculations and graphical output were produced in R (version 3.6.2; R Core Team, 2019). We utilized package vegan to calculate: Shannon's diversity (h'; biodiversity function), taxa richness (S; the number of taxonomic groups using the specnumber function), Pielou's evenness index [J; $J = h'/\log(S)$], and total and relative abundances of soil epigeic fauna organisms per plot (Odum, 1969) for both dry and rainy seasons. T-tests compared the seasonal plot means of these community variables. Pearson's correlation coefficients were calculated to verify the relationships between soil epigeic fauna community variables, monthly total litterfall and leaf fall, and mean monthly rainfall during the dry and rainy seasons. Soil chemical properties were compared by analysis of variance (one-way ANOVA) and Tukey's HSD test after assessing normality using the Shapiro-Wilk test. When normality was not achieved after transformations, a Kruskal-Wallis test was used. The remaining mass of leaf and wood litter in the decomposition bags was compared by t-test. A 95% confidence level was considered in all statistical tests.

A Mantel test for spatial autocorrelation (mantel.rtest function in package ade4 with 999 permutations) was conducted on two distance matrices: One containing spatial distances among plots — latitude and longitude of each plot — and other containing distances among annual abundances of epigeic fauna (the sum of the dry and rainy season total abundances per plot). No spatial autocorrelation among plots was detected (r = 0.08, p-value = 0.30). We then conducted non-metric multidimensional scaling (NMDS) ordinations (metaMDS function in vegan package; Dixon, 2003) based on Bray-Curtis dissimilarity (vegdist function in vegan package) and standardized data (Legendre, 2008) to compare: i) the mean abundances of soil epigeic fauna groups per plot between seasons, and ii) the annual abundances of soil fauna groups among plots. Statistically significant differences in clustering by season were determined by permutational multivariate analysis of variance (PERMANOVA) calculated with the adonis2 function in vegan package. The soil epigeic fauna group vectors that were significant at the 95% confidence level (group scores obtained by the envfit function with 999 permutations) were plotted as arrows on the seasonal and annual NMDS ordinations.

A Principal Component Analysis (PCA) was conducted to ordinate the plots regarding the main drivers of variation in soil physicochemistry, epigeic fauna community variables, and litter decomposition, using the prcomp and ggbiplot functions and stats and ggbiplot packages. We included leaf and wood k rates after 720 days of the experiment to match the soil collections during both years of this study. We averaged the mean soil diversity and evenness per plot of both dry and rainy seasons and calculated the total abundance per plot (sum of both seasons) to avoid non-integer numbers and to represent the number of organisms counted per plot. Preliminary soil PCAs were run using standardized data matrices to select the critical variables for the final PCA. In the preliminary PCA, low (< 1.0) eigenvalues (Peña-Claros et al., 2012) were found for all parameters except leaf and wood k, pH, available P, H+Al, SB, CECe, SOM, SOC stock, and mean diversity, evenness and annual total abundance per plot — which were included in the final PCA. Finally, we plotted the final soil variables significant at the 95% confidence level (group scores from function envfit with 999 permutations) as arrows into the annual NMDS ordination to verify the relationships (annual scale) among soil epigeic fauna groups with soil chemistry and litter decomposition rates using R package ggplot2 (Wickham, 2016). All data utilized in this study can be retrieved at DOI:10.17632/zvs4xm845b.1

3. Results

3.1 Seasonal variation in soil epigeic fauna abundance and diversity

We found marked seasonal differences in the mean epigeic fauna Shannon's diversity and Pielou's evenness per plot (t-test; $p < 0.05$), but not in total abundance or taxonomic group richness (Fig. 1). Across all 12 plots, Shannon's diversity was highest in the rainy season, with values ranging from 0.78 to 1.753 and a plot average of 1.41, representing 15 taxonomic groups across all plots. Taxa richness per plot ranged from 7 to 11, with a mean value of 9 taxa per plot. Pielou's evenness, indicating the uniformity of soil epigeic fauna, ranged from 0.84 to 0.34 with a plot average of 0.66. In the dry season, diversity ranged from 0.37 to 2.12, with a plot average of 1.01, representing a total of 23 orders and classes. Taxa richness per plot ranged from 5 to 17, with an average of 10 taxa per plot. Pielou's evenness ranged from 0.17 to 0.75 with a plot average of 0.44.

We counted 5,140 individuals of soil epigeic fauna in all 12 plots in the rainy season, averaging 428 per plot. Isoptera was the most abundant order with 2,021 individuals, followed by Collembola and the Formicidae family, with 995 and 819 individuals, respectively (Fig. 2a). During the dry season, we counted 4,763 soil epigeic fauna individuals, averaging 397 per plot. Overall, the Formicidae family was the most abundant taxonomic group in our study, with 2,377 individuals, followed by Isoptera with 1907 and Araneidae with 363 individuals (Fig. 2b).

3.2 Correlations among rainfall, soil epigeic fauna and litterfall

Mean monthly rainfall correlated positively with Shannon's diversity (Pearson's $r = 0.47$; $p < 0.05$) and Pielou's evenness (Pearson's $r = 0.55$; $p < 0.05$; Fig. 3). Rainfall correlated ($p < 0.05$) negatively with mean monthly leaf fall (Pearson's $r = -0.88$; $p < 0.05$) and total litterfall rates (Pearson's $r = -0.84$; $p < 0.05$).

In the first year (2018-2019), the total annual litterfall was 2.72 Mg ha^{-1}, where 81.5% were composed of leaves, 7.1% fine wood, 9.4% reproductive material, and 1.4% miscellaneous (*i.e.*, non-identifiable plant material). In the second year (2019-2020), the total annual litterfall was 3.09 Mg ha^{-1}, where 83.9% were leaves, 9% fine wood, 6.1% reproductive parts, and 0.9% miscellaneous (Supplementary Fig. S2).

3.3 Leaf and wood decomposition rates

Leaf and wood litter decomposition rates (k) were statistically similar (t-test), with mean annual k rates of 0.006 for all plots for both fractions (Fig. 4). Regarding litter half-life, leaf litter would lose 50% of the initial mass after 531 days and wood litter after 495 days of exposure. Comparing the remaining mass of both litter fractions during the whole study (five samplings), we did not find a significant difference between leaf and fine-wood k rates ($p = 0.15$).

However, we observed different temporal patterns in leaf and wood decomposition. Leaf decomposition was highest after 30 days of exposure when 8.7% of the initial mass had decayed (approximately 1.74g). In contrast, wood litter presented the highest decomposition after 120 days, decomposing approximately 1.51 and 1.60g on 240 and 365 days, respectively. During the dry season (from May to August – 30 to 120 days exposure), leaf and wood litter decomposition remained almost inactive, decomposing only 0.97% and 2.2%, respectively.

3.4 Relationships between litter decomposition and soil epigeic fauna and physicochemistry

The NMDS of plot-level soil epigeic fauna abundances showed a significant distinction among the dry and rainy seasons (Fig. 5a), where season significantly explained 33% of the variance in epigeic fauna abundance (PERMANOVA, $p = 0.001$; Supplementary Table S2). We noted that Hemiptera and Collembola groups and epigeic fauna evenness and diversity were strongly associated with rainy season collections (Fig. 5b). By contrast, Formicidae, total litterfall and leaf fall were more associated with dry season sampling, and Isoptera was closely associated with the total abundance of epigeic fauna per plot.

A PCA of litter decomposition and soil epigeic fauna and physicochemical variables explained 66.4% of the total variance in the first two principal components: PC1 explained 47.4%, and PC2 explained 19% of the variation (Fig. 5c; Supplementary Table S2). PC1 included soil fertility variables co-varying in the opposite direction relative to fine wood decomposition and Shannon's diversity, and Pielou's evenness. PC2 included the highest rates of leaf litter decomposition positively associated with soil pH and epigeic fauna abundance. Out of these soil and litter variables included in the PCA, wood decomposition was strongly associated with Hemiptera, while Isoptera, the most abundant group in the rainy season, was associated with epigeic fauna abundance (Fig. 5d).

4. Discussion

4.1 Seasonal variation in soil epigeic fauna diversity and abundance

Our results suggest that soil epigeic fauna diversity and evenness, but not abundance and taxa richness, are positively influenced by rainfall and soil water content in the studied savanna ecosystem. We expected rainfall seasonality to influence soil epigeic fauna diversity and abundance because these are generally related to soil type, climate, and vegetation (Lavelle and Pashanasi, 1989; Pinheiro et al., 2002; Santos et al., 2020), although studies in the Cerrado are scarce. Apart from soil water content, soil temperature — not measured in this study — regulates soil fauna, determining its spatial and temporal patterns (Lavelle and Spain, 2001). Our results make sense because while heavy rainfall events can cause physical damage during flight, reduce foraging efficiency, and increase migration, dry periods can lead to the desiccation of invertebrates that live at the soil-litter interface and decrease egg and larvae viability and survival (Torode et al., 2016).

Although our dry season collections presented a non-significantly higher number of soil epigeic fauna taxa, the mean Shannon's diversity and Pielou's evenness across all plots were highest during the rainy season. This finding may be explained by the fact that Shannon's diversity index considers richness and the degree of evenness in species abundances, assigning equal weights to rare and abundant species. Still, season significantly explained 33% of the variance in epigeic fauna composition.

Differences in soil epigeic fauna diversity and evenness among dry and rainy seasons make sense, given that certain groups, like Collembola, significantly increase in abundance during the rainy season due to sensitivity to low soil water content (Holmstrup, 2019). We noted that Hemiptera followed this same trend. Although comparisons with other studies in natural savanna ecosystems were not possible, Cajaíba and Silva (2017) reported that the family Cydnidae (Insecta: Hemiptera: Heteroptera) was more abundant during rainy seasons in agricultural, native forest, and cattle pasture land-use types in northern Brazil.

Formicidae, Isoptera, Araneidae, and Collembola were the most abundant soil epigeic fauna groups in the studied savanna. This finding corroborates Benito et al. (2004) in a similar savanna ecosystem but using a different methodology; in their study, soil samples were removed, and all macroinvertebrates were collected. By contrast, Pinheiro et al. (2002) found that Coleoptera, Hymenoptera, Diptera, and Isoptera were the most abundant groups in a similar savanna in the Cerrado. These authors used a combined trap method (*i.e.*, pitfall, malaise tent, and window trap), possibly explaining the differences.

Formicidae is generally reported as the most abundant group in soil fauna studies (Lima et al., 2020; Nunes et al., 2021) due to its crucial role in litter fragmentation and organic material incorporation into the soil (Tavares et al., 2020). Nunes et al. (2021) related the Formicidae dominance in the dry season due to its high mobility. Besides, soil ants become unsheltered in long rainy periods, and an increase in soil water favors the development of some fungi species that prey on Formicidae eggs, putting all ants' offspring at risk (Martins et al., 2020).

Studies on soil fauna in the Cerrado are still scarce, especially in natural ecosystems. The few existing studies were primarily conducted in silvopasture and pasture systems (Marchão et al., 2009; Portilho et al., 2011; Silveira et al., 2016; Vendrame et al., 2009). Because soil fauna embraces one-quarter of all species on Earth and provides a wide variety of functions (e.g., nutrient cycling, waste decomposition, climate regulation, pathogen resistance), it regulates aboveground diversity and functioning. Because soil fauna influence extends to human well-being, soil biodiversity and its ecosystem functions require explicit consideration when establishing nature protection priorities and policies to design new conservation areas (Guerra et al., 2021). The scarcity of studies in the Cerrado represents a major gap in soil biodiversity knowledge and reinforces the need for future studies surveying soil fauna, especially in areas covered by native savanna vegetation undergoing chronic environmental alterations.

4.2 Relationships between litterfall and soil epigeic fauna

We found an association between leaf fall and the Formicidae group, both high in the dry season. We believe that this relates to Formicidae's high mobility and that several species in this family inhabit the leaf litter layer (Bomfim et al., 2020; Nunes et al., 2021). Also, these authors found that most ant species live in the leaf litter, and only a small part of the species lives in the twigs litter.

Our findings corroborate the notion that litterfall patterns in savannas are strongly influenced by climate variables (Giweta, 2020), especially those linked to water (Ferreira and Uchiyama, 2015). Regarding the implications of water availability to plant phenology and litter production, Giweta (2020) found that plant water consumption is related to air temperature and relative humidity, affecting plant growth, development, and health status. Consequently, plant water availability strongly influences fine litter production by savanna plant species.

The Cerrado ecoregion is characterized by well-defined dry and rainy seasons, reflecting the observed well-defined seasonal litterfall peaks. Fine litter production was highest during drier months (May to September) when plants are water-stressed. This litter deposition pattern in Cerrado ecosystems can be a strategy to consume less water in dry seasons and maintain soil water content, as litter deposited on soil decreases plant transpiration surface (Moraes and Prado, 1998). Considering litterfall plays such an essential role in nutrient cycling by providing a means of supplying nutrients to the soil and serving as a niche and food for soil fauna (Giweta, 2020), global climatic changes can alter nutrient cycles in Brazilian Cerrado ecosystems.

4.3 Litter decay relates to soil epigeic fauna and chemistry

We expected leaf and wood decay rates to differ because of their contrasting chemical compositions, especially lignin content (Hall et al., 2020). By contrast, leaf and wood litter decay rates were statistically similar and very low, as fast decomposition rates usually fall between 1.0 and 4.0 (Olson, 1963). Miatto and Batalha (2016) found similar low decomposition rates (k between 0.004 and 0.043) in a savanna ecosystem in southeastern Brazil. These authors reported that litter chemistry reflected an extreme leaf economic spectrum, showing a conservative strategy with low nutrient concentrations; this could explain the similar leaf and wood litter decomposition rates, as lignin-to-nitrogen ratios highly influence decomposition. Litter decomposition rates in Cerrado soils are generally considered slow, with a half-life time greater than one year, which corroborates our findings (Bustamante et al., 2012).

While litter decomposition is a multi-factorial, cascade process that is not usually continuous (Lavelle et al., 1993), the observed low decomposition rates can generally relate to the typical rainfall seasonality and soil acidity in typical savanna ecosystems in the Cerrado. Litter decomposition correlates strongly with temperature and humidity (Lavelle et al., 1993; Wall et al., 2008) as both climate variables control soil fauna activity and, consequently, decomposition rates. We observed that litter decomposition presented a strong seasonal trend, occurring more intensively in the rainy season. This pattern corroborates studies reporting that litter decay can be three to seven times faster in rainy than in dry seasons (Peña-Peña and Irmler, 2016; Ribeiro et al., 2018).

Regarding litter decomposition association with soil epigeic fauna groups, we noted a strong association between wood litter decay and Hemiptera order abundance. The phytophagous habits of some species could explain this trend in this order that feeds on litter (Capinera, 2008). According to Goldman et al. (2020), several tropical Hemipterans are commonly found in litter, which corroborates our findings.

The PCA indicated that wood litter decay rate grouped with soil epigeic fauna diversity and evenness per plot, in opposed quadrants to soil fertility variables like SOM, SOC stock, and P availability (Fig. 5). On the other hand, leaf litter decay rate co-varied with epigeic fauna abundance and soil pH. These results may align with each soil fauna guild's specific nutrition needs (Primavesi, 1981) and the generally higher levels of lignin and recalcitrant compounds in fine wood than leaf litter. Lignin, the most complex organic compound to decompose, is broken down by a few specific organisms (Tan et al., 2020).

Therefore, we speculate that the specific need to decompose wood litter may be associated with a greater need for diversity than an abundance of soil epigeic fauna, even though both epigeic fauna diversity and Hemiptera abundance increased with rainfall in our study.

In the studied savanna, soil pH related strongly with leaf decomposition and epigeic fauna abundance. Soil pH is known to affect soil fauna activity, showing a negative correlation with the abundance of Cerrado macrofauna groups (Franco et al., 2016). This pattern can be associated with the soil epigeic fauna spatial distribution (Giweta, 2020) that leads to a slow litter decay, promoting an increase in soil organic matter and C stocks (Primavesi, 1981). Leaf litter decay is a crucial nutrient cycling process linked with soil solution P in highly-weathered soils — such as those in the studied savanna — due to strong P adsorption on soil mineral colloids (Novais et al., 2007). Savanna ecosystems in the Cerrado present low shade, soil moisture content, and available P concentration in the topsoil (Jacobson and Bustamante, 2014). Our findings indicate that key soil physicochemical variables and soil epigeic fauna diversity and abundance were strongly related to litter decomposition in the studied savanna ecosystem in the Cerrado. Therefore, the soil-plant-atmosphere interactions that promote function and ecosystem service provision in savanna ecosystems may be threatened by conversion to agriculture and mining and climate change.

5. Conclusions

In the studied Neotropical savanna, we found strong linkages between rainfall seasonality, litterfall rates, and the mean soil epigeic fauna diversity and evenness. Certain soil epigeic fauna groups, like Hemiptera and Collembola, were more related to the rainy season collections, while Formicidae was more associated with the dry season collections. Contrary to our expectation, leaf and wood litter decomposition rates were very similar, with wood decay rates positively associated with Hemiptera abundance and soil epigeic fauna diversity. Altogether, our findings highlight the close links between soils and vegetation, which are key ecosystem components influenced by climatic conditions. Future climatic changes, including longer dry season lengths, may directly affect the observed seasonal shifts in soil biodiversity and key nutrient cycling processes in Neotropical savanna ecosystems.

Our study was a pioneer in quantifying fine wood litter decomposition rates in savannas in the Cerrado and relating it to soil epigeic fauna composition and diversity. Additional studies in tropical savanna ecosystems are encouraged to further our understanding of decay patterns of litter fractions other than leaves and fine wood and the role of species composition on litter decomposition and nutrient cycling in tropical savannas. We especially encourage long-term studies linking soil epigeic fauna and topsoil parameters in the Cerrado, a conservation hotspot due to high ecological importance and rampant human threat.

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Fig. 1. Seasonal variation in the soil epigeic fauna community in 12 plots of typical Brazilian savanna (cerrado *sensu stricto*) in central Brazil. **(a)** Total soil epigeic fauna abundance (total number of individuals per plot). **(b)** Shannon's diversity and **(c)** Pielou's evenness means per plot. **(d)** Total number of taxonomic groups. In each box, the middle band is the median value of 12 plots, and the top and bottom of the box are the first and third quartiles, respectively. Whiskers indicate the maximum and minimum values. Points outside the whiskers range are outliers. One asterisk denotes a significant difference between seasons at the 95% confidence level, two asterisks indicate difference at the 99% confidence level, and 'ns' denotes no significant difference by t-tests.

Fig. 2. Soil epigeic fauna abundance (x-axes) per taxonomic group (y-axes) in **(a)** the rainy and **(b)** dry seasons in a typical savanna ecosystem in central Brazil. 'Others' indicate individuals in the larval phase, as their identification was not possible.

Fig. 3. Pearson's correlation coefficients (r) among rainfall, litter production and decomposition rates, and soil epigeic fauna community variables measured in a typical savanna ecosystem in central Brazil. Crossed squares indicate non-significance at the 95% confidence level.

Fig. 4. Leaf and fine wood decomposition rates during 365 days of the experiment in the studied savanna in Central Brazil.

Fig. 5. **(a)** Seasonal NMDS clustering of soil epigeic fauna communities. The stress value of the ordination is indicated. Ellipses indicate the 95% confidence interval of the group centroids. Each point

indicates a plot, in a total of 12 for each season, where squares represent the dry and triangles the rainy season. **(b)** Seasonal NMDS including the soil epigeic fauna taxa and community metrics, litterfall and rainfall vectors significant at the 95% confidence level. **(c)** Principal component analysis (PCA) of annual soil epigeic fauna abundance, Shannon's diversity and Pielou's evenness, leaf and wood decomposition rates (k at 720 days), soil organic matter (SOM in dag kg^{-1}), sum of bases (SB in cmolc dm^{-3}), effective cation exchange (CECe in cmolc dm^{-3}), potential acidity (H+Al in cmolc dm^{-3}), available phosphorus (P_{av} in mg dm^{-3}) and pH. Each point represents the plot averages of these variables in a total of 12 plots. PC1 (x-axis) explained 47.4%, and PC2 (y-axis) explained 19% of the total variance in the soil and litter data. **(d)** Annual NMDS including soil epigeic fauna taxa (total abundance per plot) and the variables from (c) significant at the 95% confidence level. The stress value of the ordination is indicated. The statistical results of the NMDS's and PCA are listed in Supplementary Table S2.

Table 1. Soil physical variables and carbon stocks measured in the studied savanna.

Depth (cm)	**Bulk density (kg dm^{-3})**	**Gravimetric moisture (g cm^{-3})**	**Volumetric moisture (m^3 m^{-3})**	**Total porosity (kg dm^{-3})**	**SOC stock (Mg ha^{-1})**
0–20	0.85	34.04	29.12	67.77	48.9
s.e.	0.01	1.97	2.30	1.50	1.33
20–40	0.96	32.36	30.93	63.67	39.36
s.e.	0.02	1.39	1.34	0.71	1.44

Note: s.e. = standard error.

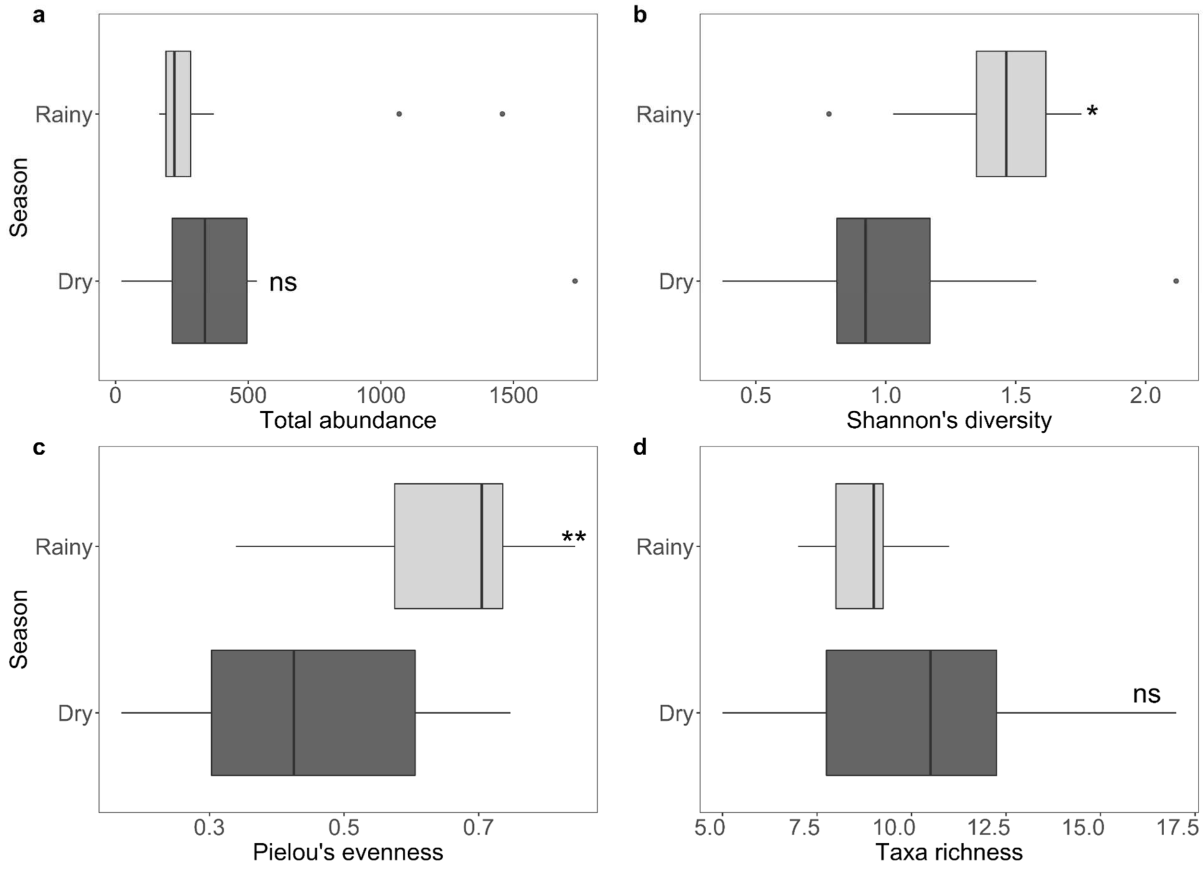
a
Season
Rainy
Dry
ns
0
500
1000
1500
Total abundance
b
Rainy
Dry
*
0.5
1.0
1.5
2.0
Shannon's diversity
c
Season
Rainy
Dry
**
0.3
0.5
0.7
Pielou's evenness
d
Rainy
Dry
ns
5.0
7.5
10.0
12.5
15.0
17.5
Taxa richness

Fig. 1.

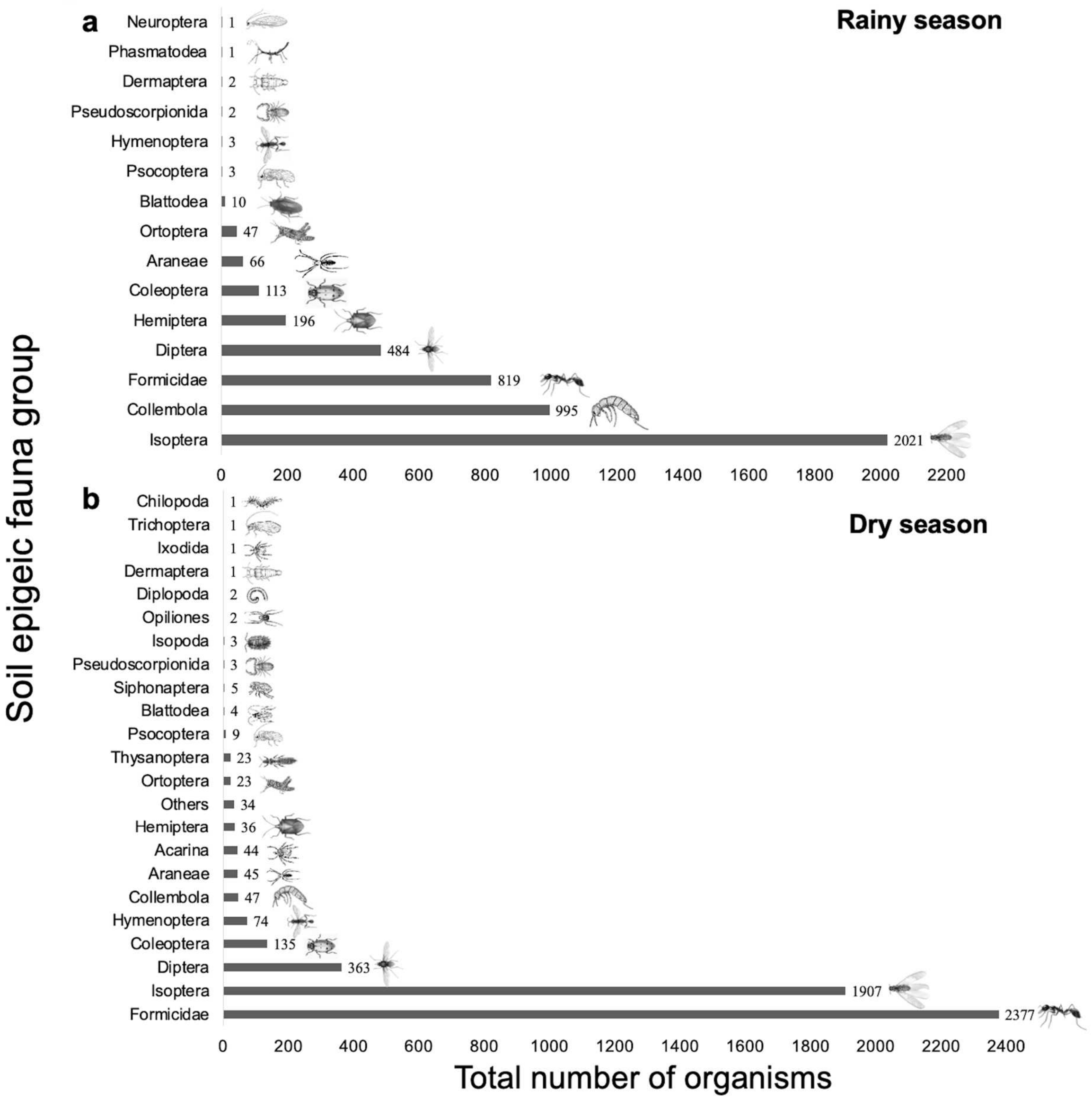
a
Rainy season
Neuroptera 1
Phasmatodea 1
Dermaptera 2
Pseudoscorpionida 2
Hymenoptera 3
Psocoptera 3
Blattodea 10
Ortoptera 47
Araneae 66
Coleoptera 113
Hemiptera 196
Diptera 484
Formicidae 819
Collembola 995
Isoptera 2021
0 200 400 600 800 1000 1200 1400 1600 1800 2000 2200
b
Dry season
Chilopoda 1
Trichoptera 1
Ixodida 1
Dermaptera 1
Diplopoda 2
Opiliones 2
Isopoda 3
Pseudoscorpionida 3
Siphonaptera 5
Blattodea 4
Psocoptera 9
Thysanoptera 23
Ortoptera 23
Others 34
Hemiptera 36
Acarina 44
Araneae 45
Collembola 47
Hymenoptera 74
Coleoptera 135
Diptera 363
Isoptera 1907
Formicidae 2377
0 200 400 600 800 1000 1200 1400 1600 1800 2000 2200 2400
Soil epigeic fauna group
Total number of organisms

Fig. 2.

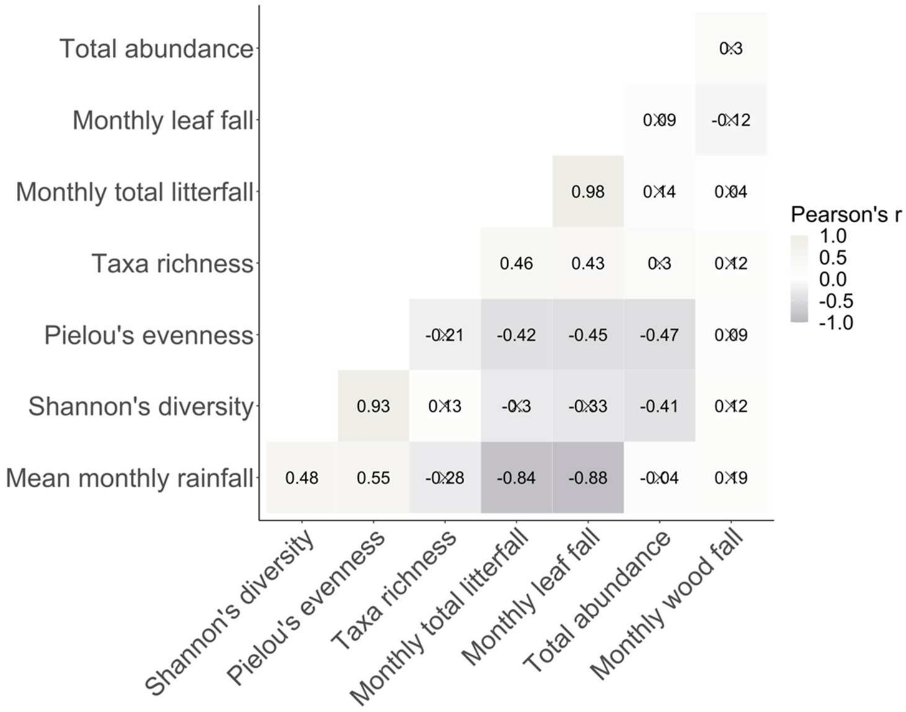
Total abundance
Monthly leaf fall
Monthly total litterfall
Taxa richness
Pielou's evenness
Shannon's diversity
Mean monthly rainfall
Shannon's diversity
Pielou's evenness
Taxa richness
Monthly total litterfall
Monthly leaf fall
Total abundance
Monthly wood fall
Pearson's r
1.0
0.5
0.0
-0.5
-1.0
0.3
0.09
-0.12
0.98
0.14
0.04
0.46
0.43
0.3
0.12
-0.21
-0.42
-0.45
-0.47
0.09
0.93
0.13
-0.3
-0.33
-0.41
0.12
0.48
0.55
-0.28
-0.84
-0.88
-0.04
0.19

Fig. 3.

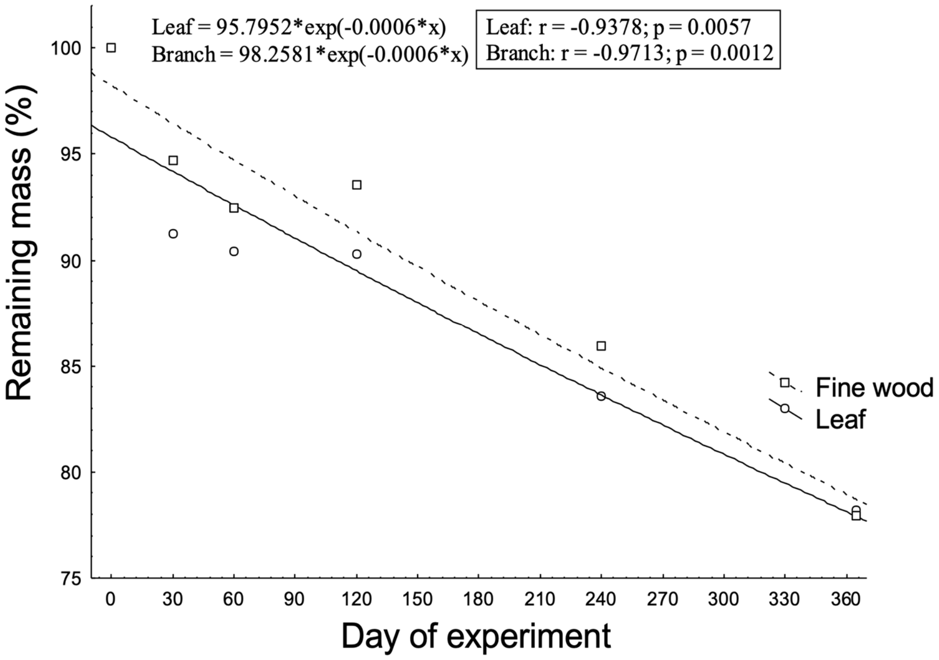
Leaf = 95.7952*exp(-0.0006*x)
Branch = 98.2581*exp(-0.0006*x)
Leaf: r = -0.9378; p = 0.0057
Branch: r = -0.9713; p = 0.0012
Remaining mass (%)
100
95
90
85
80
75
0
30
60
90
120
150
180
210
240
270
300
330
360
Day of experiment
Fine wood
Leaf

Fig. 4.

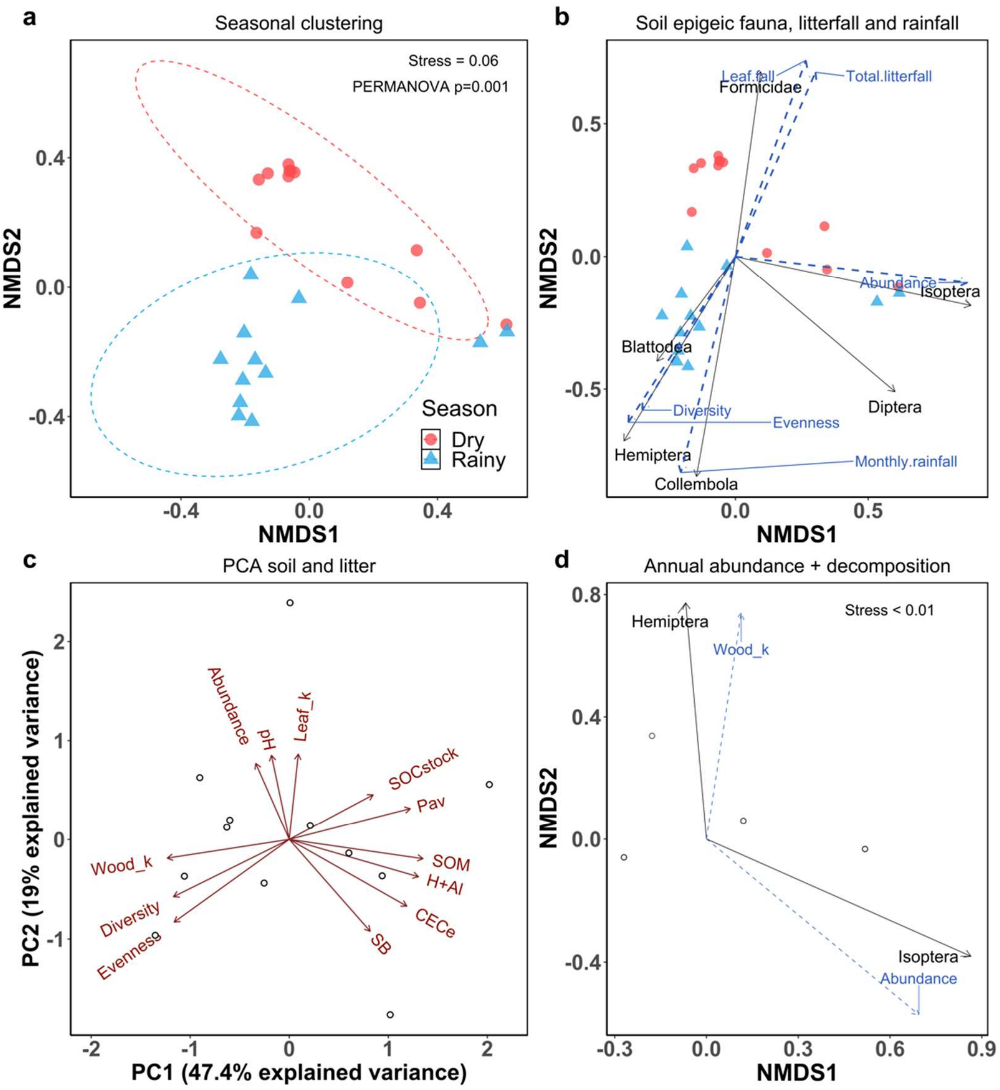
a
Seasonal clustering
Stress = 0.06
PERMANOVA p=0.001
NMDS2
NMDS1
0.4
0.0
-0.4
Season
Dry
Rainy
b
Soil epigeic fauna, litterfall and rainfall
Leaf.fall
Total.litterfall
Formicidae
Abundance
Isoptera
Blattodea
Diptera
Diversity
Evenness
Hemiptera
Monthly.rainfall
Collembola
0.5
0.0
-0.5
c
PCA soil and litter
Abundance
pH
Leaf_k
SOCstock
Pav
SOM
H+Al
CECe
SB
Wood_k
Diversity
Evenness
PC2 (19% explained variance)
PC1 (47.4% explained variance)
2
1
0
-1
-2
d
Annual abundance + decomposition
Stress < 0.01
Hemiptera
Wood_k
Isoptera
Abundance
0.8
0.4
0.0
-0.4
-0.3
0.3
0.6
0.9

Fig. 5.

Highlights

- Rainfall seasonality modulates soil epigeic fauna composition in a Brazilian savanna.
- Wood and leaf litter decomposition rates are statistically similar and very low.
- Soil epigeic fauna diversity positively relates to wood litter decomposition.