

Plant species richness increases the spatial stability of litter mass in Brazilian Pantanal

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Abstract: I used the natural gradient of plant species richness from Brazilian Pantanal to verify how plant richness and structure are related to litter mass accumulated (LMA) in the soil. Significant positive effects on LMA and on its spatial stability highlight the trait-dependent insurance in environments under cyclic disturbances. I suggest that LMA is regulated by the relationship between colonization and performance of few plant species aboveground, which also explains the species distribution in the landscape. Pantanal is one of the most interesting and diverse biomes in the biosphere, and because of its high conservation appeal and natural experimental potential, studies therein may help to predict the effects of biodiversity loss on ecosystem functioning in natural environments.

Resumen: Utilicé el gradiente natural de riqueza de especies de plantas a partir del Pantanal brasileño para verificar cómo la riqueza y la estructura vegetal están relacionadas con la masa del matillo acumulado (LMA) sobre el suelo. Los efectos positivos significativos de la riqueza de especies sobre la LMA y su estabilidad espacial resaltan el aseguramiento dependiente de los rasgos en ambientes sometidos a disturbios cíclicos. Sugiero que la LMA está regulada por la relación entre la colonización y el desempeño de pocas especies de plantas sobre el suelo, lo que también explica la distribución de las especies en el paisaje. El Pantanal es uno de los biomas más interesantes y diversos de la biosfera, y dado su gran atractivo para la conservación y su potencial experimental natural, su estudio puede ayudar a predecir los efectos de la pérdida de diversidad sobre el funcionamiento ecosistémico.

Resumo: Foi usado o gradiente natural de riqueza de espécies de plantas do Pantanal brasileiro para verificar como a comunidade de plantas está relacionada com a massa de serapilheira acumulada (LMA) no solo. Os efeitos positivos significativos da riqueza específica na LMA e na sua estabilidade espacial evidenciou a dependência das características das espécies na manutenção dos processos ecossistêmicos em ambientes sujeitos a perturbações. Sugere-se que a LMA é regulada pela relação entre a colonização e o desempenho de algumas espécies de plantas, o que também explica a distribuição destas espécies na paisagem. O Pantanal é um dos biomas mais interessantes e diversos da biosfera e seu elevado apelo para conservação e potencial experimental natural podem aumentar a previsibilidade dos estudos sobre os efeitos da perda de diversidade sobre o funcionamento dos ecossistemas.

Key words: Biodiversity-ecosystem functioning, disturbance, litter mass, Pantanal and Paratudal, plant species richness, spatial variability.

Biodiversity is an important factor in regulating the magnitude and stability of many ecosystem processes (Hillebrand & Matthiessen 2009). Recent studies have highlighted the context dependence of the Biodiversity-Ecosystem Functioning (BEF) relationship (Boyer *et al.* 2009). However, because most of this research has used very manipulative experimental designs, the potential to extrapolate these results to natural ecosystems is limited (Naeem 2008). Hence, actual efforts to predict the response to species loss have failed and, as a consequence, little has been done to improve ecosystem management (Chettri *et al.* 2012). Alternatively, there are natural ecosystems with species richness gradients mainly established by the differential relation between species traits and environmental conditions (Spooner *et al.* 2012). I suggest that studies in these natural gradients could help to explain the causes and consequences of changes on biodiversity.

The Brazilian Pantanal region provides one of the clearest examples of how environmental factors may drive community dynamics and ecosystem performance. The Pantanal oscillates between periods of fire and flood, exhibiting unique extinction and colonization dynamics in the impacted areas, as well as great plasticity of its species to adapt to new conditions (Scremin-Dias *et al.* 2011). Consequently, natural species richness gradients emerge in the landscape, including resistant monodominant plant communities, such as “Carambazal”, “Buritizal” and “Paratudal”. Paratudal is a vegetation structure dominated by *Tabebuia aurea* (Silva Manso) Benth. & Hook., and resulted by many factors, such as flooding and the association with arthropods that form wooded hills, where the species can be established (Soares & de Oliveira 2009). It arises as an interesting system that helps to verify the BEF relationship in natural ecosystems, as it exhibits trade-offs between species resistance and performance.

In this study, I examine the relationship between plant species richness and litter mass accumulation (LMA) in the soil, by investigating the natural gradient of plant richness from the Paratudal to the riparian vegetation around the Miranda river - Pantanal. Litter has a dominant role in soil ecosystem functioning, contributing to nutrient cycling below-ground and soil fauna structure (Guendehou *et al.* 2014; Portela & dos Santos 2009; Smith & Bradford 2003). Thus, litter on soil serves as a proxy for the potential effects of changing plant community structure on soil ecosystem processes.

Table 1. Linear models performed to mean litter mass accumulated (LMA) its spatial variability (coefficient of variation, $n = 5$), using plant richness and vegetation structure as main predictor variables. Plant density was used as co-variable in all models. Thus, the statistical parameters shown to the main predictors do not include the effect of density on the response variables. Bold letters mean significant F values. * $P < 0.05$; ** $P < 0.01$.

Variables	Plant species richness		Vegetation structure	
	$F_{1,22}$	$F_{Density}$	$F_{4,19}$	$F_{Density}$
Mean LMA	6.51*	8.59**	4.84**	11.55**
Spatial variability LMA	4.45*	1.13	0.50	0.90

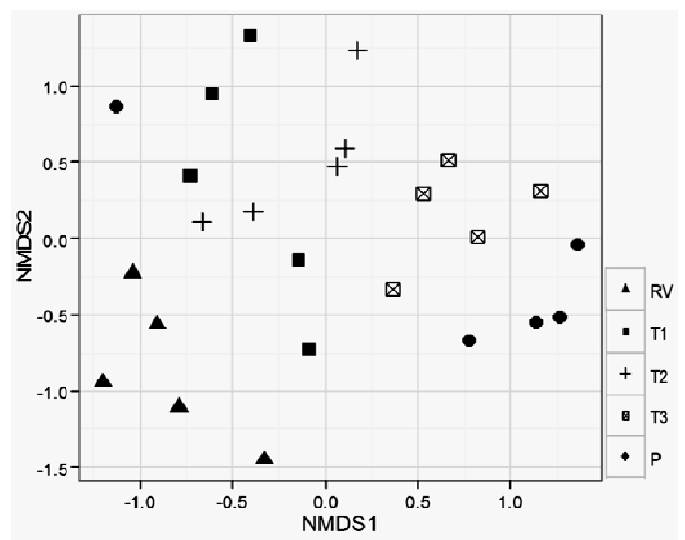


Fig. 1. Non-metric multidimensional scaling demonstrates the differences among the five vegetation structures, nearer symbols mean more similar community structure. Permutational Multivariate Analysis of Variance (PerMANOVA) shows significant differences in the community structure among the vegetation structures (PerMANOVA; $R^2: 0.304$, $P = 0.001$).

Samples were collected during the dry season around the field station “Base de Estudos do Pantanal” (BEP) (19°34’ S, 57°01’ W), a property of the Universidade Federal do Mato Grosso do Sul in southern Pantanal, Brazil. Five areas of different vegetation structure were established in the landscape: Paratudal (P), Transition 1 (T1), Transition 2 (T2), Transition 3 (T3) and Riparian

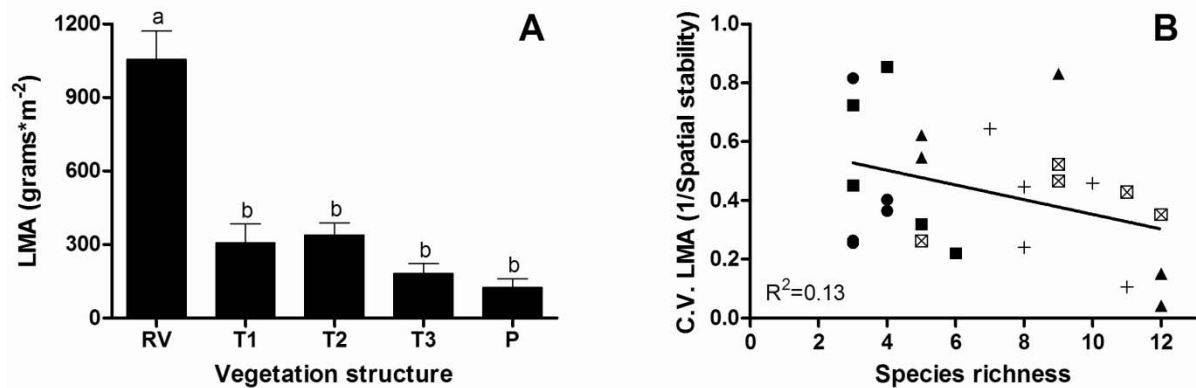


Fig. 2. Effects of vegetation structure on mean LMA (A), different letters mean significant differences among the vegetation structures (Tukey HSD, pos hoc test; $P < 0.05$). Plant richness decreases LMA spatial variability (linear regression, $P < 0.05$) (B). Symbols legend is the same of the Fig. 1.

vegetation (RV). These areas were determined by dividing the total sampling area (Paratudal to Riparian Vegetation) into five strips, oriented parallel to Miranda river. In each area, five quadrats (each, 100 m²) were established with a distance of 100 m between two quadrats. Plants with circumference at breast height greater than 2 cm and those that could contribute to LMA on soil were morphotyped. Species richness was determined by the number of different morphotypes in each quadrat. In each quadrat, five LMA samples (each, 0.25 m²) were collected and dried at 60 °C until they reached a constant weight. LMA samples were composed of leaves in different stages of decomposition, but not freshly fallen. Because plant density could be a confounding factor in the BEF relationship in natural ecosystems, it was used as a co-variable in all data analyses. I estimate the spatial stability using the coefficient of variation (CV) of the five LMA samples in each quadrat. The coefficient of variation is a common metric to establish spatial or temporal predictability, an important aspect of ecosystem stability (Weigelt *et al.* 2008). Lower CV values for LMA mean higher spatial stability in each vegetation area. Statistical details are described in the figure and table legends.

Plant community showed significant differences among the vegetation structures (Per MANOVA; $R^2: 0.304$, $P = 0.001$). Models performed to verify the direct effect of plant richness and vegetation structure on mean LMA and its spatial stability demonstrated that plant density is an important predictor of the mean LMA (GLM, $P < 0.05$), but not its spatial variability. Excluding

those effects, vegetation structure was able to explain differences in mean LMA but not its spatial variability (Table 1). The effects of vegetation structure on mean LMA are related mainly to high LMA values in Riparian Vegetation (RV) (Fig. 2A). There was no clear effect of increased plant richness from Paratudal (P) to RV (Fig. 2B). However, plant richness increased spatial stability (Fig. 2B), decreasing the coefficient of variance among replicates.

Biodiversity affects ecosystem function mainly through complementarity (niche differentiation and/or facilitation among species) and selection mechanisms (for review, see Caliman *et al.* 2010). Studies suggest that these mechanisms can work as stabilizing factors in a changing world - the insurance hypothesis of biodiversity (Yachi & Loreau 1999). The research presented herein provides evidence of how plant richness can be related to the variability of some ecosystem functions in natural environments. Changes in vegetation structure were not able to regulate the spatial stability of LMA (Table 1), indicating no dependence on community composition and species identity (Fig. 1). On the other hand, plant richness showed strong positive effects on spatial stability of LMA (Fig. 2B).

I suggest that plant species richness could minimize the differences on LMA in the soil because plant species show different strategies for surviving in this cyclic disturbed environment. Riparian vegetation is not regulated by hydric and fire disturbances, commonly observed in Paratudal, dominated by grass species and *T. aurea*. Plant communities that are subjected to cyclic

environmental changes are structured by species resistant to disturbance. Consequently, the distribution of these species in the landscape is unpredictable, since they are highly dependent on specific environmental conditions for establishment. It also explains the reason of non-clear plant richness gradient in the landscape. In addition, under these conditions, ecosystem processes should be limited by the ability of resistant species to perform these processes. In this way, the magnitude and stability of ecosystem processes in extreme environments, such as the ones that occur at Pantanal, should be driven by resistant species, highlighting their insurance trait-dependence.

The natural gradient of plant richness in the Pantanal is an interesting system to improve the predictability of BEF relationship, incorporating natural complex environments and excluding the effects of random species manipulations. However, it is important to highlight some traps of using this environment. For example, establishing categories of diversity in natural ecosystems can be challenging because species turnover is continuous. Furthermore, other important environmental factors for the Pantanal system (e.g. relief and water viability) should be considered to clarify the effect of plant richness on LMA, as well as the inclusion of other ecosystem functions. It will greatly improve the understandings about the mechanisms suggested in this study. In spite of these limitations, the Pantanal remains as one of the most interesting and diverse biomes in the biosphere, and should be incorporated into the BEF debate since it shows high conservation appeal and great potential for natural experiments.

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