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# The effect of tree-on-tree interactions and abiotic conditions on woody communities in Brazilian savannas

## Research Article

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## Abstract

Fire plays a crucial role in shaping plant communities in South American savannas. However, the impact of biotic interactions on tree communities still needs to be better explored. In this study, we evaluated the influence of tree-on-tree interactions and abiotic conditions on the structure and diversity of woody communities in savannas of Central Brazil. We used plots of 10 × 10 m in three preservation areas of savanna to assess the abundance and composition of juveniles and adults in woody communities associated with two Apocynaceae tree species: *Hancornia speciosa*, postulated to show negative interactions with the associated tree community, and *Himatanthus obovatus*, postulated to show positive interactions. Our results revealed that while abiotic factors, represented by the altitude, are more critical in shaping the community of juvenile trees, tree-on-tree interactions have a stronger influence on adult tree populations, driving community dynamics during plant recruitment. Specifically, *Hancornia speciosa* reduces the abundance of adults, whereas *Himatanthus obovatus* enhances their relative abundance; both shape the composition of tree communities. Consequently, tree-on-tree interactions create distinct mosaics at various stages of regeneration, contributing to savanna dynamics and conservation.

## Introduction

Savanna is an heterogeneous vegetation in the tropics and subtropics, usually characterised by a continuous $C_4$ herbaceous layer with a discontinuous $C_3$ tree stratum, where fire is a prevalent endogenous disturbance (Lehmann et al. 2011, 2014, Pausas and Bond, 2020). Tropical savannas are distributed in Africa, Australia and South America (Figure 1a) under different fire regimes and dynamics, covering approximately 20% of the terrestrial surface (Archibald et al. 2013, 2019, Lehmann et al. 2011). In South America, savannas are mainly distributed in the Cerrado (Borghetti et al. 2019, Critical Ecosystem Partner Fund, 2018, Lehmann et al. 2011, Olson et al. 2001), a phytogeographic domain that covers approximately 2 million km$^2$ (Figure 1b). The Cerrado harbours 12,363 species of angiosperm in Brazil; more than half of this diversity (6,939 species) belongs to savannas (cerrado *sensu lato* vegetation), which corresponds to approximately 95% of angiosperm species in the Brazilian savannas and includes over 1,000 species of trees (Flora and Funga of Brazil, 2022).

More than half of the native vegetation cover in the Cerrado domain is already converted to croplands, mainly of soybean, and pasturelands or has been changed to hydroelectric dams, urban areas or mining. Most of the remaining area (>80%) is not covered by pristine vegetation and remains under intense anthropic pressure, mainly because of the agribusiness expansion (INPE, 2019, Klink and Machado, 2005, Lahsen et al. 2016, Overbeck et al. 2022, Strassburg et al. 2017). Conservation units protect less than 10% of the Cerrado (ICMBio, 2019, Lahsen et al. 2016), which will not be effective in the face of current land use and the effects of climate change (Velazco et al. 2019). Over 30% of the remaining Cerrado is estimated to be devastated by 2050, leading to the extinction of hundreds of plant species (Strassburg et al. 2017). In the last two or three decades, the Cerrado agricultural frontiers have comprised mainly savannas in the states of Maranhão (MA), Tocantins (TO), Piauí (PI) and Bahia (BA), a region known as MATOPIBA (Pivello et al. 2021, Sano et al. 2019). This region comprises the most significant remnants of original vegetation in the Cerrado, but its flora remains little known (Santana and Simon, 2022).

The boundaries between fire-prone savannas and fire-impending forests can be sharp and dynamic. Under intermediate rainfall and mild seasonality, similar resource conditions can support contrasting fire feedback loops and lead to the establishment of either savannas or forests as alternative stable vegetation types ('biomes' in Staver et al. 2011 or 'ecosystems' in Buisson et al. 2019, see also Bond et al. 2016, Dantas et al. 2016, Le Stradic et al. 2021, Midgley et al. 2010, Pausas and Bond, 2020, Reis et al. 2015, Touboul et al. 2018, Veldman et al. 2015). A large portion of South America is estimated to be under bi-stability, showing mainly savannas (low tree cover) in the Brazilian Cerrado domain and especially forests (high tree cover) in the eastern Amazonia domain (Staver et al. 2011). On a continental scale, the savanna vegetation is often reduced to a couple of functional groups, namely graminoid (mainly C4 grasses) and woody plants (mainly C3 trees). Hence, local patterns and processes that characterise heterogeneous landscapes are usually neglected (e.g. Levick and Rodgers, 2011), and the impact of interactions within life forms in structuring and maintaining the plant community assemblage is overlooked.

Recruitment is critical to savanna structure and dynamics (e.g. Borghetti et al. 2019), but this process has yet to be further investigated (Midgley et al. 2010). Fire selectively affects recruitment more than established trees: it helps to maintain a low tree cover and favours the recruitment and persistence of savanna specialists to the detriment of forest specialists (Midgley et al. 2010). Plant–plant interactions, such as competition and facilitation, within life forms can also be essential for recruitment, community assembling and vegetation structuring (Tatsumi et al. 2019, Tilman, 2004, Vega-Álvarez et al. 2019). However, their influence in savannas remains poorly explored and discussed (see Chagas et al. 2020, Flake et al. 2022, Le Stradic et al. 2021). Here, we evaluated the influence of tree-on-tree interactions and the altitude effect (abiotic conditions) on tree recruitment in a savanna within the MATOPIBA region in Central Brazil.

First, we compare the species number, abundance and composition of juvenile and adult trees in woody communities associated with two species of non-forest trees that are commonly found in savannas: *Hancornia speciosa* Gomes and *Himatanthus obovatus* (Müll. Arg.) Woodson (Apocynaceae). While *H. speciosa* seems to interact negatively with the neighbourhood occupation, *H. obovatus* seems to interact positively. The contrasting effects of these target species in the associated plant community were inferred from field observations and supported through laboratory tests on allelopathy (Gonçalves, 2016, Uhlmann et al. 2018). More recently, the number of rare species surrounding these trees also supported their opposite influence on the selectivity of coexisting species. In particular, *H. speciosa* acted as a filter, reducing the richness and abundance of surrounding trees while promoting evenness in the associated tree communities (Chagas et al. 2020). By comparing juvenile and adult trees associated with these species, we aim to identify patterns of species turnover and changes in the community structure, providing evidence of the regional species pool and the potential factors involved in tree recruitment (Datry et al. 2015, Grime, 1998, Salles and Schiavini, 2007). Finally, we assess the relative importance of tree-on-tree interactions and abiotic conditions (on a local scale, embodied by the altitude) on the structure and diversity of woody communities.

Variation in the species number is a key parameter for assessing environmental restoration efforts. Still, it is equally important to consider species composition and abundance, as they impact the functioning and structuring of plant communities (Chagas and Pelicice, 2018, Grubb, 1977, Pausas and Bond, 2021, Ploughe et al. 2019). Both negative and positive interactions can influence species composition, increase species richness and decrease population size, albeit in different strata (Hutchinson, 1967, Tilman, 2004, Vega-Álvarez et al. 2019, Whittaker, 1969). Given the biotic filter imposed by *H. speciosa* and *H. obovatus*, we anticipate distinct patterns of tree recruitment in their surrounding compared to communities not associated with them. Consequently, we hypothesise that plant interactions will play a more significant role than altitude in shaping adult communities, whereas their influence on juvenile communities may be less pronounced.

## Materials and methods

### Study area

This study was conducted in a savanna of Central Brazil, in Porto Nacional, state of Tocantins, in 2016. The study area is in the Cerrado Biosphere Reserve (Figures 1b and 1c), delimited by the Man and the Biosphere programme of the United Nations Educational, Scientific and Cultural Organization (Brito and Silva 2019). Savanna plots were set up in three reserves of private rural properties with low anthropic activity, classified as cerrado *sensu stricto* (Ribeiro and Walter, 2008) and natural occurrences of *Hancornia speciosa* and *Himatanthus obovatus*. The reserves encompass ~ 109, 40.5 and 14.5 ha, forming a polygon of ~ 8,500 ha between 10°33'00"–10°48'30"S and 48°20'00"–48°26'00"W, with plots distributed in polygons of ~ 23.5, 33.5 and 5 ha, respectively. Soils in the three reserves are oligotrophic and acidic, with low organic matter and high levels of aluminium (Pinheiro et al. 2018). Microenvironmental differences within and between sites were homogenised by the use of replicas at local and regional scales. However, abiotic factors, such as temperature, are not expected to vary enough locally to affect our results significantly. Although often seen as a prime determinant of savannas, soil properties are extremely uniform below 10–15 cm and are not associated with changes in the Cerrado composition and physiognomy (Ruggiero et al. 2002). Fire was recorded in these three reserves in the years 2004, 2007, 2008, 2010, 2011, 2012, 2014, 2017 and 2019 (Chagas and Pelicice, 2018; INPE, 2019).

### Target species

*Hancornia speciosa* (Figure 1d), popularly known as 'mangabeira', produces fruits ('mangabas') that are used by the locals and small industries for candies, juices and jams. It is also a source of latex for traditional medicine. The species blooms from September to November, with fruit dispersal only after riped and fallen, from November to January. In Brazil, *H. speciosa* occurs in the Amazon, Caatinga, Atlantic Forest and Cerrado phytogeographic domains, reaching Paraguay, Bolivia, Peru and Venezuela (Almeida et al. 2016, Collevatti et al. 2018, Flora and Funga of Brazil, 2022, Monachino, 1945).

*Himatanthus obovatus* (Figure 1e) is popularly known as 'Tiborna'. The plant is used in folk medicine as an antitumour agent and has immunomodulatory properties. It blooms throughout the year, with a peak from October to December, and the seeds are wind dispersed. The species is also used for reforestation because of its rapid growth. In Brazil, *H. obovatus* occurs in the Amazon, Caatinga and Cerrado phytogeographic domains, reaching Bolivia (Flora and Funga of Brazil, 2022, Plumel, 1991, Soares et al. 2016).

### Sampling

In each of the three reserves, 30 plots of 10 × 10 m were set up (Figure 1f): ten plots with an adult individual of *H. speciosa* in the centre (Hancornia plots), ten with an adult individual of

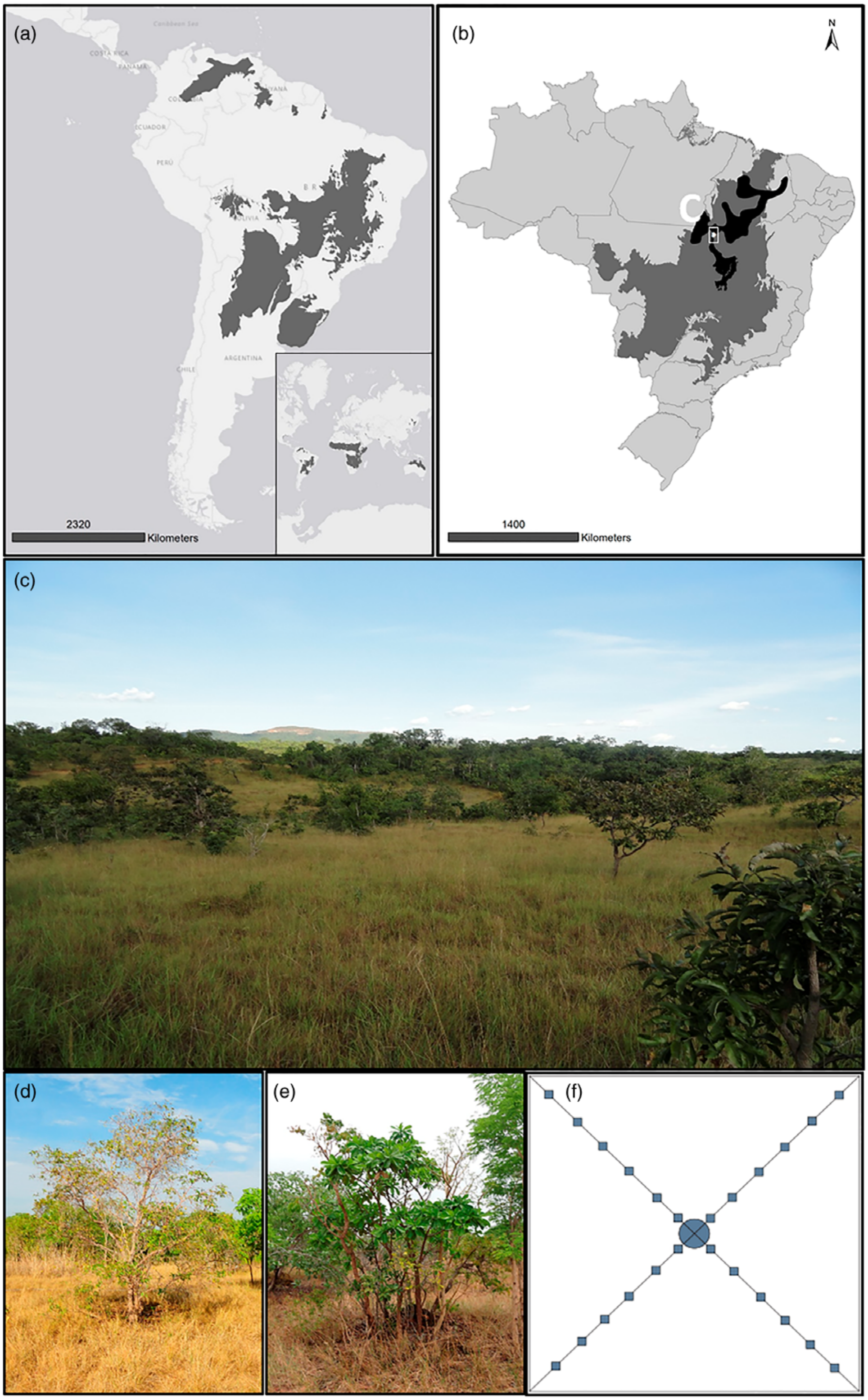

**Figure 1.** Study area, vegetation, sample design and target plants. (a) Savanna biome area (dark grey) with emphasis on South America (WWF 2019). (b) Cerrado domain area (dark grey; IBGE 2019) and Cerrado Biosphere Reserve (black; MMA, 2019) in Brazil, showing the study area. (c) Landscape in the study area. (d) *Hancornia speciosa*. (e) *Himatanthus obovatus*. (f) Scheme of sample plots: ☐ – plot limits; ● – target species; ■ – subplots.

*H. obovatus* (Himatanthus plots) and ten without any of the target species (Control plots), but with a wood species of similar height in the centre of the plot. Plots were at least 10 m distant from each other, and plots of the same type (Hancornia, Himatanthus or Control) had a minimum distance of 20 m. A map showing the plot distribution is available in Chagas et al. (2020), and the coordinates and altitude of the plots are available in Supplementary Information S1. To quantify adult trees, in each plot, we collected all plants with stem perimeter at ground ≥10 cm (3.18 cm of diameter) or height ≥1 m (Felfili et al. 2000), including dead individuals. Frames of 0.5 × 0.5 m were used to quantify seedlings and saplings (juveniles hereafter), including individuals <10 cm in circumference and <1 m in height (Mueller-Dombois and Ellenberg, 1974). The frames were distributed within the plots, from the centre to the angles of the plot, at 1 m far from each other, comprising four transects with six frames, totalling 24 frames per plot (Figure 1f). We recorded all woody species within each subplot (Felfili et al. 2000) and counted the number of individuals for each species. The vouchers are deposited in the herbarium of Universidade Estadual de Feira de Santana (HUEFS), with duplicates sent to the herbarium of Universidade Federal do Tocantins (HTO). The species were identified in the least inclusive taxonomic categories and classified according to the APG IV (2016).

### *Data analysis*

For each type of plot (Hancornia, Himatanthus or Control), we calculated species richness (number of species; Tokeshi, 1993) and abundance (number of individuals; Magurran, 2004). To standardise species richness, we calculated rarefaction curves based on plot sampling effort and 500 randomisations of the original matrix of each plant stage (juvenile and adult trees) separately, using the Jackknife1 estimator implemented in the package EstimateSWin910 (Colwell, 2017). For adult trees, we used the rarefaction curves of Chagas et al. (2020). We also evaluated the species richness extrapolated to twice the sampling effort using the package *iNEXT* (*iNterpolation and EXTrapolation*; Chao et al. 2014). The relative abundance was calculated for each species (Mueller-Dombois and Ellenberg, 1974). We tested the data distribution using the Shapiro–Wilk test to corroborate the normality assumption (Crawley, 2013). We then used the Kruskal–Wallis H test (non-parametric test for non-normally distributed data) to compare the median and interquartile range of measures among plot types and plant stages ($p \leq 0.05$). We applied a posteriori Dunn's test to compare the median using Bonferroni adjustment to control the error rate (Dinno, 2017). The analyses were performed in R3.4.4 (R Core Team, 2019).

Generalised linear models were used to test the effect of target species, height of the central tree and altitude on the number of individuals, species richness and relative abundance of juveniles and adults in the communities. The link function for normal distribution and residual distributions of models was evaluated to select the quasi-Poisson distribution as the most suitable (Crawley, 2013). The number of individuals, species richness and relative abundance was selected as response variables in separate models for juveniles and adults. The predictors were represented by two continuous explanatory variables (altitude as an abiotic factor and height of the central plant as a biotic factor) and one categorical variable factor (i.e. plot). We also obtained a null model with only the intercept, and all variables in a single model formed the global model.

The models were compared using the Akaike information criterion (AIC). Those with the lowest AIC correction value for finite samples (Δ AICc) were considered the most suitable for the data (Burnham and Anderson, 2002). Models with Δ AICc<2.0 were considered equally plausible to explain the variation in observed data (Burnham and Anderson, 2002, Burnham et al. 2011). We also obtained the corrected Akaike weight (wAICc), indicating the relative suitability of the models (Portet, 2020). Analyses were performed in R3.4.4, using the packages vegan, APE and lme4. To estimate predictor coefficients on a comparable scale, we used the package jtools (Long, 2020).

To assess the similarity in species composition and abundance among plots, we applied the UPMGA (unweighted pair group method with arithmetic mean) based on Jaccard (Jaccard, 1908) and Bray–Curtis coefficients (Bray and Curtis, 1957). Cluster confidence was calculated based on bootstrap, using 1000 replications in PAST 3.23 (Hammer et al. 2001). For each plot, we calculated beta diversity and its turnover and nestedness components between juveniles and adults using the package *betapart* (Baselga, 2010), also implemented in R3.4.4.

## Results

We recorded 5,173 individuals belonging to 110 tree species: 76 species (2,264 individuals) as juveniles and 101 (2,909 individuals) as adults. Fifty-seven species (804 individuals) of juveniles and 85 species of adults (598) were recorded in Hancornia plots, 60 (746) of juveniles and 76 (1,077) of adults in Himatanthus plots and 60 (714) of juveniles and 78 (1,232) of adults in Control plots (Figure 2; Supplementary Information S2). Considering juvenile and adult trees in the three types of plots, 34 species (29.35%) were found exclusively as adults and nine (7.33%) exclusively as juveniles; 67 species (63.30%) were recorded in both stages. Hancornia plots had more exclusive species (15) than Himatanthus (5) and Control (3) plots; the three types of plots shared 33 (30.27%) species. Control plots showed more dead individuals (11) than Hancornia (5) and Himatanthus (9) plots (Supplementary Information S2).

The three plot types showed similar richness for juveniles when the sampling effort is controlled, tending to stabilisation after a rapid initial accumulation (Figure 3a). If twice the number of plots was collected for each type (extrapolated species richness), we expected an increase of seven species (64 vs 57) for juveniles in Hancornia plots, five (65 vs 60) in Himatanthus plots and 15 (75 vs 60) in Control plots (Figure 3a). The Hancornia plots showed higher richness for adult tree species when sampling effort is controlled; Himatanthus and Control plots showed similar richness, with the three types of plots tending to stabilise after a rapid initial accumulation (Figure 3b). If twice the number of plots was collected for each type (species richness extrapolated), increases of seven (92 vs 85) species were estimated for adults in Hancornia plots, five (81 vs 76) in Himatanthus plots and 15 (93 vs 78) in Control plots (Figure 3b).

Compared to Control plots, Hancornia plots showed lower abundance (number of individuals) and Himatanthus plots higher relative abundance in adults. No parameter analysed here showed significant differences between Control and Hancornia or Himatanthus plots for juveniles (Table 1). Relative abundance was higher in adults than in juveniles in all types of plots. However, Control plots showed relatively higher numbers of adult individuals (abundance) and species (richness), a difference not observed in Hancornia and Himatanthus plots. In contrast, Himatanthus plots showed a higher adult relative abundance, a relative difference not shared with Control and Hancornia plots (Table 2).

In juvenile trees, the best-fit models contained only the altitude variable with a significant positive effect for the number of individuals (~ 85%, Est. 0.008 $p < 0.001$), number of species (~ 65%, Est. 0.005 $p < 0.001$) and relative abundance (~ 65%, Est. 0.005 $p < 0.001$) (Fig. 4; Table 3). In adults, the best-fit models for

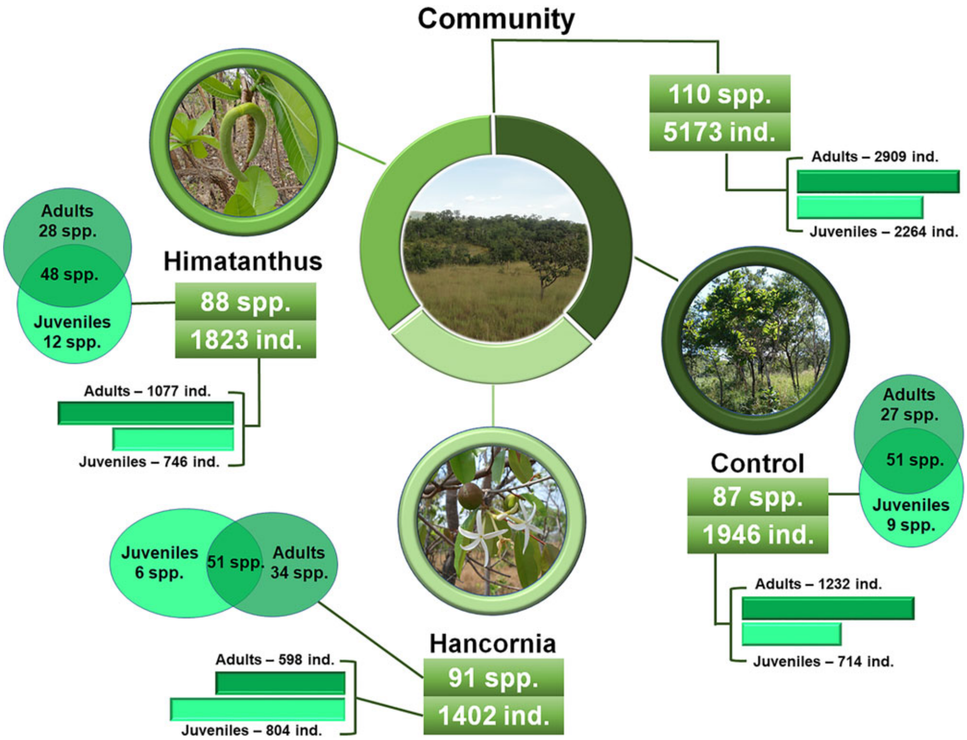

**Figure 2.** Sample design and results. Number of individuals (ind.) and species (spp.) in the woody community and associations of Hancornia, Himatanthus and Control plots, according to juvenile and adult trees.

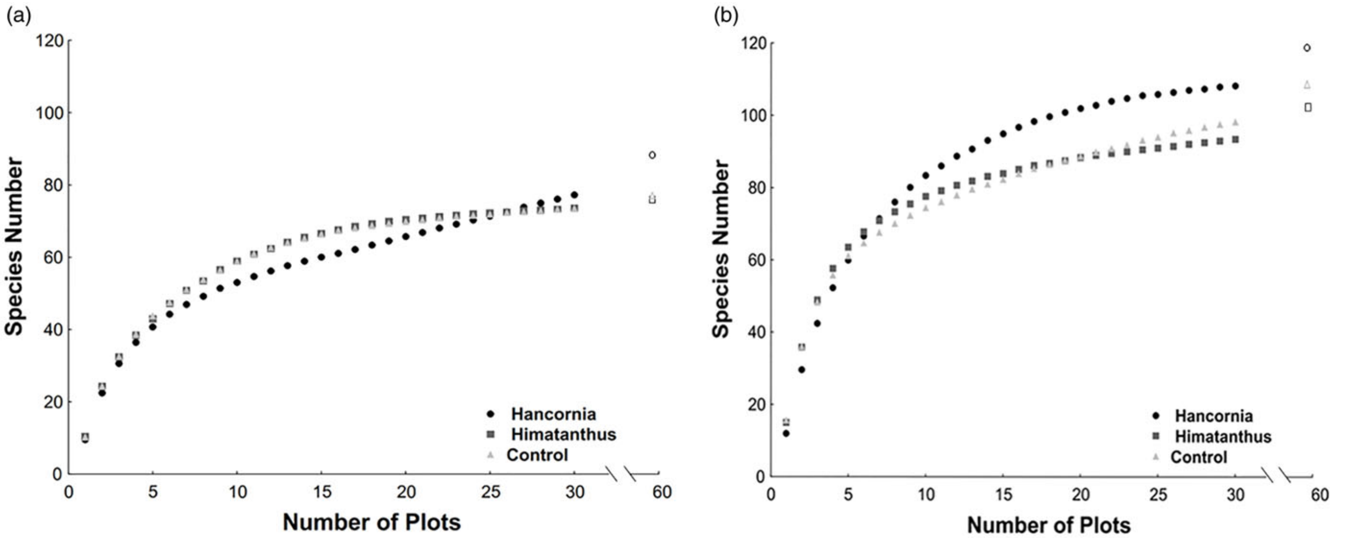

**Figure 3.** Expected number of species obtained from a rarefaction analysis based on the sampling effort (10 × 10 m plots) in Hancornia, Himatanthus and Control plots: (a) juvenile and (b) adult trees.

the number of individuals (~ 50%), number of species (~ 27%) and relative abundance (~ 53%) contained the variable plot (target species), in combination with altitude and height of the central plant, only altitude (though not significantly better than a null hypothesis) or alone, respectively (Figure 4; Table 3). For adults, the significant effects observed in the number of individuals were produced by Hancornia (Est. −0,682 $p < 0.001$) and the height of central plant (Est. −0,150 $p < 0.01$), in the number of species by Hancornia (Est. −0.306 $p < 0.05$) and altitude (Est. 0.004 $p < 0.05$) and in relative abundance by Himatanthus (Est. 0.378 $p < 0.01$; Table 3).

Similarity coefficients, both Jaccard and Bray–Curtis, highly supported clusters of juvenile and adult trees (Figure 5). Within these groups, Himatanthus plots were more dissimilar for juveniles and Hancornia plots more dissimilar for adults when compared to Control plots (Figure 5a); the higher dissimilarity of Hancornia plots for juveniles with Bray–Curtis was not supported (i.e. <50% bootstrap; Figure 5b)

Beta diversity between juveniles and adults was similar in the three types of plots, ranging from 0.281 in Hancornia plots to 0.294 in Himatanthus plots. However, the dissimilarity between juveniles and adults in Hancornia plots was mainly due to nestedness than

**Table 1.** Comparison between plot types (Hancornia, Himatanthus and Control) according to plant stages (juveniles and adults), showing median and interquartile range of number of individuals (abundance), number of species (richness) and relative (species) abundance

| | Juveniles | | | |
|---|---|---|---|---|
| | Hancornia | Himatanthus | Control | *P* |
| Number of individuals | 24.50 ± 21.00$^{a}$ | 25.0 ± 24.75$^{a}$ | 19.50 ± 17.25$^{a}$ | 0.781 |
| Number of species | 9.50 ± 4.00$^{a}$ | 9.50 ± 7.00$^{a}$ | 9.00 ± 4.75$^{a}$ | 1.000 |
| Relative abundance | 9.50 ± 4.00$^{a}$ | 9.50 ± 7.00$^{a}$ | 9.50 ± 0.82$^{a}$ | 0.936 |
| Adults | | | | |
| Number of individuals | 18.5 ± 15.5$^{a}$ | 25 ± 34.8$^{ab}$ | 45.00 ± 43.00$^{b}$ | 0.006** |
| Number of species | 10.00 ± 8.50$^{a}$ | 11.00 ± 11.80$^{a}$ | 18.00 ± 10.80$^{a}$ | 0.069 |
| Relative abundance | 11.5 ± 12.2$^{a}$ | 17.5 ± 6.75$^{b}$ | 9.00 ± 10.20$^{a}$ | 0.003** |

Medians and interquartile ranges followed by the same letter did not differ based on Kruskal–Wallis H test (i.e. $p > 0.05$); ** indicates $p < 0.01$.
$^{ab}$Medians and interquartile ranges followed by the same letter did not differ based on Kruskal–Wallis H test ($p < 0.05$).

**Table 2.** Comparison between life stages (juveniles and adults) according to each type of plot (Hancornia, Himatanthus and Control), showing median and interquartile range of number of individuals (abundance), number of species (richness) and relative (species) abundance

| | | Plant stages | | |
|---|---|---|---|---|
| Plots | Measures | Juveniles | Adults | *P* |
| Hancornia | Number of individuals | 24.50 ± 21.00 | 18.50 ± 15.50 | 0.131 |
| | Number of species | 9.50 ± 4.00 | 10.00 ± 8.50 | 0.402 |
| | Relative abundance | 9.50 ± 4.00 | 11.50 ± 12.20 | 0.235 |
| Himatanthus | Number of individuals | 25.00 ± 24.75 | 25.00 ± 34.8 | 0.168 |
| | Number of species | 9.50 ± 7.00 | 11.00 ± 11.80 | 0.175 |
| | Relative abundance | 9.50 ± 7.00 | 17.50 ± 6.75 | <0.001*** |
| Control | Number of individuals | 19.50 ± 17.25 | 45.00 ± 43.00 | 0.011* |
| | Number of species | 9.00 ± 4.75 | 18.00 ± 10.80 | 0.002** |
| | Relative abundance | 9.50 ± 0.82 | 9.00 ± 10.20 | 0.923 |

* Indicates $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$, based on Kruskal–Wallis H test.

turnover, whereas turnover in Himatanthus and Control plots was higher than nestedness (Table 4).

## Discussion

Our results support the hypothesis that *Hancornia speciosa* and *Himatanthus obovatus* act as biotic filters, influencing tree recruitment in woody communities within savannas. Therefore, they confirm that plant–plant interactions, extending beyond the extensively discussed complex tree–grass coexistence (e.g. Archibald et al. 2013, Chagas and Pelicice, 2018, Dantas et al. 2016, Flake et al. 2022, Holdo and Nippert, 2023, Lehmann et al. 2011, Levick and Rogers, 2011, Midgley et al. 2010, Sankaran, 2019, Sankaran et al. 2004, Scholes and Archer, 1997, Sharpe, 1992), also play a role in shaping savanna dynamics within life forms.

The distinct species composition patterns observed in juveniles and adults, along with lower tree abundance and a higher number of rare tree species during the adult stage, resulting in higher evenness (see Chagas et al. 2020), provide further evidence for the selective impact of *Hancornia speciosa* on the woody community. The beta diversity between juveniles and adults in *H. speciosa*-associated communities, primarily driven by nestedness, strengthens this hypothesis. Hence, *Hancornia speciosa* seems to restrict the coexistence of tree species and limit their abundance, as traditionally expected in communities primarily driven by negative interactions (Hutchinson, 1967, Tilman, 2004, Whittaker, 1967, 1969). Consequently, *H. speciosa* appears to function as a biotic filter during the development of woody plants.

The negative interactions of *H. speciosa* with neighbouring communities during the recruitment result in the exclusion of less-tolerant species, reducing tree richness and constraining populations of tolerant species. Consequently, the abundance of adults in the vicinity is kept lower, reducing the direct competition with other trees (see references in Schöb et al. 2014, Verdú et al. 2010). The lower abundance associated with *H. speciosa* possibly explains why fewer dead trees are found closer to this species. The vacant space and increased light resulting from plant exclusion in its vicinity are expected to facilitate new colonisations and the dominance of tolerant species, leading to higher abundances of juvenile trees and herbs (Grime, 1998, Lima and Gandolfi, 2009). The reduced tree cover favours the grass layer and consequently the likelihood of fires occurring closer to *H. speciosa*. However, no significant differences were found in the richness and abundance of herbs (Chagas et al. 2020) and juvenile trees associated with this species. Since germination is generally less affected by the negative influence of allelochemicals compared to plant growth (Gui Ferreira and Aquila, 2000, and references therein), selection pressure is probably more intense during development. This could

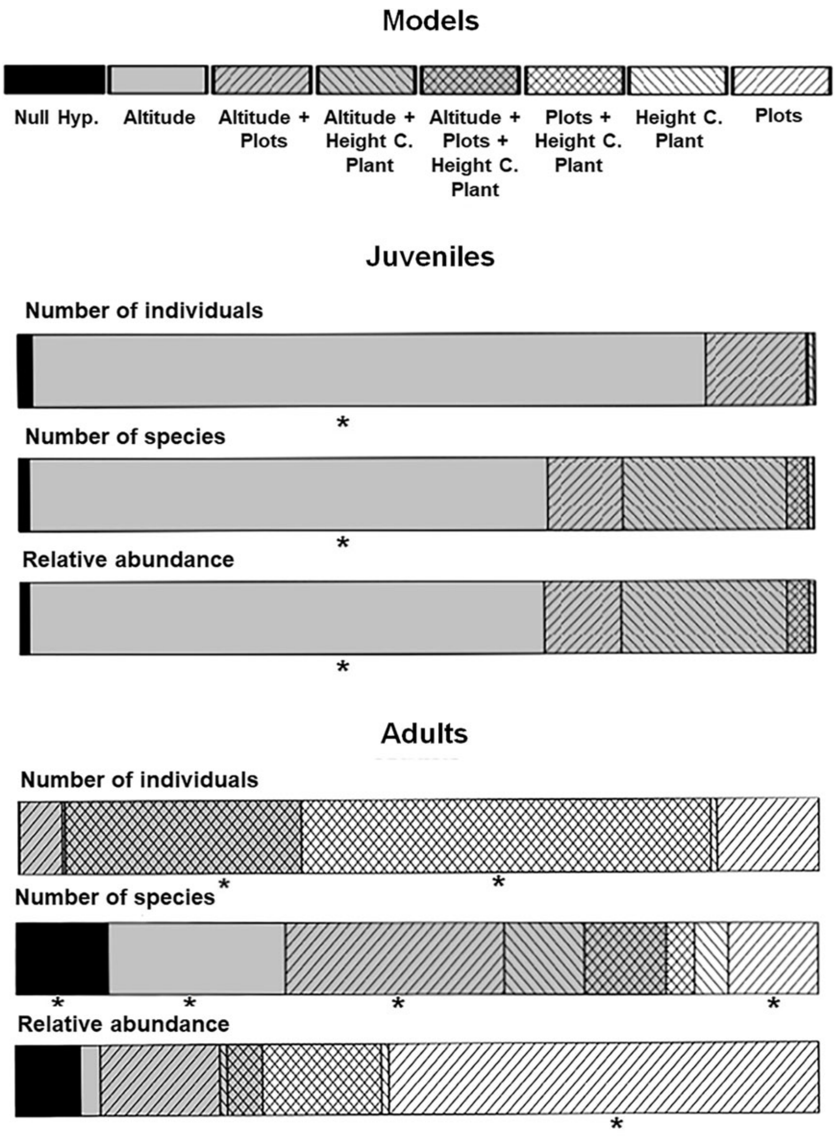

**Figure 4.** Influence of abiotic (altitude) and biotic (plots and height of the central plant) factors in explanatory models for the number of individuals (abundance), number of species (richness) and relative (species) abundance of (a) juvenile and (b) adult trees in Hancornia, Himatanthus and Control plots indicated by the corrected Akaike weight (wAICc); * indicates the most suitable models (Table 4 and Supplementary Information S3).

explain the observed differences in species composition and abundance between juvenile and adult trees (Barnes and Archer, 1999, Salles and Schiavini, 2007).

The higher dissimilarity of juvenile composition in the community surrounding *Himatanthus obovatus* suggests that this species has a greater influence on initial recruitment compared to *Hancornia speciosa* (Barnes and Archer, 1999, Peláez et al. 2019). It likely modifies the environment by providing shading, which in turn reduces surrounding temperature and water loss, thereby facilitating initial recruitment (Bruno et al. 2003, Stachowicz, 2001). Positive plant–plant interactions typically involve individuals from the upper strata (shrubs and trees) influencing the components of the lower stratum (herbs and juvenile trees; Barnes and Archer, 1999, Peláez et al. 2019, Vega-Álvarez et al. 2019). However, altitude was found to have a greater influence than target species in explaining the variation in communities of juvenile trees.

These positive or negative effects of biotic interactions observed in this study may have implications beyond the taxonomic attributes of plant communities (i.e. species richness, species composition, dissimilarity pattern) under different target species and control treatment. For example, it has been shown that density-dependent biotic factors can affect the phylogenetic structure of plant communities (Campos et al. 2021, Carrión et al. 2017, Galván-Cineros et al. 2023). Specifically, in a scenario of high floristic similarity (i.e. phylogenetically related species are ecologically more similar), their ecological traits can be conserved within evolutionary niches, and then facilitation can be the primary process determining phylogenetic overdispersion (Cavender-Bares et al. 2009, Webb et al. 2002). However, facilitation also can promote phylogenetic evenness if ecological traits are predominantly convergent (Carrión et al. 2017, Cavender-Bares et al. 2009). Furthermore, we presume that the higher dissimilarity of juveniles is shaped by colonisations and stochastic recruitment processes (i.e. under neutrality-based stochastic hypotheses; Cavender-Bares et al., 2009; Webb et al., 2002), which can determine a random phylogenetic structure simultaneously with environmental factors in the Cerrado.

## Implications for conservation

The MATOPIBA region intersects the Amazon agricultural frontier within the eastern and southern Amazonia, commonly

**Table 3.** Parameters and *p*-values estimated in the generalised linear model explaining the number of individuals, number of species and relative abundance of the influence of abiotic (altitude) and biotic (plots and height of central plant) factors in juvenile and adult trees

| | | Juveniles | | Adults | |
|---|---|---|---|---|---|
| | Fixed factors | Estimate | *p*-value | Estimate | *p*-value |
| Number of individuals | (Intercept) | 1.243008 | 0.03915* | 3.432108 | 1.33E-06*** |
| | Plots Han[1] | 0.156134 | 0.31786 | −0.68168 | 0.00025*** |
| | Plots Him[1] | 0.154442 | 0.32775 | −0.07458 | 0.68775 |
| | Altitude | 0.008077 | 0.00052*** | 0.003306 | 0.23003 |
| | Height of central plant | −0.05036 | 0.29914 | −0.1501 | 0.00922** |
| Number of species | (Intercept) | 0.984471 | 0.01665* | 1.657348 | 0.00239** |
| | Plots Han[1] | −0.05947 | 0.57247 | −0.30627 | 0.03145* |
| | Plots Him[1] | 0.041036 | 0.69662 | −0.0494 | 0.72668 |
| | Altitude | 0.005122 | 0.00116** | 0.004669 | 0.02699* |
| | Height of central plant | 0.00504 | 0.87524 | −0.03461 | 0.42992 |
| Relative abundance | (Intercept) | 0.969748 | 0.01845* | 2.365168 | 9.57E-06*** |
| | Plots Han[1] | −0.06288 | 0.55094 | 0.06596 | 0.64017 |
| | Plots Him[1] | 0.04054 | 0.70027 | 0.377768 | 0.00686** |
| | Altitude | 0.005157 | 0.00108* | 0.000287 | 0.88975 |
| | Height of central plant | 0.007259 | 0.82109 | 0.004189 | 0.92144 |

[1] Difference between Control plots and Hancornia (Han) and Himatanthus (Him) plots.

* Indicates *p*-values < 0.05, ** *p*-values < 0.01 and *** *p*-values < 0.001.

**Table 4.** Beta diversity (total dissimilarity) and their components (turnover and nestedness) between juvenile and adult trees in Hancornia, Himatanthus and Control plots

| Plots | Turnover | Nestedness | Total dissimilarity |
|---|---|---|---|
| Hancornia | 0.105 | 0.176 | 0.281 |
| Himatanthus | 0.200 | 0.094 | 0.294 |
| Control | 0.183 | 0.101 | 0.284 |

called the 'arc of deforestation'. This vast area is experiencing intense degradation in the Cerrado–Amazonia transition (Marques et al. 2020). The deforestation in this region can have implications for the climate, potentially leading to prolonged and warmer dry seasons in the region (Costa and Pires, 2010, Marengo et al. 2022). The savannas of Tocantins studied here are located in the centre of an extensive area characterised by bi-stable tree cover conditions (Staver et al. 2011), at the interface between two phytogeographic domains, one currently covered mainly by savannas and the other dominated by forests; they are under significant threats from land use (Marques et al. 2020, Pivello et al. 2021, Sano et al. 2019) and local climate change (Costa and Pires, 2010).

Fire is a recurrent disturbance in this region, impacting areas of varying sizes and resulting in landscapes with patches at different stages of regeneration. Consequently, the savannas consist of mosaics of associations at different successional stages, with distinct species composition and abundance (Chagas and Pelicice, 2018, Silva et al. 2011). Effective fire management is essential for maintaining the diversity of vegetation types and plant diversity within this mosaic (Abreu et al. 2017, Arnan et al. 2020, Buisson et al. 2019, Durigan et al. 2020, Pivello et al. 2021). However, the composition and structure of plant communities can also influence soil nutrients as well as nutrient turnover and availability (Pellegrini, 2016). Consequently, they play a role in shaping the heterogeneity of tree cover and the distribution of fire regimes in savanna landscapes.

Differences observed between juvenile and adult trees in our study support the negative influence of *H. speciosa* on the neighbouring plant community and suggest the possibility of a positive interaction between *H. obovatus* and the surrounding plant community (Barnes and Archer, 1999, Peláez et al. 2019). In regions where *H. speciosa* is more prevalent, there is a tendency for trees to be less abundant compared to the average savanna, which potentially increases the risk of fires and reduces the likelihood of forest encroachment. Both species act as structuring agents in regenerating communities and contribute to the formation of successional mosaics of associations, resulting in higher levels of beta diversities in fire-prone savannas.

Tree recruitment in savannas can be directly influenced by the composition and abundance of adult trees, but it is also shaped by environmental filters and limiting biotic interactions (Cadotte and Tucker, 2017, Lortie et al. 2004). In the absence of disturbance, tree-on-tree competition is a potential limiting factor for tree cover, thereby impacting tree–grass ratios (Sankaran et al. 2004). This study demonstrated that local tree-on-tree interactions can also drive the composition and structure of woody communities in savannas with intense fire regimes. These interactions affect tree cover and contribute to landscape heterogeneity at a regional scale. Considering the spatial distribution of tree species and their associated communities is crucial for understanding savanna dynamics and should be noticed in management plans and restoration projects. Therefore, tree-on-tree interactions should be taken into account when implementing burning patch mosaics in

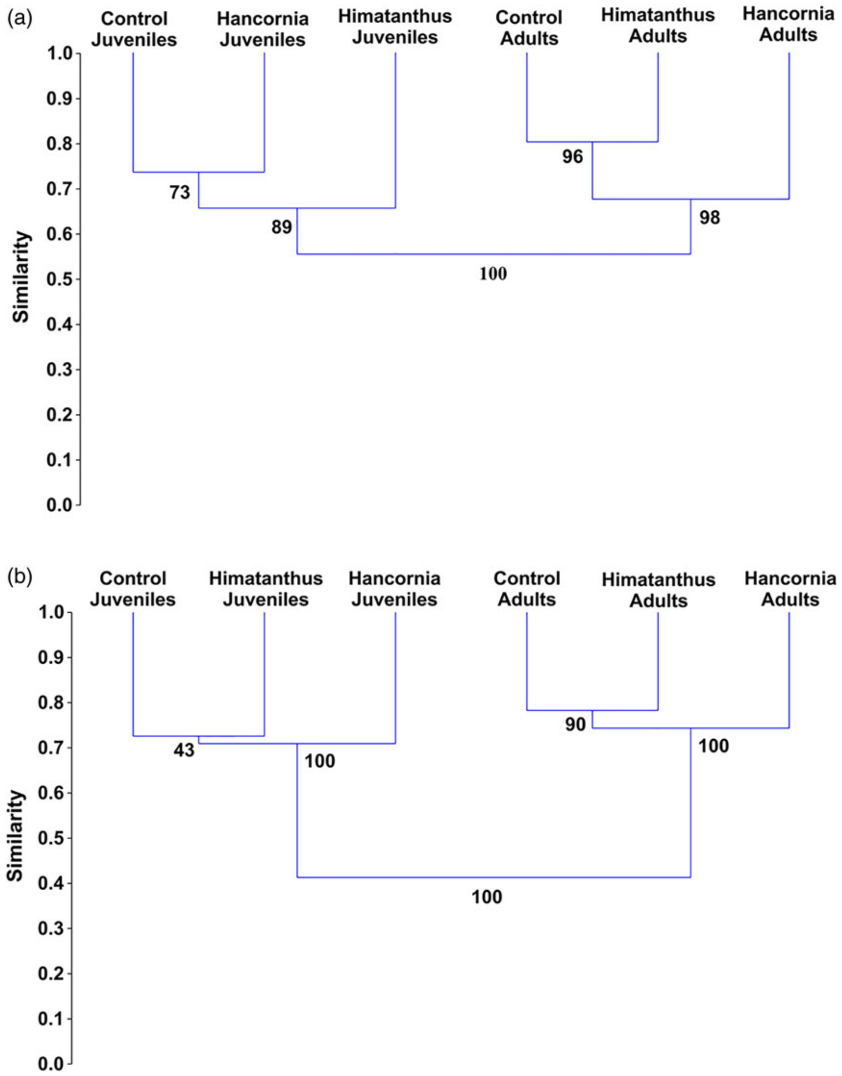

**Figure 5.** Dendrogram of similarity between woody species for juvenile and adult trees: (a) Jaccard coefficient, based on species presence and absence matrix and (b) Bray–Curtis coefficient, based on species abundance matrix.

savannas to ensure the persistence of ecological processes essential for biodiversity maintenance.

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