UNDERSTANDING THE COMMUNITY STRUCTURE OF DUNG BEETLES IN AMAZONIAN SAVANNAS: THE ROLE OF FIRE DISTURBANCE, VEGETATION AND LANDSCAPE STRUCTURE

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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. The role of fires is an integral part of this understanding as they affect the temporal and spatial dynamics of tropical ecosystems, including savannas (Sanaiotti and Magnusson 1995) and more seasonal humid tropical forests (Barlow and Peres 2006).

The cover of trees, shrubs, and grasses is highly variable in Amazonian savannas, even within relatively small areas (Magnusson *et al*., 2008), and often relates to the frequency and intensity of fire. However, the effect of this variation on the distribution and abundance of savanna insect communities is poorly understood. This is important, as these savannas are increasingly used for pasture and crops, often resulting in an increased incidence of fire in remaining areas of native vegetation (Sanaiotti and Magnusson 1995).

We examine how fire, local vegetation structure and landscape configuration interact to influence the dung - beetle communities in Amazonian savannas. We focus on dung beetles (Coleoptera: Scarabaeinae), which are broadly distributed across the tropics. 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 review in Nichols *et al*., 2008).

OBJECTIVES

In this study, we examine how fire, local vegetation structure and landscape configuration interact to influence the dung - beetle communities in Amazonian savannas, and quantify the explanatory role of environmental and spatial variables. Specifically, we investigate to what extent environmental and spatial variables can explain: (1) the structure and diversity of dung beetle assemblages in Amazonian savanna patches, and (2) how the variation in dung beetle assemblage composition is partitioned between the influence of environmental and spatial factors.).

MATERIAL AND METHODS

Study area

This study was undertaken in a 16 x 16 km region of semi - deciduous forest and patches of savanna that surrounds the village of Alter do Chão. The village is located on the eastern bank of the Tapajós River, 35 km southwest of the city of Santarém, in the Brazilian Amazon (2o 30'S; 54o 57'W). The mean annual temperature in Santarém is about 27.5 o C, with mean annual precipitation of 2215 mm. There is a pronounced dry season between June and November, when monthly precipitation is less than 65 mm on average. 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).

Dung beetle sampling

We used 22 plots established in 1997 as part of a long term study of savanna dynamics by INPA (Magnusson, *et al*., 2008), spread over the existing savanna patches all of which were sampled during the dry season of 2003 (between July and September). Each plot encompassed an area of 3.75 ha, and was composed of four parallel line - transects, 250 - m long and separated by 50 m. Dung beetle were sampled using pitfall traps baited with either cow dung, human faeces, or carrion, and each trap was left in the field for a full 24 hours. Traps with each bait type were grouped into arrays with one trap per bait type (with individual traps spaced 0.5 m apart) and trap arrays were spaced every 50 m, so that in each plot there was a total of 22 sampling points and 66 traps. The pitfall traps consisted of plastic containers (diameter 05 cm, height 10 cm) with an inner receptacle containing the bait. Dung beetles attracted by the bait fell into a 5% detergent solution. For the purpose of this paper we grouped the dung beetles from each plot, reducing the influence of stochastic variation from the small sample sizes.

Environmental variables

We used the point - quadrat method to measure the cover by each of the following vegetation strata: large (> 2 m in height) trees (TRE), small trees and shrubs (< 2m tall) (SHR), tall grasses (mostly Trachypogon plumosus), and short grasses (mostly Paspalum carinatum) (GRA). We spaced the sampling points at 2 - m intervals along transects, with 500 points per plot. (for further details on vegetation measurements see Magnusson *et al.*, 2008). The landscape was classified in a GIS using semi - supervised classification of a 2003 Landsat 7 (30 - m pixel) satellite image. In each plot we calculated the percentage of forest cover within a 450m buffer (FOR) as a proxy of the importance of distance to the surrounding forest. We used the number and extent of burns in each plot as a measure of the fire regime across short - term and medium time intervals. Burn extent was estimated in each plot after the dry - seasons of 1999, 2000, 2001, and 2002 by noting the 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 number of sample points (500). Medium - term fires effect (FMT) was calculated as the mean percentage of area burned during the 4 evaluations. Short - term (FST) was calculated as the percentage of area burned in the year immediately before the sampling period.

Spatial variables and data analysis

Because environmental variables such as fire can be spatially discrete, we submitted the sites geographical position to a spectral decomposition by computing a Principal Coordinates of Neighbour Matrices (PCNM) analysis. The PCNM functions were constructed using the 'give.thresh' function of the R software 'spacemaker' library to truncate a matrix of Euclidean distances among the sites across the landscape.

We used individual - based rarefaction analysis to describe patterns of species richness amongst sites. We plotted species - abundance distributions (Whittaker - plots) to elucidate dominance patterns within local communities. We used hierarchical partitioning to examine the independent effects of the six key environmental variables (FST, FMT, SHR, TRE, GRA, and FOR) on 8 dependent local community descriptors (abundance, observed richness, Shannon index, evenness, rollers and tunnelers richness, and rollers and tunnelers abundance). The significance of independent effects was calculated using a randomization test with 1000 iterations (Mac Nally 2002).

In order to estimate the fraction of variation of the dung beetle community data attributable to the environmental effects (fires and vegetation aspects) and spatial geographical position in the landscape (captured by PCNMs) we performed a canonical partitioning analysis through multiple Redundancy Analysis (RDAs).

RESULTS AND DISCUSSION

Patterns of community richness and species abundance

We captured a total of 3,334 dung beetles from 15 species at 22 sampled savanna sites. Capture success was highly variable across plots, ranging from as few as 17 to as many as 410 individuals. Capture success was also unevenly distributed across species: most of the plots were dominated by just 3 species which accounted for 87.7% of all individuals sampled. Canthon sp.1 was the only species present in all sites, the most abundant overall (50.7% of total captures), and was dominant numerically at 14 of 22 sampled sites. The beta - diversity partition 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.

Effects of vegetation cover, fires, and landscape structure on dung beetle communities

Hierarchical partitioning revealed the strong independent effect of percentage forest cover in the surrounding landscape on total dung beetle species richness, total abundance, evenness, and the species richness of the tunnelers guild. The species richness of rollers was influenced by the frequency of short term fires incidences. None of the other local environmental variables affected individual dung beetles community metrics.

Effects of geographical position and environmental variability on patterns of species composition

Three environmental variables (FST, FMT and FOR) and 5 PCNM's (4, 5, 6, 8 and 9) were retained as significant predictors of variation in dung beetle community composition. The effect of environmental factors and space was contrasting when analysed as isolated factors (environment, space and environment and space together) versus when we partitioned out the effect of geographical location. In isolation, the environmental variables explained 10 % (R2a = 0.10) of variation in dung beetle community structure, spatial variables explained 26% (R2a = 0.26), and spatial and environmental variables together explained 31% (R2a = 0.31). Partitioning out the influence of spatial position reduced the importance of environmental variables, which explained 5% (R2a = 0.05), while 5% of the variance was explained by spatially and environmental variables together (R2a = 0.05), and 20% (R2a = 0.20) was due to spatial influence alone. Sixty - nine percent (R2a = 0.69) of the variance remained unexplained.

Discussion

This work presents novel information about patterns of dung beetles diversity and distribution in an Amazonian Savanna landscape, and is the first to evaluate the influence of environmental variables whilst simultaneously accounting for spatial autocorrelation in the distribution of an insect assemblage in this system. Overall, the species richness of dung beetles in these Amazonian savanna patches was low when compared to either primary forest sites from other Amazonian locations (which usually support more than 50 species in a given locality (Gardner *et al.*, 2008) or the central Brazilian savannas (Cerrado), where it is usual to sample more than 45 species of dung beetle in each locality. Vulinec *et al.*, (2008) also report low species richness of the dung beetle community (17 species) in continuous and fragmented forests from Alter do Chão. The low richness of intra - Amazonian savannas may be due to the historical isolation of these patches, their relatively small size, and the high frequency of fire disturbance. These historical and ecological factors may have acted as an extinction filter, reducing the community to a pool of disturbance - tolerant species.

The community structure of the individual sample plots was highly uneven, and most plots were dominated by just one or two very abundant species. This pattern is relatively common in open and climatically unstable environments and illustrates the unpredictable nature of fire - affected landscapes (Barbosa and Fearnside 2005). The level of apparent rarity shown by most of the dung beetle species in this landscape suggests there is a high turnover in local communities and consequently an elevated level of beta diversity. This pattern is found also in introduced pasture lands in southern Brazil (Louzada and Carvalho - Silva in press), 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 both strongly positive, and negative, weak, or have no detectable effect. This variation in responses is likely related to inter - taxa differences, fire severity, and time since fire, among other variables (Barlow and Silveira 2009). Our data clearly revealed strong intra - taxa differences, depending on ecological guild, as fire had a significant effect on the diversity of dung beetles that roll dung, but no effect on the tunnellers (or other community response metrics).

However, none of the local vegetation characteristics we measured appeared to have a strong influence on dung beetle communities. Moreover, recent advances in landscape ecology have revealed the potentially important role of landscape configuration on local diversity and community structure. Our results support this dominating landscape - level role, as the percentage of forest in a 450 m buffer around the site was the most important variable influencing the abundance, total species richness, species richness of tunellers, and community evenness.

Our environmental variables accounted for a small percentage of the explained variation in dung beetle community structure at the smallest local - scale, and this can be attributed to spatially dependent processes such as fire and the percentage of forest in surrounding buffers.

CONCLUSION

This study indicates that while environmental factors like vegetation and fires can explain some community - level aspects of dung - beetle assemblages in savannas, much of this variation in species composition and abundance may be strongly affected by the spatial location of sites, and environmental variables that are also dependent on spatial location. We suggest that comparative work using similar analyses may reveal similar patterns in different environments and regions, providing a broader understanding of community structure at local and regional scales that will prove more useful for testing ecological theory and its application to conservation.

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