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The introduced tree *Prosopis juliflora* is a serious threat to native species of the Brazilian Caatinga vegetation

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HIGHLIGHTS

- *Prosopis juliflora* reduced growth of native Caatinga species tested.
- *P. juliflora* increased the mortality of all species of native plants tested.
- *Mimosa tenuiflora* and *Caesalpinia ferrea* had the lowest mortality and highest height.
- *M. tenuiflora* and *C. ferrea* may present a viable option to management systems.

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ABSTRACT

Despite its economic importance in the rural context, the *Prosopis juliflora* tree species has already invaded millions of hectares globally (particularly rangelands), threatening native biodiversity and rural sustainability. Here we examine seedling growth (leaf area, stem diameter, plant height) and seedling mortality across five native plant species of the Caatinga vegetation in response to competition with *P. juliflora*. Two sowing treatments with 10 replications were adopted within a factorial 2 × 5 randomized block design. Treatments consisted of *P. juliflora* seeds sowed with seeds of *Caesalpinia ferrea*, *Caesalpinia microphylla*, *Erythrina velutina*, *Mimosa bimucronata* and *Mimosa tenuiflora* (one single native species per treatment), while seeds of native species sowed without *P. juliflora* were adopted as controls. Overall, our results suggest that *P. juliflora* can reduce seedling growth by half and cause increased seedling mortality among woody plant species. Moreover, native species exhibit different levels of susceptibility to competition with *P. juliflora*, particularly in terms of plant growth. Such a superior competitive ability apparently permits *P. juliflora* to establish monospecific stands of adult trees, locally displacing native species or limiting their recruitment. The use of less sensitive species, such as *C. ferrea* and *M. tenuiflora*, to restore native vegetation before intensive colonization by *P. juliflora* should be investigated as an effective approach for avoiding its continuous spread across the Caatinga region.

1. Introduction

Biological invasions have emerged as a major threat for global biodiversity as they already represent one of the main causes of species extinction (Vitousek et al., 1996, 1997; Lenda et al., 2013). In addition to species extinction and biotic homogenization at multiple spatial scales, synergisms between human-mediated disturbances and biological invasions may threaten ecosystem integrity further by providing biomass for intense fires, for example (van Wilgen et al., 2008). In the case of plants, deliberate introductions of "useful species" represent the major source for the increment of exotic floras, from which many species achieve invasive status (Pyšek, 1998; Chapple et al., 2012).

Prosopis juliflora (Sw.) DC L., 1753 is an evergreen tree species, which is native of rangelands (i.e. steppe and savanna-like vegetation types) in South America, Central America and the Caribbean. It refers to a fast growing species, which is tolerant to arid conditions and saline soils; i.e. a drought-resistant species (Pasiecznik et al., 2004; El-Keblawy and

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Al-Rawai, 2005) like others within this genus (Adams et al., 2010). In addition to its aggressive nature, *P. juliflora* can provide valuable goods and services, such as timber, firewood and soil rehabilitation (Pasiecznik et al., 2001). These "desirable" characteristics have fuelled intentional introductions of *P. juliflora* across rural areas globally, with the consequent invasion of millions of hectares of rangelands in South Africa, East Africa, Australia, coastal Asia (Pasiecznik, 1999), and America (Kemp and Michalk, 2005). *P. juliflora* is now one of the top global invasive plant species according to the International Union for Conservation of Nature (IUCN).

One of the key attributes frequently exhibited by invasive species is their superior competitive ability as compared to native species (Rejmánek and Richardson, 1996). For example, *P. juliflora* can displace both agricultural and exotic plants and native species (Mwangi and Swallow, 2005) by delaying seed germination and reducing plant growth in terms of roots, shoots, leaf area, stem diameter, and plant height (Inderjit et al., 2008). Studies suggest that allelopathic substances produced by *P. juliflora*'s leaves, fruits, seeds, roots and flowers (Noor et al., 1995) affect species such as *Bambusa arundinacea* (Retz.) Willd. (Poaceae) (Inderjit et al., 2008) and *Echinochloa crus-galli* (L.) Beauv (Poaceae) (Goel et al., 1989; Nakano et al., 2003, 2004). Direct competition in addition to allelopathy may be the forces behind the successful invasion of sedimentary lowlands and alluvial river plains by *P. juliflora* (Pegado et al., 2006; Siddiqui et al., 2009), although evidence in favor of such a superior competitive ability is still scarce. In these more humid habitats (wetlands, riverbanks, alluvial plains), the first individuals form small agglomerates, from which *P. juliflora* expands and forms monospecific and persistent stands (Archer, 1995; Rajwant et al., 2012).

The Caatinga vegetation is a mosaic of scrub vegetation and patches of dry forest (Leal et al., 2005), which has been considered as a seasonally dry tropical forest in northeast Brazil (Bullock et al., 1995; Pennington, 2006; Santos et al., 2011). This singular biogeographic area (covering ca. 800,000 km^2) supports more than 1500 plant species, including a myriad of endemics; i.e. nearly 1/3 of the Caatinga flora consists of endemic species (Araújo et al., 2007; Albuquerque et al., 2012). As a semiarid region devoted primarily to activities such as agriculture and cattle-raising, the Caatinga has experienced deliberate species introductions as attempts to improve or turn viable farming-based activities (Cavalcante and Major, 2006). This region has also faced intensive habitat degradation from soil exhaustion, particularly in the case of low-input agriculture and over grazing by livestock, creating a sort of synergism between human poverty and environmental degradation (Leal et al., 2005; Santos et al., 2011).

In this socio-ecological context, *P. juliflora* was introduced in the Caatinga region in the 1940s (Pegado et al., 2006) as a source of forage for livestock, charcoal, firewood, cuttings and stakes, among other uses (Pometti et al., 2007). Economically, *P. juliflora* is a key element across several land use systems that apparently have improved rural livelihoods (Rajwant et al., 2012) and prevented further soil degradation (El-Keblawy and Abdelfatah, 2014). Conversely, *P. juliflora* has naturally spread over degraded river banks and other habitats previously disturbed by human activities (i.e. *P. juliflora* has achieved the invasive status), establishing monospecific stands which, in the case of the Caatinga vegetation, compete with a myriad of native plant species such as *Caesalpinia pyramidalis* Tul. (Fabaceae) (Pegado et al., 2006) and *Pilosocereus tillianus* R. Gruber & Schatzl (Cactaceae) (Larrea-Alcázar and Soriano, 2006). In this region, *P. juliflora* is also able to compete with traditional short-cycle crops such as maize (*Zea mays* L., Poaceae) and cotton (*Gossypium hirsutum* L., Malvaceae) (Porto Filho, 1981). One single *P. juliflora* tree is able to produce between 630,000 and 980,000 seeds per year (Hardin, 1988) which are then consumed and scarified by livestock, with a subsequent deposition in the ground and mixed with manure, resulting in increased germination and invasive potential (Felker, 2003).

For the sake of both the Caatinga biodiversity and rural sustainability we must understand the mechanisms providing the increased invasive potential exhibited by *P. juliflora* and inform stakeholders about restoration and/or management techniques to mitigate potential negative impacts resulting from spread of this plant at regional scale. Here we examine the seedling performance across five native woody plant species of the Caatinga vegetation as exposed to competition with *P. juliflora* in two experimental conditions: native species growing alone (controls) or in mixed stands with *P. julifora* (treatments). Seedling growth (height, stem diameter and leaf area) and mortality were monitored during a six-month period. We hypothesize that plants experiencing interspecific competition will exhibit lower total biomass than those that grow alone (Laird and Aarssen, 2005). We discuss the uncovered patterns in the context of biological invasion, particularly the ecology of *P. juliflora* and sustainable development of the Caatinga region.

2. Materials and methods

2.1. Experimental site and native plant species

The study was carried out in 2006 at the experimental station of the Center for Agricultural Research in the Semi-Arid Tropic, which is located in the Petrolina municipality (09° 23′S and 40° 30′W, 376 m a.s.l.), Northeast Brazil (Fig. 1). Five woody species from the Fabaceae family were selected because species of this family usually form symbiotic associations with *Rhizobium* (Rhizobiales: Rhizobiaceae). In fact, most of the Fabaceae species are able to establish symbiotic relationships with nitrogen-fixing bacteria in the Caatinga vegetation, helping to maintain soil fertility (Teixeira et al., 2006). Additionally, Fabaceae species represent a substantial portion of the Caatinga flora (from herbs to tree species), with characteristic taxa inhabiting the majority of the Caatinga

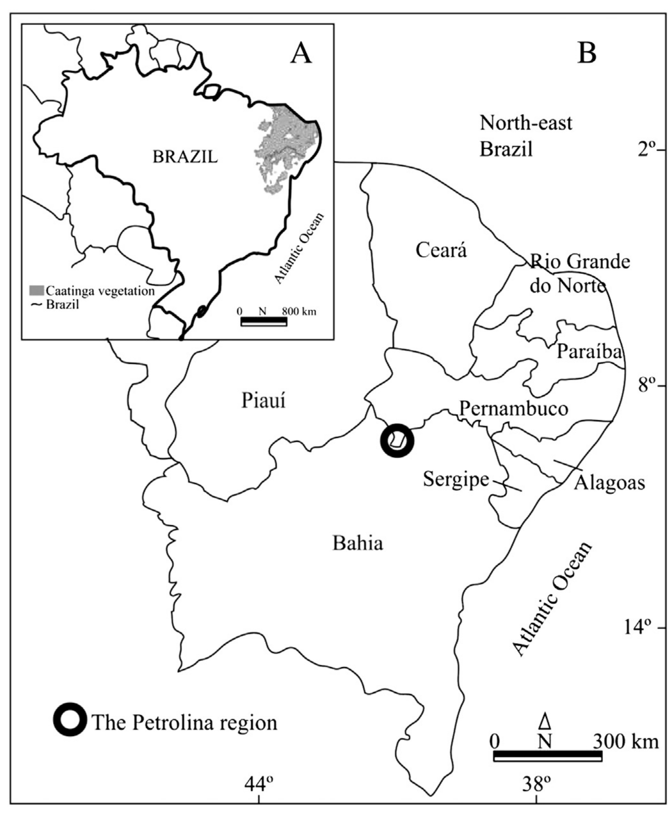

Fig. 1. The area covered by the Caatinga vegetation (A), and location of the Petrolina region, north-east Brazil (B).
Source: adapted from Leal et al. (2007).

habitats, including degraded areas (Leal et al., 2003, 2005). Fabaceae, Euphorbiaceae, Cactaceae and Bromeliaceae account for the majority of native plant species in the Caatinga vegetation (Giulietti et al., 2004). We adopted: *Mimosa tenuiflora* (Willd.) Poir., *Erythrina velutina* Willd., *Mimosa bimucronata* (De Candolle, O. Kuntze), *Caesalpinia microphylla* Mart. ex G. Don and *Caesalpinia ferrea* Mart. ex Tul.

2.2. Experimental design and plant parameters

The experiment consisted of a randomized block and factorial design with 2 × 5 treatments with 10 replications which consisted of two types of sowing methods: (1) seeds of each native species sowed separately (controls), and (2) seeds of *P. juliflora* interspersed with seeds of each native species. Across controls (one for each native species), fifty-six seeds per plot were sown at 6 × 6 cm spacing, leaving 26 seeds as a margin. In the treatments, half of the seeds were from *P. juliflora* and the other half from native species, resulting in five combinations of *P. juliflora* and native species. Seed dormancy was artificially broken by a small cutting with blunt scissors into the seed side opposite to the micropylar region. This procedure usually facilitates water absorption and standardizes seed germination (Bastos et al., 1992). Seeds were then sown into iron barrels measuring 56 cm in diameter and 50 cm in height and filled with Caatinga soils. Irrigation was carried out three times a day using two liters of water per plot. The effects of interspecific competition between plants may be inferred from the relationship between distance and size of neighboring plants on the assumption that competition among them is density-dependent; i.e. the smaller the spacing, the lower the development and survival (Larrea-Alcázar and Soriano, 2006).

Fifteen randomly selected seedlings were assessed per plot and species every 20 days along a six-month period. Height, stem diameter and seedling mortality were recorded. Plant height and stem diameter were measured with a ruler and digital caliper, respectively. Leaf area was determined for two central plants in each plot for each treatment, using an area meter LI-3100, LI-COR. Leaf area, stem diameter, plant height and mortality among native species at the end of the experimental period were used for statistical analyses. By examining the impact caused by *P. juliflora* across five species we are able to address the generality of uncovered patterns. We chose an experimental approach versus a field approach to better control environmental variations, such as soil conditions for example. Note that allelopathy is a potential mechanism influencing interspecific competition in this biological system. Finally, our mixed flocks of seeds mimic those occurring in the natural conditions as flocks of *P. juliflora* reach the ground via feces of livestock (Nascimento, 2008).

2.3. Data analyses

Cross-treatment and cross-species differences in terms of seedling growth and mortality were compared via analyses of variance followed by Student–Newman–Keuls tests available from the Statistical Analysis System and Genetics package (SAEG) (Ribeiro Júnior, 2001).

3. Results

Leaf area differed among sowing methods ($F = 140.89$, $p < 0.0001$) and species examined ($F = 7.89$, $p < 0.0001$), with a significant interaction between these two explanatory variables ($F = 12.05$, $p < 0.0001$; Table 1). Mean leaf area was similar across native species whether or not they were interspersed with *P. juliflora*. However, native species exhibited reduced leaf area when interspersed with *P. juliflora* (Fig. 2). *E. velutina* and *C. ferrea* exhibited the highest and lowest leaf areas when growing alone, respectively.

The sowing treatment ($F = 42.34$, $p < 0.0001$) and species tested ($F = 493.42$, $p < 0.0001$) affected plant growth in terms of stem diameter. However, there was no interaction between these variables ($F = 1.72$, $p < 0.152$; Table 1), indicating similar responses among plant species. Overall, seedlings exhibited lower stem diameter in the presence of *P. juliflora* as compared to the controls (Fig. 3A). *E. velutina* exhibited the highest stem diameter while *C. microphylla* and *C. ferrea* exhibited the lowest (Fig. 3B).

Mean increments in seedling height followed the same pattern observed for stem diameter, with differences occurring between sowing treatment ($F = 79.36$, $p < 0.0001$) and plant species ($F = 79.75$, $p < 0.0001$). Again, the interaction between species and sowing treatment was not significant ($F = 0.19$, $p < 0.530$; Table 1). Lower growth rates were recorded among native seedlings interspersed with *P. juliflora* (Fig. 4A). Major increments were recorded for *M. tenuiflora* and *C. ferrea,* while there was only a minor increment in height for *C. microphylla* (Fig. 4B). Finally, sowing treatment affected plant mortality ($F = 25.67$, $p < 0.0001$) and species tested ($F = 21.67$, $p < 0.0001$), without interaction between these variables ($F = 0.19$, $p < 0.442$; Table 1). Seedlings interspersed with *P. juliflora* experienced higher mortality (Fig. 5A), with the lowest scores for *M. tenuiflora* and *C. ferrea* and the highest for *M. bimucronata* (Fig. 5B).

4. Discussion

Overall, *P. juliflora* can reduce seedling growth in terms of leaf area, stem diameter and plant height, as well as increase seedling mortality among native woody plant species of the Caatinga vegetation. Moreover, native species exhibit different levels of susceptibility to the presence of *P. juliflora*, particularly in terms of plant growth. Our results showed a 30%-reduction on plant growth (i.e. lower total biomass) with a similar decrease in seedling survivorship. Finally, such tangible and biologically relevant impacts emerge rapidly as seedlings were monitored for a short six-month period following seed germination. In case such trends are maintained, our results represent an underestimate of the total impact imposed on the recruitment of native species by *P. juliflora*.

P. juliflora negatively affected the early establishment of native plant species under certain conditions, although at this moment we are not able to separate those effects from direct competition for resources (e.g. water, nutrients and lights) from those resulting from allelopathic substances potentially produced by *P. juliflora* seedlings

Table 1
Summary of analysis of variance for leaf area, stem diameter, plant height and mortality of native plants according to sowing treatment and plant species. Petrolina, Pernambuco State, Brazil.

Variation source	Degrees of freedom average square		*F*	*P*
Leaf area [a]				
Sowing	1	1790.58	140.89	0.0001
Native species	4	100.29	7.89	0.0001
Sowing × native species	4	153.12	12.05	0.0001
Residue	90	12.71		
Diameter				
Sowing	1	47.53	42.34	0.0001
Native species	4	553.81	493.42	0.0001
Sowing × native species	4	1.93	1.72	0.152
Residue	90	1.12		
Height				
Sowing	1	391121.40	79.36	0.0001
Native species	4	393076.80	79.75	0.0001
Sowing × native species	4	2614.30	0.19	0.530
Residue	90	4928.70		
Mortality [a]				
Sowing	1	10.93	25.67	0.0001
Native species	4	9.22	21.67	0.0001
Sowing × native species	4	0.19	0.19	0.442
Residue	90	0.43		

[a] Data transformed to chi square root (x +0.5) for statistical analysis.

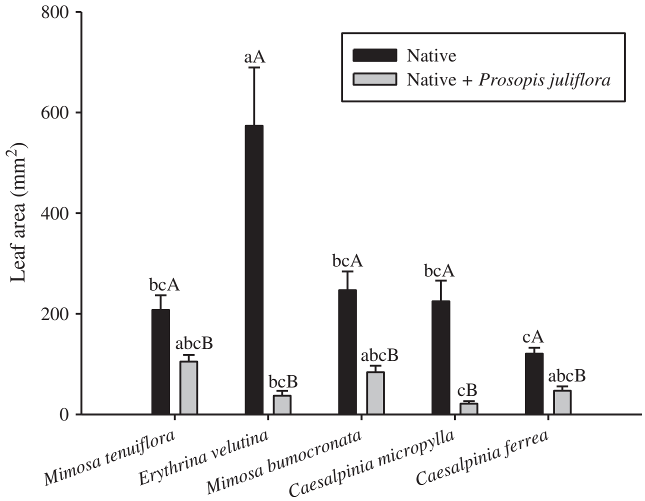

Fig. 2. Average seedling leaf area (±SE) exhibited by native plant species of the Caatinga vegetation per sowing treatment Student–Newman–Keuls test: columns followed by the same lower case letter per plant species or upper case letter per sowing treatment are not different (P = 0.05). Bars indicate the standard error.

(Pometti et al., 2007). Such a superior competitive ability is also supported by the reduced abundance of some Cactaceae species [*Stenocereus griseus* (Haw.) Buxb., *Cereus repandus* Haw. and *P. tillianus*] beneath adults of *P. juliflora* as compared to adults of Caatinga native species (Larrea-Alcázar and Soriano, 2006). Conversely, even seedlings of *P. juliflora* may respond negatively to light competition as they reduce biomass production and leaf area (Perez et al., 1999) beneath tree canopies or while growing in pastures (Pasiecznik, 2002). Similar results have been found for *Prosopis glandulosa* Torr. (Fabaceae) (Bush and Van Auken, 1987, 1990).

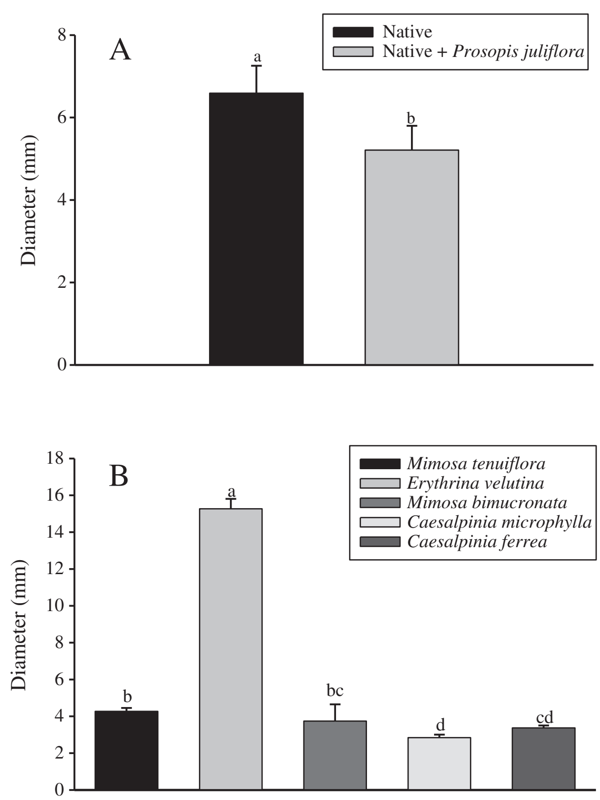

Fig. 3. Average seedling stem diameter (±SE) per sowing treatment (A) and plant species of the Caatinga vegetation (B). Student–Newman–Keuls test: columns followed by the same small letter are not different (P = 0.05).

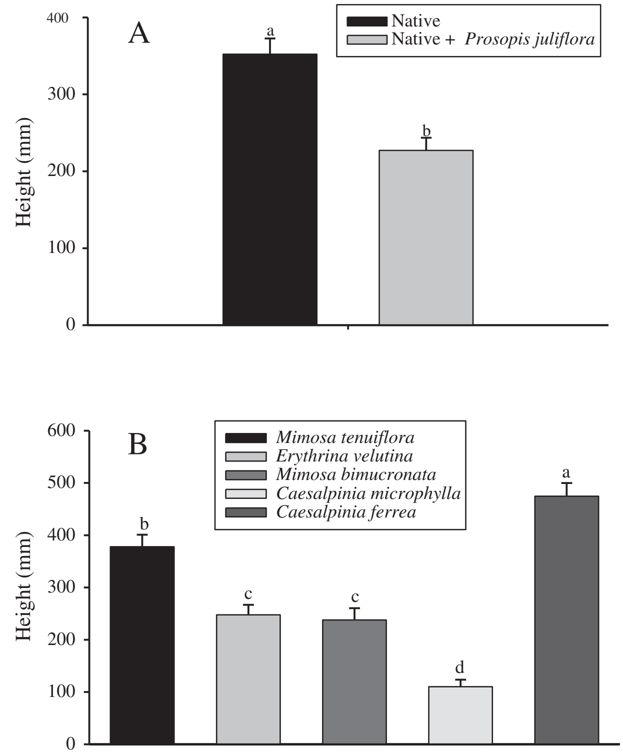

Fig. 4. Average seedling height (±SE) per sowing treatment (A) and plant species of the Caatinga vegetation (B). Student–Newman–Keuls test: columns followed by the same small letter are not different (P = 0.05).

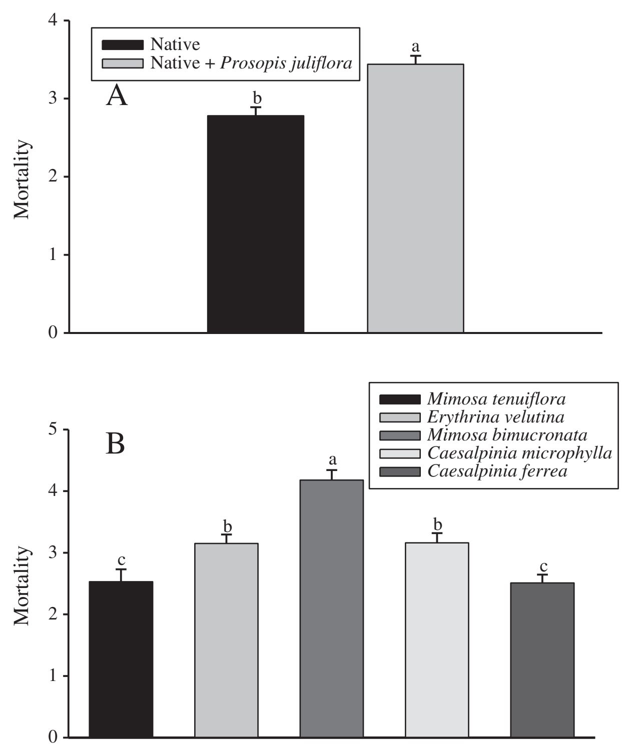

Fig. 5. Average seedling mortality (±SE) per sowing treatment (A) and plant species of the Caatinga vegetation (B). Student–Newman–Keuls test: columns followed by the same small letter are not different (P = 0.05).

Despite the scarcity of research addressing the invasion ecology of *P. juliflora* in the Caatinga region, we hypothesize the following scenario. Through intentional introductions in rural landholdings, *P. juliflora* reaches river banks/alluvial areas previously degraded by agriculture or overgrazing by livestock, most notably through gut seed dispersal by domestic animals (Nascimento, 2008). In these illuminated and humid habitats, a superior competitive ability (as suggested here) may permit *P. juliflora* to establish monospecific stands of adult trees (over 100 adult trees and 3000 saplings per hectare), locally displacing native species or limiting their recruitment (Lins e Silva, 1997; Pegado et al., 2006; Nascimento, 2008). Such "gallery forest stands" dominated by *P. juliflora* already represent a "typical" physiognomy across thousands of hectares in the entire Caatinga region (Negreiros et al., 1991). Stands result from a synergic relationship with rural activities as they provide (1), diaspore sources, (2) domestic animals acting as effective seed dispersers, and (3) degraded/open habitats to be colonized. However, even with a "superior" competitive ability, *P. juliflora* is not able to invade undisturbed stands of Caatinga vegetation, probably due to reduced light availability (Nascimento, 2008).

Humid areas represent key habitats for native biodiversity in semiarid regions (Bullock et al., 1995; Rodal et al., 2005). The Caatinga socio-ecological scenario is very similar to those described for rural areas in Africa, where there have been public appeals and intense debates for the appropriate management or even eradication of *P. julifora* stands for a series of reasons, including invasion of crop fields and communal grazing areas (Mwangi and Swallow, 2005). The use of less sensitive species, such as *M. tenuiflora* and *C. ferrea*, to restore native vegetation before intensive colonization by *P. juliflora* is one among many approaches probably required for avoiding its continuous spread across the Caatinga region (Lacerda et al., 2010). Further studies should investigate the efficiency of such approach.

Conflict of interest statement

The authors declare that they have no competing financial interests.

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