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***Comunicación breve***

# Spatial relationships between *Ananas ananassoides* (Bromeliaceae) and *Tachigali vulgaris* (Fabaceae) influencing the structure of the Amazon/Cerrado transition in Brazil

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**Abstract.** In the present study, we tested the hypothesis that: a) bromeliad *Ananas ananassoides* individuals and *Tachigali vulgaris* tree individual have an aggregate distribution pattern, and b) are spatially dissociated. To this effect, we quantified all *A. ananassoides* and *T. vulgaris* individuals (DBH of at least 30 cm) in large plot (1 ha) composed by 100 subplots measuring 10×10 m in a savanna woodland in the Bacaba Municipal Park, Nova Xavantina, Mato Grosso. The spatial pattern of *A. ananassoides* and *T. vulgaris*, and their spatial relationships, were measured using the aggregation and the association index, respectively. Both species had an aggregate distribution pattern and were spatially dissociated, which corroborates the hypotheses of this study. In this case, the preferred occupation in gaps by both species and the growth of the bromeliad in clumps may be conditioning the populations' spatial dependence. On the other hand, the bromeliad's clump formation and the tree species shading may be mutually exclusive factors, which intensify their competition for space and light and reveal spatial incompatibility by these populations. Further studies should be conducted to better understand the interactions between the herbaceous and tree layer, incorporating the temporal dynamics of natural regeneration and habitat conditions.

[Keywords: interspecific competition; spatial dynamics, gaps, environmental heterogeneity]

**Resumo. Relações espaciais entre *Ananas ananassoides* (Bromeliaceae) e *Tachigali vulgaris* (Fabaceae) influenciando a estrutura florestal na transição Amazônia/Cerrado no Brasil.** No presente estudo testamos as hipóteses de que: a) os indivíduos da bromélia *Ananas ananassoides* e da árvore *Tachigali vulgaris* distribuem-se de forma agregada, e b) dissociados no espaço. Para tanto, quantificamos todos os indivíduos de *A. ananassoides* e de *T. vulgaris* (DAP mínimo de 30 cm) em uma grande parcela (1 ha) composta por 100 subparcelas de 10x10 m em um cerradão no Parque Municipal do Bacaba, Nova Xavantina, Mato Grosso. O padrão espacial de *A. ananassoides* e *T. vulgaris*, e suas relações no espaço, foram mensurados pelo índice de agregação e associação, respectivamente. As duas espécies distribuíram-se de forma agregada e apresentaram-se dissociadas no espaço, corroborando as hipóteses do presente estudo. Neste caso, a ocupação preferencial em clareiras de ambas as espécies e o crescimento em touceiras da bromélia, pode estar condicionando a dependência espacial das populações. Por outro lado, a formação de touceiras da bromélia e o sombreamento da espécie arbórea podem ser fatores mutuamente excludentes, os quais intensificam a competição por espaço e luz entre essas espécies e revelam incompatibilidade espacial das duas populações. Novos estudos devem ser realizados para melhor compreender as interações entre os estratos herbáceo e arbóreo, incorporando a dinâmica temporal da regeneração natural e as condições do hábitat.

[Palabras clave: competição interespecífica, dinâmica espacial, clareiras, heterogeneidade ambiental]

## Introduction

The intraspecific spatial distribution of plants can be an important factor driving the interspecific spatial arrangement in the community (Bulleri et al. 2016) and, consequently, the structure of the vegetation (Budke et al. 2010). For example, the intraspecific spatial patterns of bromeliads can be connected with different mechanisms (biotic and abiotic) governing the occupation of natural communities by plant species, such as facilitation (Beduschi and Castellani 2008; Tsuda et al. 2016), competition (Oliveira et al. 2007; Beduschi and Castellani 2013), clump formation (Cogliatti-Carvalho and Rocha 2001), microclimatic conditions (Cogliatti-Carvalho et al. 2010), soil characteristics and litter composition (Barberis et al. 1998). Most of these factors promote the spatial dependence of bromeliad individuals and can account for spatial repulsion with other species, including

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trees (Oliveira et al. 2007; Brancalion et al. 2009).

*Ananas ananassoides* (Baker) LB Sm., also known as wild pineapple, is a terrestrial bromeliad, perennial, and pollinated by animals (e.g., birds and tortoises), with an annual or intermediate flowering period (Jerozolimski et al. 2009; Silveira et al. 2010; Stahl et al. 2012). This species is considered a pioneer once it presents small and photoblastic seeds and higher germination rates in areas with high luminosity (Silveira et al. 2010). However, *A. ananassoides* does not show differences in photosynthetic rates in different light conditions, indicating shade tolerance (Keller and Lüttge 2005). Thus, the factors responsible for establishment and growth (sexual and asexual) of *A. ananassoides* are complex, and may be related to the germination conditions determined by the dynamics of gaps (Silveira et al. 2010). The species grow individually or in clumps, being generally found in areas of Cerrado 'sensu stricto', but occurs in forests (Proença and Sajo 2007; Silveira et al. 2010). The plasticity in the establishment and colonization in different environments can condition changes in the patterns of spatial distribution of this species, in view of the direct competition for space and light with tree species (Oliveira et al. 2007).

The savanna woodland ("cerradão") is a rare, transitional phytophysiognomy between savanna and forest at Amazonia-Cerrado transition, and *Tachigali vulgaris* L. G. Silva and R. Lima is a typical tree species of such formations (Ratter et al. 1973; Marimon-Junior and Haridasan 2005; Araújo et al. 2011; Solórzano et al. 2012). This species controls the structural dynamics of the savanna woodland due to its pioneer characteristic, high dispersal capacity (anemochoric), quick germination, short life cycle and high annual recruitment and mortality rates (Felfili et al. 1999; Franczak et al. 2011; Morandi et al. 2015; Reis et al. 2015). Gaps caused by *T. vulgaris* in the savanna woodland can provide feedback to its own establishment (Franczak et al. 2011).

In this study we describe the intraspecific distribution pattern and the spatial relationships between *A. ananassoides* and *T. vulgaris* in a savanna woodland area in the Cerrado/Amazon transition in Brazil. We hypothesize that: a) the populations are aggregately distributed as a consequence of the pioneer characteristic of both species and as a result of clump formation by the bromeliad (Benzing 1980; Felfili et al. 1999; Cogliatti-Carvalho and Rocha 2001), which limits recruitment and conditions the spatial dependence of individuals in the site, as observed for tree species (Dalling et al. 2002), and b) both populations are negatively associated in the site due to mutually exclusive factors such as shading by the tree species and the bromeliad's clump formation strategy, which inhibits other plants from establishing themselves within the limits of bromeliads (Oliveira et al. 2007; Barberis et al. 2014).

## MATERIALS AND METHODS

### *Area of study and data collection*

The present study was conducted within a savanna woodland (14°42′02.3′′ S - 52°21′02.6′′ W) in the Bacaba Municipal Park. The park has approximately 500 ha and is situated in eastern Mato Grosso, an Amazon/Cerrado biome transition region (Marimon-Junior and Haridasan 2005). This particular type of forest is very rare and has a peculiar floristic composition, usually displaying greater alpha diversity when compared with other savanna woodlands of Central Brazil (Ratter et al. 1973; Solórzano et al. 2012).

According to Köppen's classification, the climate of the region is Aw, with a rainy season between October and April and a dry season from May to September (Alvares et al. 2013). Annual precipitation is ~1500 mm, and average annual temperature is 25 °C (Ministry of Agriculture, Meteorology Institute - INMET, 9th Meteorology District). The soil under the savanna studied is alic and acid dystrophic Yellow Oxisol, with a clay content ranging between 28 and 40% (Marimon-Junior and Haridasan 2005). These soils are associated with flat relief and soft-wavy relief, with an average elevation of 300 m (Marimon-Junior and Haridasan 2005).

Sampling was conducted in 100 contiguous plots measuring 10x10 m, in February 2015. At the time, all *Tachigali vulgaris* individuals with a minimum DBH of 30 cm and all genets of *Ananas ananassoides* larger than 10 cm were duly counted. The stolons of individual plants were identified through superficial excavations. Samples of both species were collected and compared with vouchers from the NX Herbarium (Nova Xavantina campus).

### *Data analysis*

We assessed the spatial pattern of *Tachigali vulgaris* and *Ananas ananassoides* abundance using the aggregation index (AI) (Perry 1995). This index tells the spatial aggregation, regularity and randomness when values are significantly higher, lower and equal to 1, respectively. Calculation of the AI is based on the two-dimensional coordinates (in this case, the centroid of each sample unit). Its significance is assessed by Monte Carlo permutations (Perry 1998). To complement the spatial assessment and to better visualize the layout of groupings and gaps in the distribution of individuals of both species, we constructed a contour map using program SURFER.

The spatial relationships between the two populations were determined with the help of statistical program SADIE (Spatial Analysis by Distance Indices) through the association index ($\chi$) (Perry 1998; Perry and Dixon 2002). The null hypothesis of $\chi$ is the lack of associations (i.e., the gaps and groupings of the number of *A. ananassoides* and *T. vulgaris* individuals do not coincide spatially). The values of $\chi$ vary from +1 (positive association, $P<0.025$) and -1 (negative association, $P>0.975$), and zero indicates total spatial independence. Positive associations occur when there is an overlap of groupings or gaps in two sets of data. On the other hand, negative associations are indicated by the coincidence of groupings in a dataset with the gaps in another (i.e., when there is spatial repulsion [Perry and Dixon 2002]). The aggregation and association indices were calculated utilizing SADIE Shell 1.2 (Perry et al. 1996).

## RESULTS AND DISCUSSION

We recorded 649 *A. ananassoides* and 58 *T. vulgaris* individuals in the assessed plots. The high abundance and frequency of *A. ananassoides* in the studied savanna woodland areas was consistent with the density of dominant bromeliads (terrestrial/epiphytic) in the resting forests and floodplain forests of Rio de Janeiro and Pará states (Cogliatti-Carvalho et al. 2001; Nunes-Freitas et al. 2006; Quaresma and Jardim 2012). In this case, the morphophysiological adaptations of species, such as leaf stiffness and CAM (Medina et al. 1993; Crayn et al. 2015), ensure mechanical support and resistance to water stress and high temperatures, favoring their occupation in savannic and forest areas (Proença and Sajo 2007) and contributing to the high abundance found in the present study. On the other hand, the abundance values found for *T. vulgaris* are lower than in other studies conducted in savanna woodlands with inclusion limits lower than those used in the present study (≥5 cm DBH) (Marimon-Junior and Haridasan 2005; Araújo et al. 2011; Bueno et al. 2013).

The spatial distributions of *A. ananassoides* (AI=1.29, $P$=0.025; Figures 1A and 1C) and *T. vulgaris* (AI=1.46; $P$=0.013; Figures 1B and 1C) were aggregated. The species were negatively associated with one another ($\chi$=-0.311, $P$=0.997; Figure 1D), with small groupings of up to 15 m and large groupings measuring between 30 and 60 m (Figures 1A and 1B). The aggregate pattern of both species may be connected with their pioneer characteristic and preferential occupation of places with greater availability of light or forest gaps (Proença and Sajo 2007; Silveira et al. 2010). This explains the formation of groups of varying sizes along the habitat, which may be related to the size of the forest gaps. On the other hand, the aggregation of bromeliad individuals may also be enhanced by the formation of clumps, which limits recruitment of tree species (potential competitors) and increases the spatial dependence of the individuals (Cogliatti-Carvalho and Rocha 2001; Benot et al. 2013). This strategy monopolizes resources along the habitat and has been observed in other herbaceous species, such as ferns (Walker and Sharpe 2010).

Spatial repulsion between the species can also be explained by the similar occupation of forest gaps, since the bromeliad clumps may be inhibiting the establishment of the tree species within its boundaries and causing the spatial dissociation between the two species. Elias et al. (2015) found similar results when assessing the influence of *Actinocladum verticillatum* bamboo shrubs on the natural regeneration of a savanna woodland area and a typical cerrado area. The authors revealed that the bamboo densification inhibited the grow than destablishment of tree species as a result of competition for resources such as space and light. However, the spatial dissociation between the assessed species may be linked with inhibition of the bromeliad growth caused by shading by the tree species. Similar results were found by Oliveira et al. (2007) between the populations of *Bromelia balansae* and *Dimorphandra mollis* in a typical cerrado. The authors connected this

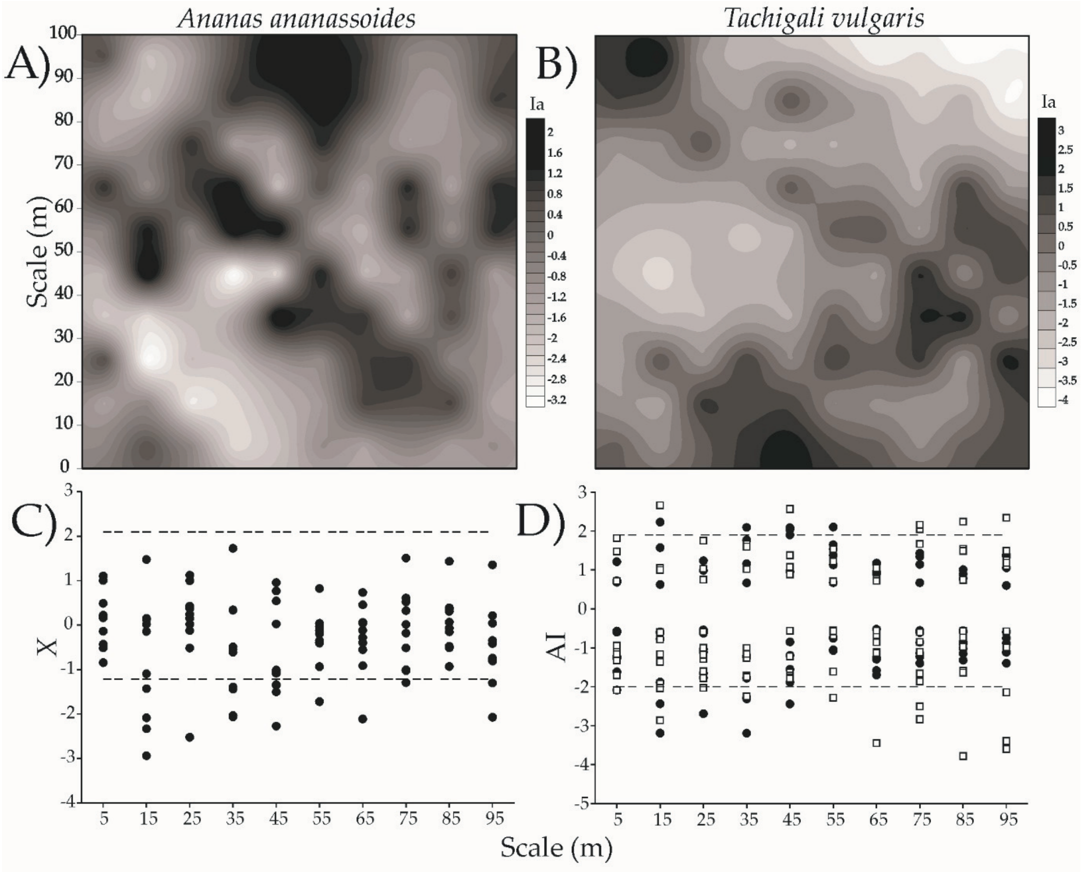

**Figure 1**. Kriging of spatial distribution of *Ananas ananassoides* (Baker) L. B. Sm. (Figure 1A) and *Tachigali vulgaris* L. G. Silva and H. C. (Figure 1B), values of association index (Figure 1C, $\chi$) and aggregation index (AI, ●=*A. ananassoides*; □=*T. vulgaris*, Figure 1D) in different scales in a savanna woodland area in the Bacaba City Park, Nova Xavantina-MT. The critical interval of the values of spatial association and aggregation indexes were constructed from 100 permutations of Monte Carlo, and are represented by dashed lines.

**Figura 1**. Krigagem da distribuição espacial *Ananas ananassoides* (Baker) L. B. Sm. (Figura 1A) e *Tachigali vulgaris* L. G. Silva and H. C. (Figura 1B), valores dos índices de associação (Figura 1C, $\chi$) e agregação espacial (IA, ●=*A. ananassoides*; □=*T. vulgaris*, Figura 1D) em diferentes escalas em um cerradão no Parque Municipal do Bacaba, Nova Xavantina-MT. O intervalo crítico dos valores dos índices de agregação e associação espacial foram construídos a partir de 100 permutações de Monte Carlo, e estão representados por linhas tracejadas.

result with the direct competition for light by the plant species.

Therefore, the formation of clumps by *A. ananassoides* and the shading by *T. vulgaris* may be mutually exclusive factors, which intensify the competition for space and light among these species and reveal spatial incompatibility by the two populations. We suggest that on a micro-scale, the bromeliad's spatial distribution is driven by clump formation and on a large scale by the dynamics of forest gaps and the interspecific competition with tree populations such as *T. vulgaris*. We can conclude that the intraspecific spatial distribution can be an important factor driving the interspecific spatial arrangement in the community (i.e., mutual repulsion), influencing the structure and possible the dynamics of the vegetation. Further studies must be conducted to verify whether this pattern is repeated with other tree and herbaceous populations, incorporating the temporal dynamics of natural regeneration and evaluating the effects of strata interaction due to habitat conditions.

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