HONEYCOMB RIPPLING MODEL: TEST IN A CERRADO FRAGMENT

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INTRODUCTION

Savannas are tropical formations in which trees and grasses coexist; in which fire is frequent; and in which the main patterns in growth and reproduction are strongly associated to alternating wet and dry seasons (Bourlière & Hadley 1983). Savannas cover a great part of Earth's surface and they contain a large and rapidly growing proportion of world's human population; consequently, they are under considerable pressure (Archer *et al.,* 2000). In savannas the balance between the grassy and woody components changes in time and space (Bourlière & Hadley 1983). The coexistence of grassy and woody plants in savannas has often been attributed to a rooting - niche separation (Walker *et al.,* 1981), but this theory is controversial (Jeltsch *et al.*, 996).

Wiegand *et al.*, 2006) presented an alternative theory for tree–grass coexistence in arid savannas: they could be patch - dynamic systems driven by rainfall and inter - tree competition for water; and a dense savanna patch could be converted into an open one. The so - called "honeycomb rippling model" predicts that evenness of inter - tree distances increase with tree size; and that inter - tree distances increase with increasing tree size. Since the model predicts that trees are patchily distributed, one would expect tree height and inter - tree distance to be spatially autocorrelated. There is an ongoing debate concerning the stability of savannas (Scholes & Archer 1997), which are ideal systems for studies on patch - dynamics,because of their clear spatial and temporal heterogeneity (Gillson 2004).Wiegand *et al.*, 2006)tested and corroborated their theory in arid savannas,but only postulated its applicability to fire dominated and seasonal savannas,as is the cerrado.

OBJECTIVES

Our aim is to test the honeycomb rippling model in a cerrado fragment, trying to answer the questions: i) Does evenness of inter - tree distances increase with tree size?; ii) Do inter - tree distances increase with increasing tree size?; and iii) Are height and intertree distance spatially autocorrelated?

MATERIAL AND METHODS

We placed 80 25 m2 quadrats in a woodland cerrado site (São Carlos, Brazil). In each quadrat, we sampled all tree individuals, measuring their height and inter - tree distance. We calculate average height and inter - tree distance evenness for each quadrat.

We did correlation analyses between height and inter - tree distance evenness and between height and inter - tree distance to answer first and the second questions. To answer the third question, we did spatial autocorrelation analyses for average height and inter - tree distance.We used the semivariance statistics y(h), available in the Gstat package for R (R Development Team 2008).

RESULTS AND DISCUSSION

We found 803 individuals of 54 tree species site. Tree height was not correlated neither with intertree distance evenness, nor with intertree distance. On the one hand, intertree distance was spatially structured; on the other hand, tree height was not spatially autocorrelated.

We refuted the honeycomb rippling model, since we did not find relationships between tree height and neither with evenness of inter - tree distances nor with inter - tree distances. The honeycomb

rippling model was initially postulated to explain arid savanna dynamics, in which rainfall is patchily distributed both in time and space. According to our results, this model does not seem to fit seasonal savannas. If, in arid savannas, rainfall events are rare and unpredictable, in seasonal savannas, the rainy season is well - defined and rainfall is considerable, up to 2000 mm (Eiten 1972, Gardner 2006). The model assumes that there is competition for water among seedlings. However, positive local interactions among individual may shape community dynamics (Pueyo *et al., .,* 2008). Besides that, in cerrado communities, trees can access water all year long (Goodland & Pollard 1972). Thus, the competition for water shall not be intense enough to result in the honeycomb rippling effect. Moreover, even for arid savannas, the coexistence of grasses and tress is not due exclusively to water competition (Jeltsch *et al.,*

1996). Other important factors that play roles in community structuring are heterogeneity of soil resources, vegetative reproduction, limited dispersal, and disturbances such as fire (Meyer *et al.*, 2008; Moustakas *et al.*, 2008; Pueyo *et al.*, , 2008; Perry *et al.*, , 2009; Rodrigues *et al.*, , 2009; Jeltsch *et al.*, , 1996). In seasonal savannas, soil has a poor nutrient content, and nutrient availability is determinant to savanna species, especially in more humid regions (Gardner 2006).

The importance of nutrients to horizontal structuring in the studied cerrado can be inferred by the spatial autocorrelation in the inter - tree distances. Spatial patterning in plant communities can be a response to heterogeneity in the abiotic environment, such as topographic gradients; or the result of local biological processes (Perry *et al.*, , 2009). Distribution of soil resource availability for plants play a crucial role in the structure, composition, and productivity of many terrestrial communities: the more clustered pattern in soil nutrients leads to a more clumped plant distribution, with higher spatial dependence (Rodrígues *et al.*, , 2009).

Tree height was not spatially structured, suggesting that competition for light in the community is not as important as competition for soil resources. This is expected, since in savannas, trees are sparsely distributed (Sarmiento 1984; Archibald & Bond 2003) and light interception is not limiting (Archibald & Bond 2003).

CONCLUSION

It is important to understand the factors that govern spatial patterns of savanna communities, because they cover a large area and are being heavily exploited by human populations (Hoffmann *et al.*, 2002; Archer *et al.*, , 2000). The honeycomb rippling model does not seem to apply to seasonal savannas, such as the Brazilian cerrado. According to our results, water and light do not seem to structure cerrado plant communities, but nutrients do.

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