

## Spatial pattern analysis and demography of two tropical trees in the Brazilian Caatinga

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**Abstract** - *Aspidosperma pyrifolium* (Apocynaceae) and *Caesalpinia pyramidalis* (Fabaceae) share the same habitat in the Brazilian Caatinga domain. In this paper, we investigate the intra and inter-species interactions between these two plants using spatial pattern analysis among cohorts. The results showed that the adult trees of each species present higher densities at distances shorter than 9 m to 12 m. However, due to seed dispersal via autochory, we expected a more aggregate density for *C. pyramidalis* than *A. pyrifolium* as the later disperses seeds through anemochory. Difference in spatial aggregation among cohorts was not observed and therefore the results contradict the expectations of the Janzen-Connell hypothesis. It is likely that this is associated with anthropogenic factors in the past such as fire, animal husbandry and logging. Using a bivariate analysis of the neighborhood density, we also confirmed the significant coexistence between the two species. This coexistence could be explained by the process of positive interspecific interactions, such as facilitation, which is common in semi-arid regions under stressful conditions.

### Padrão espacial e demografia de duas espécies arbóreas tropicais do bioma Caatinga

**Resumo** - *Aspidosperma pyrifolium* (Apocynaceae) e *Caesalpinia pyramidalis* (Fabaceae) compartilham o mesmo habitat no bioma Caatinga. Neste trabalho, investigamos as interações intra e interespecíficas por meio do padrão espacial entre coortes. Os resultados mostraram que as plantas adultas de cada espécie apresentam elevados níveis de densidade em curtas distâncias (9 m e 12 m). No entanto, devido à dispersão de sementes via autocoria, esperávamos uma densidade mais agregada para *C. pyramidalis* do que em *A. pyrifolium*, que tem dispersão anemocórica. Não foi observada diferença de agregação espacial entre coortes e, portanto, os resultados contradizem as expectativas da hipótese de Janzen-Connell. É provável que isto esteja associado a fatores antrópicos no passado, tais como incêndio, pecuária e exploração madeireira. Por meio da análise bivariada da densidade de vizinhos, foi confirmada a coexistência significativa das duas espécies. Isto pode ser explicado pelo processo de interações interespecíficas positivas, tais como a facilitação, que é comum em regiões semiáridas, sob condições estressantes.

## Introduction

The Caatinga domain occupies 11% of the Brazilian territory with an area of approximately 800,000 km<sup>2</sup>. It occurs across the states of Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia and in the north of Minas Gerais, covering 70% of Northeast region (Santos et al., 2011b). This domain occurs in areas with marked seasonality and low precipitation. It is an exclusive Brazilian domain and has shrub-tree vegetation composed mainly of xerophytic species (Costa et al., 2007). Recently, the flora of the Caatinga has received more detailed attention (Leal et al., 2005), but ecological studies are still in their early stages (Santos et al., 2011a). In relation to flora, for example, there are 932 recorded plants of which 380 are endemic species (Giulietti et al., 2004). Furthermore, eight floristic units were identified in the flora of the Caatinga, including the Arboreal Caatinga (Santos et al., 2012).

*Aspidosperma pyriforme* Mart. (Apocynaceae) occurs in the Caatinga and is known as “pereiro”, “pau-de-coaru” and “pequiá-da-mata”. It has winged seeds that are anemochorous. The tree grows up to 8 m in height. It is a heliophyte that occurs during secondary succession stages (Andrade et al., 2005). *Caesalpinia pyramidalis* Tul. (Fabaceae), known as “catingueira”, is an endemic tree species that is characteristic of the Caatinga domain (Leite et al., 2009). It is a pioneer and autochorous species (Santana & Souto, 2006).

*A. pyriforme* and *C. pyramidalis* coexist in the same habitat in these dry forests. Thus, we investigated the intra and interspecific interactions between plants of these two species through an analysis of spatial pattern in order to evaluate the ecological traits and the processes shaping the distribution of plants (Vieira et al., 2010). The expectation is that the spatial distribution of the autochorous species is more aggregated than the anemochorous one (Vekemans & Hardy, 2004). Furthermore, smaller trees (younger tree cohorts) must show a more aggregated spatial pattern than larger trees (adult tree cohorts) as mortality is a density-dependent (Vieira et al., 2012). Such a dependence is expected based on the so-called Janzen (1970) and Connell (1971) effect.

Generally, spatial patterning analyses have shown that the majority of tropical tree species exhibit a decrease in aggregation with an increase in age (Epperson &

Alvarez-Buylla, 1997, Ng et al., 2004, Vieira et al., 2012), determined primarily by the intra and interspecific competition (Condit et al., 2000). However, low densities of reproductive adults and anthropogenic factors (e.g. grazing by domesticated animals) can limit recruitment and the species capacity for regeneration (Perevolotsky & Haimov, 1992; Oba, 1998). Thus, we evaluated the spatial distribution and demography of *A. pyriforme* and *C. pyramidalis* and used the spatial analysis to assess the existence of interspecific spatial interaction.

## Material and methods

### Study site and sampling

The study site is an 0.25 ha area in the *Estação Ecológica do Seridó* (ESEC), an area of the Caatinga domain in the municipality of Serra Negra do Norte, Rio Grande do Norte State, Brazil. The local flora is characterized by small trees, often with less than 7 m in height, with sparse distribution and fewer species than other types of caatinga (Santana & Souto, 2006). However, the open characteristic does not match the original condition of vegetation, as a result from environmental degradation caused by human action, possibly through the successive burning carried out since the human colonization for the formation of pastures. The ESEC has a total area of 1,166 ha, altitude of 249 m and it is located between the geographic coordinates 06°36'40''S and 06°33'50''S and 37°17'10''W and 37°14'20''W. The semiarid local climate, according to the Thornthwaite & Mather (1955) classification, is a dry DdA'a' with an average annual precipitation of 733.7 mm and average annual temperature of 27.5 °C (Santana et al., 2006).

Within the studying plot, individuals of *A. pyriforme* and *C. pyramidalis* were recorded and their positions mapped ( $x$  and  $y$ ). The plot included 285 individuals which were divided into three classes (cohorts) according to circumference at soil height (csh). For *A. pyriforme*, the size classes of the cohorts (csh) were adults (26 cm to 79 cm) and juveniles (5 cm to 25 cm). For *C. pyramidalis*, the cohorts were adults (27 cm to 83 cm), juveniles (7 cm to 26 cm) and seedlings (1 cm to 6 cm).

### Spatial pattern analysis

To determine if the spatial pattern for a single species is aggregated (univariate analysis) and if there is a spatial

association between both species (bivariate analysis), we used a second order *neighborhood density function* (NDF; Condit et al., 2000). The NDF is statistically similar to Ripley's K function; however, it is not cumulative (Perry et al., 2006). Distance classes ( $t$ ) between 2 m and 24 m were used based on Haase (1995) suggestion that they do not exceed approximately  $\frac{1}{2}$  the length of the smallest plot dimension. Additionally, we corrected the edge effect based on Goreaud & Pelissier (1999). The NDF values were plotted in correlograms based on the distance ( $t$ ). The 99% confidence interval (CI) was estimated using a Monte Carlo method with 499 replicates for a  $\alpha = 0.01$ . We used a Cramer-von Mises ( $CvM$ ), which is the sum of the squared difference between the observed and expected values under the null hypothesis, across all distance classes (0–24 m). These calculations were analyzed with SpPack 1.38 (Perry, 2004).

In order to examine if the spatial pattern of the two species are correlated, the sampled area was subdivided into 100 plots of 5 m x 5 m and we calculated the number of individuals of each species within each sub-plot. A non-parametric correlation test was performed using Spearman correlation coefficient ( $r_s$ ) in the Statistica software (StatSoft, 2004).

## Results

### Demography

We sampled a total of 89 individuals of *A. pyrifolium*; of these 72 were adults (BIG), 16 juveniles (MED), and no seedlings (SMA) were recorded (Figure 1A). For *C. pyramidalis* we found 196 individuals: 126 adults, 61 juveniles and nine seedlings (Figure 1B). The densities

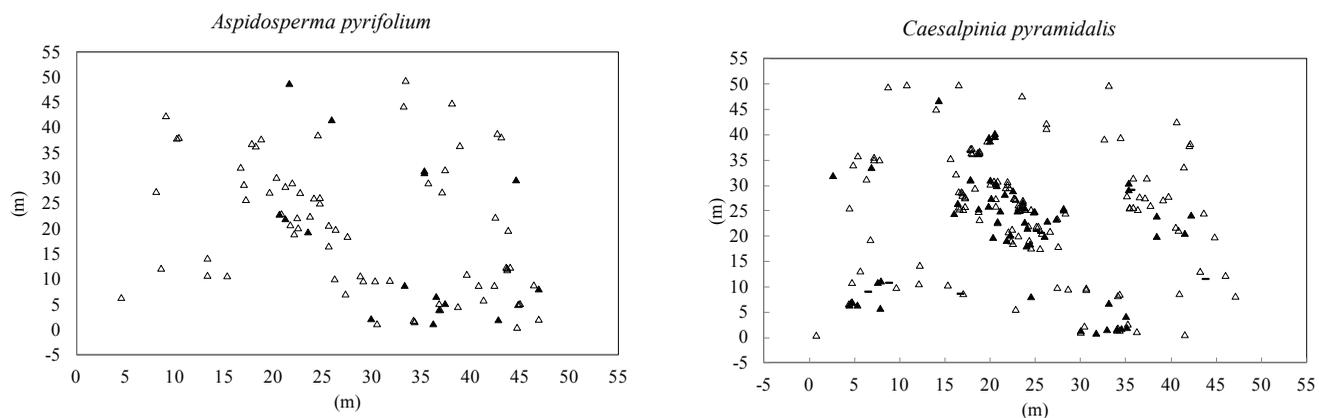
within the 0.25 ha plot were 504 trees  $\text{ha}^{-1}$  (BIG), 244 trees  $\text{ha}^{-1}$  (MED) and 36 trees  $\text{ha}^{-1}$  (SMA) for *C. pyramidalis*, and 288 trees  $\text{ha}^{-1}$  (BIG) and 64 tree  $\text{ha}^{-1}$  (MED) for *A. pyrifolium*.

### Spatial Pattern

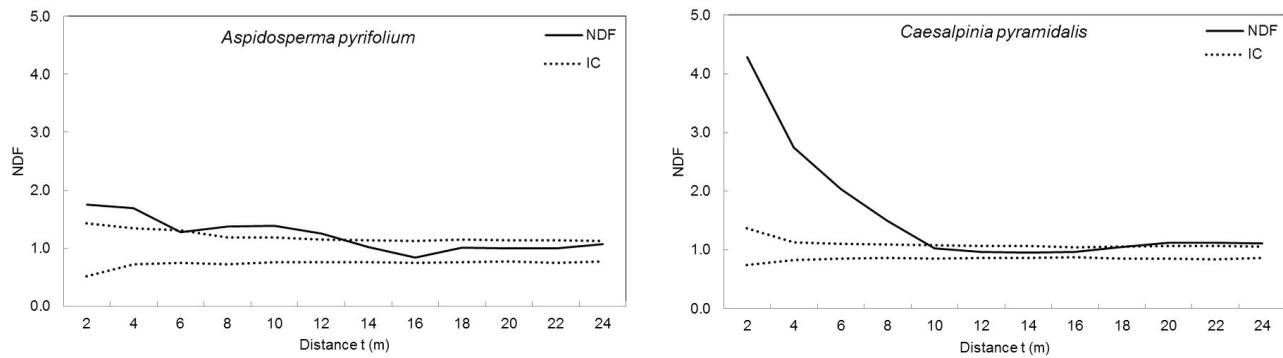
The analysis of the spatial pattern of all *A. pyrifolium* ( $N = 89$ ) individuals showed the density within a radius of 12 m was higher than expected for a hypothesis of complete randomness ( $CvM = 15.39$ ,  $P = 0.002$ ) and a random spatial pattern was observed for all other distance classes (Figure 2A). For *C. pyramidalis* ( $N = 196$ ), our results showed significant levels of aggregation below the radius of 9 m from the focal individual ( $CvM = 1.57$ ,  $P = 0.002$ ) and random spatial pattern in the subsequent distance classes (Figure 2B).

The spatial distribution of seedling (SMA) and juvenile (MED) individuals ( $N = 70$ ) of *C. pyramidalis* was significantly different from that expected for a random distribution ( $CvM = 5.49$ ,  $P = 0.002$ ) (Figure 3A). For this analysis we combined the SMA and MED classes, since the smallest class included only nine individuals. For the adult cohort (BIG,  $N = 126$ ) we observed a similar spatial pattern within a radius of 9 m from the focal individual ( $CvM = 6.99$ ,  $P = 0.002$ , Figure 3B). *A. pyrifolium* was not analyzed here because of reduced recruitment.

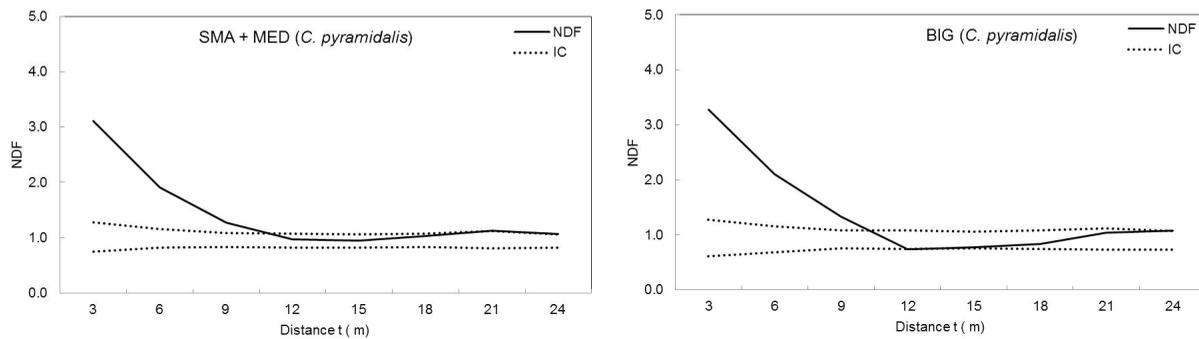
The spatial association between *A. pyrifolium* and *C. pyramidalis* (bivariate analysis) was positive within a radius of 8 m ( $CvM = 3.02$ ,  $P = 0.002$ ) and for the higher distance classes there was a random spatial pattern (Figure 4). Additionally, we found a significant correlation ( $r_s = 0.464$ ,  $P < 0.05$ ) between the spatial distribution of *A. pyrifolium* and *C. pyramidalis*.



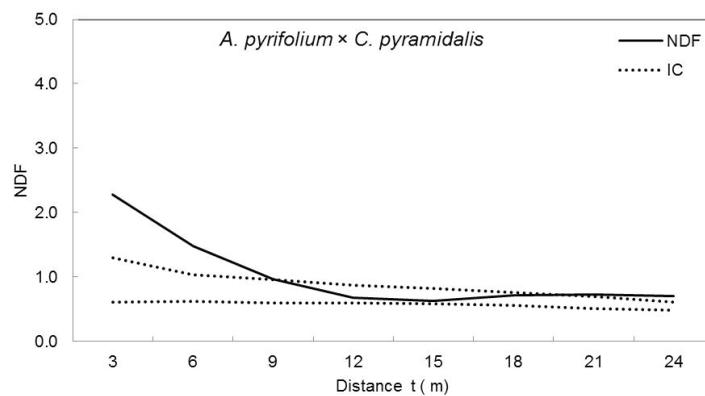
**Figure 1.** Distribution of the sampled adults ( $\Delta$ ), juveniles ( $\blacktriangle$ ) and seedlings ( $-$ ) of *A. pyrifolium* (A) and *C. pyramidalis* (B) in the sampled area of 2,500  $\text{m}^2$ .



**Figure 2.** Spatial pattern obtained by univariate analysis of the neighborhood density function (NDF) of all plants of *A. pyrifolium* (A) and *C. pyramidalis* (B). Dotted lines correspond to the 99% range for the null hypothesis of completely random spatial distribution.



**Figure 3.** Spatial pattern obtained by univariate analysis of the neighborhood density function (NDF) for seedlings and juveniles (A) and for adults (B) of *C. pyramidalis*. Dotted lines correspond to the 99% range for the null hypothesis of completely random spatial distribution.



**Figure 4.** Bivariate analysis between *C. pyramidalis* and *A. pyrifolium*. Dotted lines correspond to the 99% range of for the null hypothesis of completely random spatial distribution.

## Discussion

The spatial patterning found is likely a reflection of the reproductive strategies of each species and the historical use of the site (Vieira et al., 2010). Due to autochorous dispersal, and based on theoretical predictions (Vekemans & Hardy, 2004), we expected a more aggregate spatial pattern for *C. pyramidalis* than *A. pyriformis*, which is anemochorous. However, the results showed that both *C. pyramidalis* and *A. pyriformis* adults presented high neighbor density at short distances of up to 912 m; however, the neighborhood density function was higher for the autochorous *C. pyramidalis* species (Figure 2).

As for the spatial patterning of cohorts, there was no difference between seedlings/juveniles (SMA + MED) and adults of the *C. pyramidalis* (BIG). This result differs from what is expected, as the literature reports that most tree species have aggregated spatial distribution during early life-stages and a random pattern for older life-stages (Hamrick et al., 1993, Epperson & Alvarez-Buylla, 1997). Furthermore, our result contradicts the Janzen-Connell hypothesis (Figure 3). It is likely that the similar aggregation values of the *C. pyramidalis* cohorts are associated with anthropogenic factors or abiotic conditions (periods of water-deficiency). The demographic structure reflects the history of the forest as well as past disturbances, including fire, herbivory and logging (Barot et al., 1999; Condit et al., 2000). More specifically, grazing by domesticated animals is associated with reduced recruitment and plant growth (Oba, 1998), as well as a reduced capacity for plant regeneration (Perevolotsky & Haimov, 1992). In the studied site, there is intense grazing by domesticated animals that is associated with reduced recruitment or regeneration. Despite the fact that this area has been designated as conservation unit for more than 30 years, the reduced species richness in the ESEC compared with other areas of Caatinga reflects the effect of past anthropogenic activities in the site, such as logging for timber and charcoal (Santana & Souto, 2006).

In addition to the short distance aggregation pattern, there is considerable coexistence between the two species, as observed in the bivariate analysis of the neighbor density and the positive correlation of the Spearman coefficient. The magnitude of interspecific competition is still unknown but there is generally weak competition among some neotropical tree species (Paine et al., 2008). According to Byrne et al. (2007) the intensity with which individuals are aggregated

affects the reproductive system and also how plants use available resources (Getzin et al., 2008). Thus, the aggregation of species could be explained by positive interspecific interactions such as facilitation. This process is common in semiarid regions with high stress conditions (Smit et al., 2009). It can also be explained simply by heterogeneity in the distribution of nutrients in the soil in the sample area which creates areas of greater fertility and therefore contributes to the association between *A. pyriformis* and *C. pyramidalis*. However, future studies must move beyond spatial genetic structure and reproductive biology of these species to better understand such interactions.

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