

Community structure of dung beetles in Amazonian savannas: role of fire disturbance, vegetation and landscape structure

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Abstract Understanding the relative influence of environmental and spatial variables in driving variation in species diversity and composition is an important and growing area of ecological research. We examined how fire, local vegetation structure and landscape configuration interact to influence dung beetle communities in Amazonian savannas, using both hierarchical partitioning and variance partitioning techniques to quantify independent effects. We captured a total of 3,334 dung beetles from 15 species

at 22 savanna plots in 2003. The species accumulation curve was close to reaching an asymptote at a regional scale, but curves were variable at the plot level where total abundance ranged from 17 to 410 individuals. Most plots were dominated by just three species that accounted for 87.7% of all individuals sampled. Hierarchical partitioning revealed the strong independent and positive effect of percentage forest cover in the surrounding landscape on total dung beetle abundance and species richness, and richness of uncommon species and the tunneler guild. Forest cover also had a negative effect on community evenness. None of the variables that related to fire affected community metrics. The minimal direct influence of fire was supported by variance partitioning: partialling out the influence of spatial position and vegetation removed all of the individual explanation attributable to fire, whereas 8% of the variance was explained by vegetation and 28% was explained by spatial variables (when partialling out effects of the other two variables). Space-fire and vegetation-fire joint effects explained 14 and 10% of the dung beetle community variability, respectively. These results suggest that much of the variation in dung beetle assemblages in savannas can be attributed to the spatial location of sites, forest cover (which increased the occurrence of uncommon species), and the indirect effects of fires on vegetation (that was also dependent on spatial location). Our study also highlights the utility of partitioning techniques for examining the importance of environment variables

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such as fire that can be strongly influenced by spatial location.

Keywords Tropical ecosystem · Partial redundancy analysis · Hierarchical partitioning · Spatial variation · Beta diversity

Introduction

Understanding the relative influence of environmental and spatial variables in driving variation in species diversity is an important and growing area of ecological research (Jones et al. 2008). In particular, scientific interest in the importance of landscape-level patterns and the ecological processes that generate spatial variation in species diversity has increased considerably during the last decade (Legendre et al. 2004; Arias-Gonzalez et al. 2008). The role of fires is an integral part of this understanding as fires affect the temporal and spatial dynamics of tropical ecosystems (Bond et al. 2004), including savannas (Sanaiotti and Magnusson 1995) and more seasonal humid tropical forests (Barlow and Peres 2006). By changing vegetation structure, fires can induce cascading effects that alter animal populations and the structure and function of the landscape itself (Lindenmayer et al. 2008).

We examine how fire, local vegetation structure and landscape configuration interact to influence dung beetle communities in Amazonian savannas. These savannas probably originated during the Pleistocene period, following expansion and retraction cycles of the Amazon Forest and Cerrado (Brazilian savannas; Ab'Saber 1982; Bigarella and Andrade-Lima 1982; Behling 2001). The isolated vegetation patches cover ~150,000 km² of the Amazon region (Pires 1973) and are species-poor when compared to savannas of the Cerrado (Eiten 1978). The percentage cover of bare ground, trees, shrubs, and grasses is highly variable in Amazonian savannas (Magnusson et al. 2008) and often related to the frequency and intensity of fires (Sanaiotti et al. 2002). However, the effect of this variation in fire frequency and vegetation structure on distribution and abundance of savanna insect communities is poorly understood. These interactions are important for conservation and habitat management as these savannas are increasingly used for agriculture, often resulting in an increased incidence of fire in

remaining areas of native vegetation (Sanaiotti and Magnusson 1995).

We focus on dung beetles (Coleoptera: Scarabaeinae), which are broadly distributed across the tropics (Hanski and Cambefort 1991). Many species feed on vertebrate dung and influence a diverse array of ecological processes including secondary seed dispersal, control of detritus-feeding flies and intestinal parasites, mixing of organic matter in the soil and nutrient cycling (see Nichols et al. 2008). Furthermore, most species can be assigned to broad functional groups based on their food relocation strategies (Halffter and Edmonds 1982). Rollers (or telecoprids) construct balls that they roll apart from the original food source (dung or carcass). Tunnelers (or paracoprids) dig tunnels directly beneath the food source from where they relocate food for feeding and reproduction. Dwellers (or endocoprids) live and reproduce inside or immediately beneath the food source and rarely construct nests.

Savannas of South America support relatively diverse (15–50 species) dung beetle communities (Milhomem et al. 2003), but little is known about the dung beetles communities associated with isolated savanna patches within the Amazon forest (Matavelli and Louzada 2008), or what factors influence the structure and dynamics of those communities. Vegetation structure is a good predictor of the distribution and abundance of dung beetles in both temperate and tropical habitats (Davis et al. 2003; Menendez and Gutierrez 2004; Andresen 2005). Vegetation can affect dung beetles directly by acting as a regulator of microclimatic conditions (Menendez and Gutierrez 2004), or indirectly by changing the vertebrate fauna and affecting the availability of faecal resources for dung beetles (e.g., Williams et al. 2002; Nichols et al. 2009). Dung beetles are also sensitive to changes in landscape structure, and the flux of individuals between neighbouring sites can be interrupted when habitat changes are imposed by human activities (Estrada and Coates-Estrada 2002; Halffter and Arellano 2002; Vieira et al. 2008). Finally, dung beetles from different functional groups may respond to changes in vegetation structure in different ways, as habitat openness can directly increase the desiccation rate of dung pats and nest balls, potentially restricting the rollers and dwellers to more shaded areas (Halffter and Edmonds 1982; Hanski and Cambefort 1991).

We examined dung beetle community structure in patches of Amazonian savanna by quantifying the

explanatory role of environmental and spatial variables. Specifically, we investigated to what extent vegetation, fire and spatial location can explain the structure and diversity of these dung beetle communities by using hierarchical partitioning and variance partitioning techniques. Although the lack of background information on these tropical savannas makes it difficult to construct biologically meaningful a priori hypotheses, we developed the study around the general hypothesis that fire would affect the dung beetle community through imposing changes in vegetation structure, but would have little or no additional direct effect on the species composition or community properties. We test this idea using a variety of community metrics including abundance, species richness, evenness, and functional guilds, as these measures can respond to environmental gradients in different ways (Escobar et al. 2007; Vieira et al. 2008).

Materials and methods

Study area

This study was undertaken in a 16 × 16 km landscape of semi-deciduous forest and savanna patches that surrounds the village of Alter do Chão, on the eastern bank of the Tapajós River, 35 km southwest of the city of Santarém, in the Brazilian Amazon (2°30'S; 54°57'W; Fig. 1). The mean annual temperature in Santarém is 27.5°C, and annual precipitation averages 2,215 mm (INFRAERO reports 1984–2002). A pronounced dry season occurs during August, September and October, when monthly precipitation is <65 mm on average (INFRAERO reports 1984–2002, see Barlow and Peres 2006). The savannas of Alter do Chão are structurally and floristically similar to the Cerrado vegetation of Central Brazil, and harbour a rich assemblage of trees and bushes that form islands in the grassland (Magnusson et al. 2008). The incidence of fires in these savannas is particularly high towards the end of the dry season, often burning 70–80% of the savannas.

Dung beetle sampling

We used 22 plots established in 1997 as part of a long-term study of savanna dynamics coordinated by INPA—Instituto Nacional de Pesquisas da Amazônia (Magnusson et al. 2008). Plots were distributed across

the existing savanna patches (Fig. 1) and sampled during the transition between the wet and dry season of 2003 (June–July). For our analysis, we considered each plot as a replicate. Each sample plot was 3.75 ha and included four parallel line-transects, 250-m long each and separated by 50 m. Dung beetles were sampled using pitfall traps baited with cow dung, human faeces, or carrion. Each trap was left in the field for 48 h. Each transect had six sample points (spaced 50 m apart) for a total of 24 sampling points per plot. At each sampling point, we placed three traps (spaced 0.5 m apart) in an array with one trap per bait type. Hence, each plot was sampled by a total of 72 traps. The pitfall traps consisted of plastic containers (diameter 15 cm, height 10 cm) with an inner receptacle containing the bait. Dung beetles attracted by the bait fell into a 5% detergent solution.

Dung beetles were sorted, mounted, assigned to a functional guild (tunneler or roller), and identified to genus and species level using identification keys and the taxonomic support of Dr. Fernando Zagury Vaz de Mello (FZVM). When species identification was not possible, we sorted beetles into morphospecies according to their external morphology. Voucher specimens were deposited at the Entomological Collection of Universidade Federal de Lavras (UFLA) and in FZVM's personal collection (Universidade Federal de Mato Grosso).

Environmental variables

Vegetation parameters in each plot were sampled in the wet season of 2003. We used the point-quadrat method to measure cover by each of the following vegetation strata: large (>2 m tall) trees (TRE), small trees and shrubs (<2 m tall) (SHR), and both tall (mostly *Trachypogon plumosus*) and short grasses (mostly *Paspalum carinatum*) (GRA). We spaced the sampling points at 2-m intervals along transects for a total of 500 points per plot. Details on these vegetation measurements are provided by Magnusson et al. (2008).

The landscape was classified in a GIS using a semi-supervised (non-automatic) classification of a 2003 Landsat 7 (30-m pixel) satellite image. In each plot, we calculated the percentage of forest cover within three buffers (150, 300 and 450 m). Because of colinearity, we retained the 450-m buffer (FOR) as a proxy of the forest influence on the savanna plot.

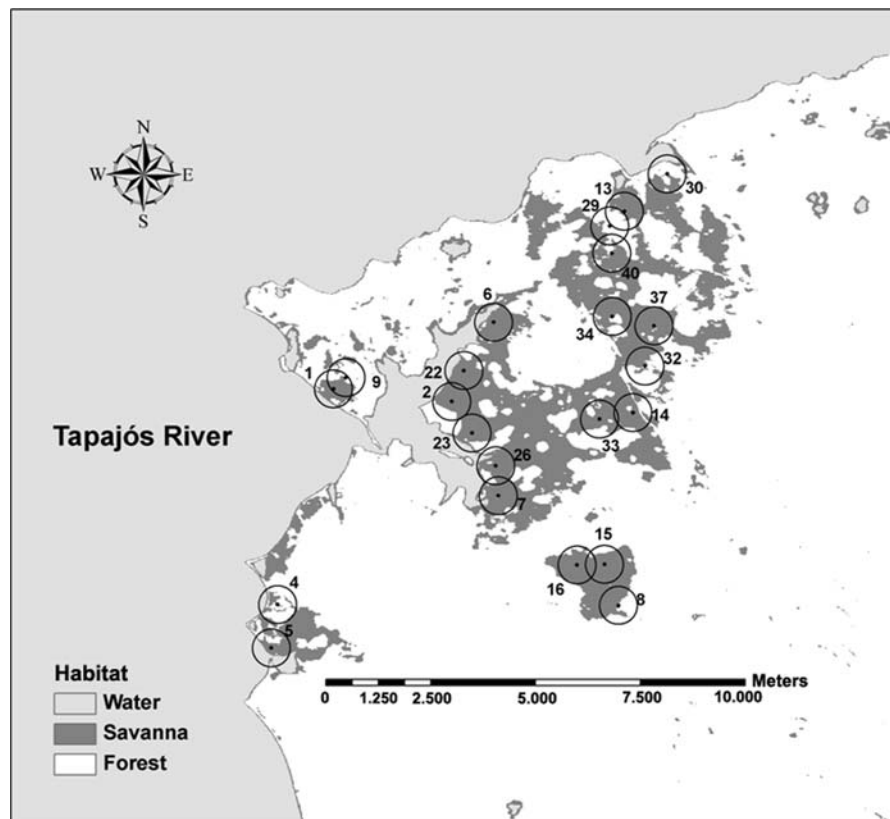


Fig. 1 The 22 sample plots at Alter do Chão, Pará, Brazil. Circles around plots represent 450-m landscape buffers used to measure surrounding forest cover

We used the number and extent of burns in each plot as a measure of the fire regime across short- and medium-term intervals. Burn extent was estimated in each plot after the dry seasons of 1999, 2000, 2001, and 2002 by recording presence or absence of recently burned vegetation at 2-m intervals along transects in each plot. The percentage of the plot area affected by fire in each year was determined as the number of sampling points with burned vegetation divided by the total number of sample points (500). Effect of medium-term fires (FMT) was calculated as the mean percentage of area burned during the four evaluations. Effect of short-term fires (FST) was calculated as the percentage of area burned in the year immediately before the sampling period.

Spatial variables and data analysis

Geographical position of sites were entered into a principal coordinates of neighbour matrices (PCNM)

analysis (Borcard and Legendre 2002; Borcard et al. 2004). PCNM variables represent a spectral decomposition of the spatial relationships among the study sites that can be computed for regular or irregular sets of points in space (Borcard et al. 2004). The PCNM functions were constructed using the ‘give.thresh’ function from the R software ‘spacemakeR’ library (Dray et al. 2006) to truncate a matrix of Euclidean distances among sites across the landscape. Distances larger than the threshold value were replaced by an arbitrarily large distance following Borcard and Legendre (2002). We then computed a principal coordinate analysis (PCoA) of the modified distance matrix using the ‘pcnm’ function of the ‘spacemakeR’ library and kept only coordinates corresponding to positive eigenvalues.

We used individual-based rarefaction analysis to describe patterns of species richness among sites (Colwell and Coddington 1994; Gotelli and Colwell 2001). We plotted species-abundance distributions

(“Whittaker plots”) to elucidate dominance patterns within local communities. These curves are cumulative ranked-abundances plots in which the cumulative ranked abundance of each species is plotted against the species rank in order from most abundant to least abundant species.

We used hierarchical partitioning (Chevan and Sutherland 1991) to examine the independent effects of the six key environmental variables (FST, FMT, SHR, TRE, GRA, and FOR) on eight metrics that describe the local dung beetle community: the observed species richness of all beetles, rollers and tunnelers, and uncommon species (occurred at <4 of the sample plots or <10 individuals overall); abundance of all dung beetles and of rollers and tunnelers; and community evenness (Pielou’s index). Hierarchical partitioning is a multiple-regression technique in which all possible linear models are jointly considered to identify the most likely causal factors, providing a measure of the effect of each variable that is largely independent from effects of other variables (Chevan and Sutherland 1991; Mac Nally 2000). Models included Poisson errors, and we evaluated competing models based on the R^2 goodness of fit statistic. The significance of independent effects was calculated using a randomization test with 1,000 iterations (Mac Nally 2002). Hierarchical partitioning and associated randomization tests were implemented using the hier.part package freely available in the R statistical program (R Development Core Team 2008).

Prior to performing the analysis of community composition variation, we transformed the species abundance table using the Hellinger transformation (square root of the relative abundance of each species in the quadrat). This transformation made the data (containing many zeros) amenable to analysis by multivariate methods that preserved Euclidean distances between points in the multi-dimensional space (Legendre and Gallagher 2001) and avoided overestimating the influence of uncommon species.

To estimate the fraction of variation of the dung beetle community data attributable to the vegetation, fire and spatial location in the landscape (captured by PCNMs), we performed a canonical partitioning analysis using multiple redundancy analysis (RDAs; Borcard et al. 1992; Borcard and Legendre 1994; Legendre et al. 2005). Ecological variance in canonical partitioning is split into eight fractions using

partial ordination methods (Borcard et al. 2004): (a) two individual non-spatially structured components explained by vegetation or fire variables respectively, (b) two spatially structured components of vegetation or fire variance, (c) a fraction of vegetation-fire explained variance, (d) a fraction of spatially structured variance not explained by vegetation or fire, (e) a joint fraction of space-vegetation-fire explained variance, and (f) a residual fraction (the unexplained variance). To reduce Type I errors and overestimation of the amount of explained variance, we performed a forward selection of the significant PCNMs and environmental variables using ‘forward.sel’ function available in the R ‘packfor’ library (Blanchet et al. 2008). This function performs a forward selection under the reduced model using Monte Carlo permutation tests (999 random permutations), retaining the variables with $P < 0.10$ (3 PCNM in this study and all environmental variables).

Adjusted bi-multivariate redundancy statistics (R_a^2 ; Peres-Neto et al. 2006) were computed by the ‘varpart’ partitioning function of the R ‘vegan’ library. The R_a^2 statistics were shown to produce unbiased estimates of the contributions of the independent variables (vegetation, fire and space) to the explanation of the response variables, correcting for the number of objects and explanatory variables in the analysis (Peres-Neto et al. 2006). The adjusted form corrects for the explanation that would be provided by the same number of random explanatory variables measured over the same number of observation points. Statistical analyses were performed using the freely available R software (R Development Core Team 2008).

Results

Species richness, abundances, and turnover

We captured a total of 3,334 dung beetles from 15 species at 22 savanna plots (see Table 1 in Matavelli and Louzada 2008). With the exception of two unknown species, all sampled species could be classified to rollers (five species) or tunnelers (eight species) guilds. We did not classify any species as dwellers. For all samples combined, the species accumulation curve was close to reaching an asymptote (Fig. 2a), but this pattern was variable at the plot

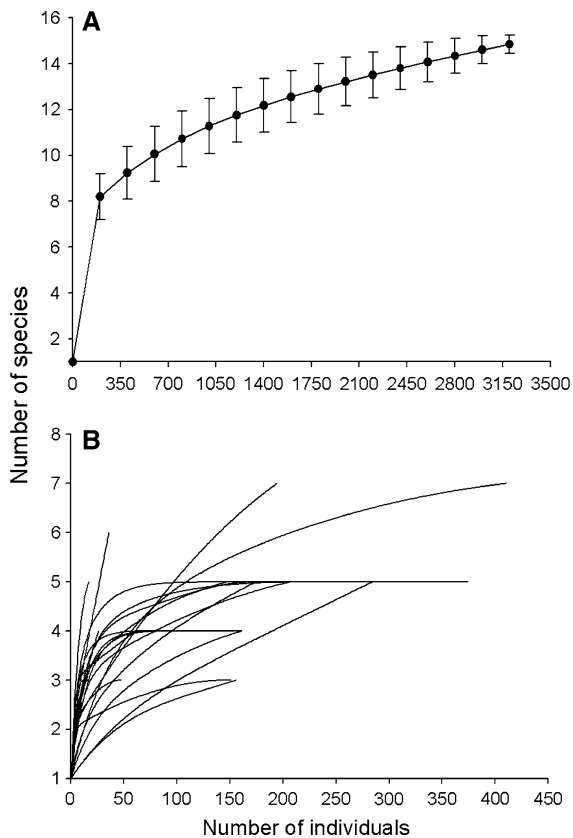


Fig. 2 Rarefaction curves for dung beetles at Amazonian savanna sites. **a** Sample-based rarefaction curve at the regional scale (all plots combined); **b** individual-based rarefaction curves at the plot-level

level (Fig. 2b). Total abundance was highly variable across plots, ranging from 17 to 410 individuals. Abundance was also unevenly distributed across species, and most of the plots were dominated by just three species (Fig. 3) that accounted for 87.7% of all individuals sampled. *Canthon* sp.1 was the only species present at all sites, the most abundant overall (50.7% of total captures), and dominant numerically at 14 of 22 sampled sites (Fig. 3). The beta-diversity partition (Lande 1996) was 71.3% (average of 10.7 species not present in any given site), implying a potential turnover of 100% in species composition between local communities.

Vegetation cover, fires, and landscape structure

Hierarchical partitioning revealed the strong, independent and positive effect of percentage forest cover in the surrounding landscape on total dung beetle

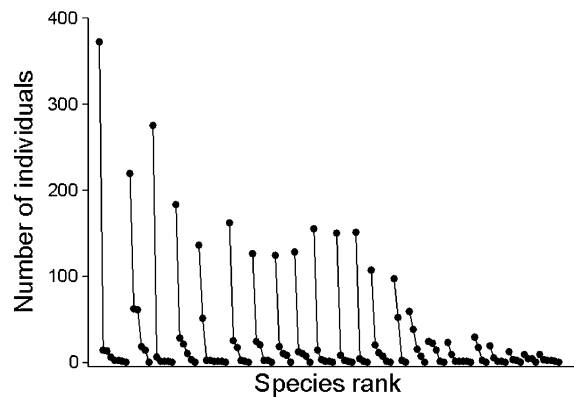


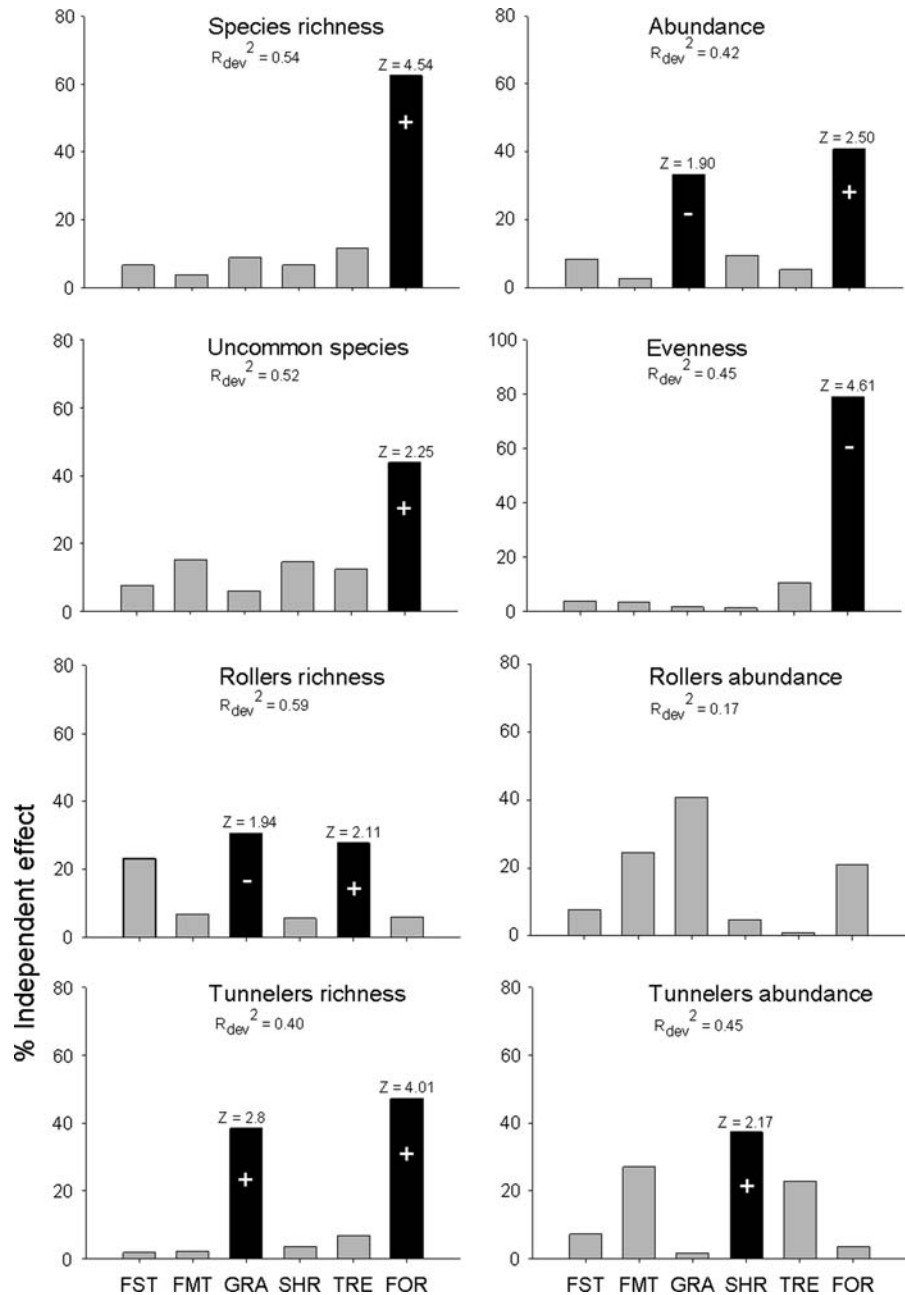
Fig. 3 Rank abundance plots for dung beetle communities in Amazonian savanna. The most abundant species were (1) *Canthon* sp1, (2) *Canthon* sp2, and (3) *Trichillum externepunctatum*

abundance and species richness, and the richness of uncommon species and the tunneler guild (Fig. 4). Forest cover also had a negative effect on community evenness (Fig. 4). Grass cover had an independent negative effect on total abundance and on the species richness of rollers, but a positive effect on the species richness of tunnelers. The richness of rollers was also influenced positively by tree cover, whereas shrub cover affected positively the abundance of tunnelers. None of the fire-related variables affected individual dung beetle community metrics (Fig. 4).

Geographical position and environmental variability

All environmental variables (FST, FMT, GRA, SHR, TRE and FOR) and 5 PCNM's (4, 5, 6, 8 and 9) were retained as significant predictors of variation in dung beetle community composition. Effects of vegetation, fire and space differed when analysed as isolated factors (Fig. 5a) versus when we partitioned out effects of factors upon each other (Fig. 5b). In isolation, R_a^2 scores reveal that the vegetation variables explained 6.0% of variation in dung beetle community composition, fire explained 15%, spatial variables explained 30%, vegetation and fire variables together explained 14%, vegetation and spatial variables together explained 48%, and fire and spatial variables together explained 34% ($R_a^2 = 0.34$; Fig. 5a). Partialling out the influence of spatial position and vegetation removed all of the individual explanation attributable to the fire variables, whereas

Fig. 4 Distribution of percentage of independent effects of measured environmental variables on dung beetles at Amazonian savanna sites as determined by hierarchical partitioning. *Black bars* represent significant effects ($P < 0.05$) as determined by randomization tests. Positive or negative relationships are shown by + or – symbols, respectively. R_{dev}^2 is the total deviance explained by a generalized linear model including the six measured variables. Short-term fires (FST), medium-term fires (FMT), grass cover (GRA), shrub cover (SHR), tree cover (TRE), and percentage of forest cover within a 450-m buffer (FOR)



8% of the variance was explained by vegetation and 28% was explained by spatial variables when partialling out the effects of the others two variables. Spatial and fire variables together accounted for 14% of the explained variation, and 20% was due to vegetation and fire variables together. Fifty-seven percent of the variance in the species composition among plots remained unexplained (Fig. 5b).

Discussion

This work describes novel patterns of dung beetle diversity and distribution in Amazonian savanna landscapes. Our study is the first to evaluate influences of vegetation and fire while simultaneously accounting for spatial autocorrelation in the distribution of insect assemblages in this system. Species

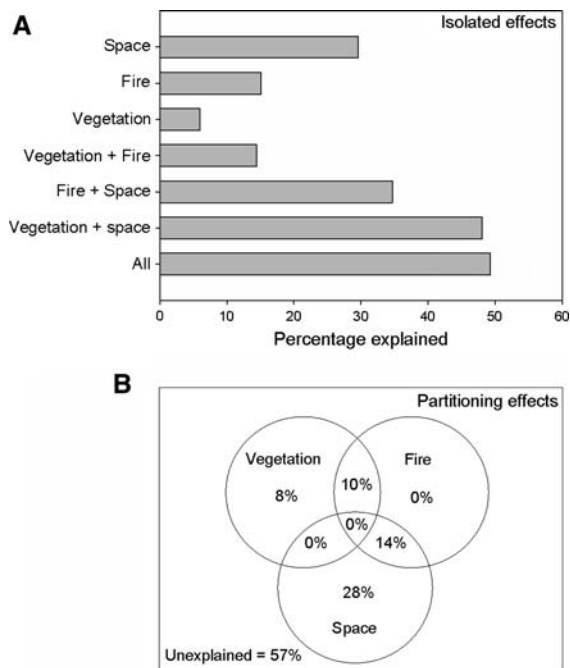


Fig. 5 Partitioning of the variation in dung beetle community composition using vegetation, fire and spatial variables. An individual variables effect **a** and the variables effects when partitioning out the effects of other variables **b** were calculated using redundancy analysis

richness of dung beetles in these Amazonian savanna patches (4.5 species per plot) was lower than in continuous and fragmented forests from the same region (12 species per plot; Vulinec et al. 2008) despite a similar total diversity within each system (15 species in savanna, 17 species in forest). However, these richness values are low when compared to either primary forest sites from other Amazonian locations, which usually support >50 species in a given locality (Klein 1989; Quintero and Roslin 2005; Gardner et al. 2008), the central Brazilian savannas (Cerrado) where >45 species of dung beetle in each locality is usual (Milhomem et al. 2003), or even introduced pastures from Southern-Central Brazil where ≤ 20 dung beetle species per site is common (Louzada and Carvalho-Silva 2009).

The low richness of intra-Amazonian savannas may be due to the historical isolation of these patches from the Cerrado savannas in Central Brazil (which occurred in the late Pleistocene; Sanaiotti et al. 2002), their relatively small size, the high frequency of fire disturbance, and lack of overlap with the beetle fauna from forested areas (sampled in the same seasonal

period and region; Vulinec et al. 2008). For example, many of the species we recorded are common in Cerrado areas, and include some species (*Canthon lituratum*; *Dichotomius nisus*; *Ontherus appendiculatus*, and *Trichillum externepunctatum*) that also occur in introduced pastures from Central and Southern Brazil (Almeida and Louzada 2009; Louzada and Carvalho-Silva 2009).

The community structure of the individual sample plots was highly uneven, and most plots were dominated by just one or two abundant species (Fig. 3). This pattern is relatively common in open and climatically unstable environments (Magurran 1988) and illustrates the unpredictable nature of fire-affected landscapes (Barbosa and Fearnside 2005). The community evenness was negatively related to the percentage of forest cover around the sampled site. This contrasts with the positive effect of forest cover on species richness and abundance, which could theoretically increase community evenness. However, the reduction in community evenness seemed to be a consequence of the positive effect that forest cover had on the number of uncommon species rather than any decrease in dominance of the most abundant species (Fig. 4).

The level of apparent rarity of most of the dung beetle species in this landscape suggests a high level of turnover and an elevated level of beta diversity. This pattern is also found in introduced pastures in southern Brazil (Louzada and Carvalho-Silva 2009), and may be frequent in open Neotropical ecosystems. The influence of fire on the species richness of tropical fauna is highly variable, and can be strongly positive (Andersen 1991) or negative (Louzada and Schiffler 1996; Cintra and Sanaiotti 2005), weak (Parr et al. 2002; Vasconcelos et al. 2008), or have no detectable effect (Farji-Brener et al. 2002). This variation in responses is likely related to inter-taxa differences, fire severity, time since fire, and other variables (Barlow and Peres 2006). Our data also revealed strong intra-taxa differences between resource-relocation guilds, as grass cover density had significant but contrasting effects on species richness of dung beetles that either roll or bury dung (Fig. 4), suggesting potential habitat partitioning at the guild level.

Dung beetles are known to respond strongly to changes in vegetation structure (Davis et al. 2002; Ford et al. 2003; Escobar et al. 2007), microclimate

and soil characteristics (Sowig 1995), and the quantity and quality of vertebrate faeces (Nichols et al. 2009). The local vegetation characteristics we measured appeared to influence different aspects of the dung beetle community (Fig. 4). Moreover, recent research has revealed the important role of landscape configuration on local diversity and community structure (Harvey et al. 2006; Nichols et al. 2007; Taki et al. 2007; Leonard et al. 2008). Our results support this landscape-level role as the percentage of forest in a 450-m buffer around sites was the most important variable influencing the abundance, community evenness, and species richness of all species, uncommon species and tunnelers (Fig. 4). This strong landscape-scale effect of forest cover could be related to dung availability as forest fragments support medium-sized mammal species (Sampaio 2007) including some that may forage in savanna sites that are close to forest (Albernaz and Magnusson 1999).

There is a growing interest in modelling beta diversity using both environmental and spatial explanatory variables, allowing their relative contributions to be assessed (Michel et al. 2007; Leonard et al. 2008). Our results support the utility of this approach, as many of the environmental factors that influence beetle composition were collinear with spatial location. For example, vegetation variables accounted for a small percentage of the explained variation in dung beetle community composition at the finest local scale, and this result can be attributed to spatially dependent processes such as fire and the percentage of forest in surrounding buffers. Furthermore, although a significant amount of the variation explained by vegetation is related to the incidence and frequency of fire, fire itself had no independent effects. Instead, fire seems to affect dung beetle communities indirectly through its interaction with vegetation structure and the spatial location of sites (Fig. 5).

Conclusion

This study indicates that much of the variation in species composition of dung beetle assemblages in savannas can be attributed to the spatial location of sites and the indirect effects of fires on vegetation (that are also dependent on spatial location). Forest cover affected community metrics by increasing the presence of rare species. Comparative work

using similar analyses could reveal parallel patterns in different environments and regions, providing a broader understanding of community structure at local and regional scales that should be useful for testing ecological theory and its application to conservation.

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