

Biological invasion of *Leucaena leucocephala* (Lam.) de Wit (Fabaceae) in the "Parque Nacional de Brasília", Brazil¹

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ABSTRACT - (Biological invasion of *Leucaena leucocephala* (Lam.) de Wit (Fabaceae) in the "Parque Nacional de Brasília", Brazil). This paper evaluated the occurrence of *Leucaena leucocephala* (Lam.) de Wit in an area located inside the Brasília National Park (Distrito Federal). Local environmental characteristics were examined to determine how they influenced the plant's dispersal and the distance traveled by the species', in addition to identifying the classes of invasive individuals, according to their height. The ANCOVA test was used to assess the effect of distance and to show how this effect depends on the environment. Results show that the number of classes does not depend on the distance from the point of introduction and that the population behaves as an invader, according to the criteria used to measure the invasiveness of woody plants with seeds. It was also found that the status of the environment (particularly the degree of conservation of the native flora and exposure to sunlight) is the strongest limiting factor affecting the number of classes of individuals and the production of fruits. Knowledge of these biophysical factors can guide park staff in making decisions about management options for controlling or eradicating invasive populations.

Keywords: biological invasions, Cerrado, invasive species, protected areas

RESUMO - (Invasão biológica de *Leucaena leucocephala* (Lam.) de Wit (Fabaceae) no Parque Nacional de Brasília, Brasil). Este artigo avaliou a ocorrência de *Leucaena leucocephala* (Lam.) de Wit em uma área localizada dentro do Parque Nacional de Brasília (Distrito Federal). Foi examinado como as características ambientais locais influenciaram a dispersão da planta e a distância percorrida pela população. Foram identificadas as classes dos indivíduos invasores de acordo com suas alturas. Para verificar o efeito da distância e como esse efeito depende do tipo de ambiente foi usado o teste ANCOVA. Os resultados mostram que o número de classes não depende da distância do ponto de introdução e que a população se comporta como invasora, de acordo com os critérios utilizados para medir a capacidade invasiva de plantas lenhosas com sementes. Constatou-se também que o estado do ambiente (particularmente o grau de conservação da flora nativa e a exposição à luz solar) é um forte fator limitante que afeta o número de classes de indivíduos e a produção de frutos. O conhecimento desses fatores biofísicos pode orientar as decisões da equipe gestora do parque sobre as opções de manejo para controlar ou erradicar as populações invasoras.

Palavras-chave: áreas protegidas, Cerrado, espécies invasoras, invasão biológica

Introduction

Biological invasions figure among current major global environmental changes. Human activities enable and even cause many invasive episodes (Chong *et al.* 2006, Meyerson & Mooney 2007, Hulme 2009, IPBES 2019). An environment's potential to be

invaded by exotic species rests on three factors: (i) number and frequency of propagules introduced into the new environment, (ii) biological characteristics of the invasive species and (iii) the environment's susceptibility to invasion (Lonsdale 1999, Blackburn *et al.* 2011). Invasive species can cause changes in communities and entire ecosystems, *e.g.* through

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biodiversity loss and changes in ecosystem services and functions (e.g. Sala *et al.* 2000, Butchart *et al.* 2010, IPBES 2019). There is a wide consensus about the fact that disturbed environments are particularly susceptible to invasions (Simberloff 2013). For Davis *et al.* (2000), disturbances make resources (soil nutrients or luminosity) available to introduced exotic species, supporting their establishment. To be considered invasive, an exotic species must prosper in natural ecosystems (disturbed or not), unaided by humans, and reduce the abundance and richness of native species (Richardson *et al.* 2000, Blackburn *et al.* 2011).

Historically, research on biological invasions and exotic species with invasive potentials has addressed three themes: (i) the species' reproductive and establishment properties, combined with their genetic and eco-physiological attributes (Barret & Richardson 1986 apud Chong *et al.* 2006, Werle 2012, p. 197, Simberloff 2013 p. 29); (ii) habitat characteristics and properties of invaded communities (Rejmánek 1996, Simberloff 2013, p. 56); and (iii) social, economic and ecological impacts of invasions (Office of Technology Assessment (OTA) 1993, Vitousek *et al.* 1997, Werle 2012, p. 196, Simberloff *et al.* 2013). This study focuses on the second theme. It considers that interactions between exotic species and invaded environments can determine whether invasions will be successful, as reported by Lodge (1993). For plants, the ability of invasive species to reproduce, in association with local environmental conditions, is regarded as an important and necessary driver to predict and control biological invasions (Albert *et al.* 2015).

This research was motivated by the occurrence of the species *Leucaena leucocephala* (Lam.) de Wit. in the Brasília National Park (BNP), a fully protected area¹ featuring both preserved and disturbed Cerrado formations. BNP is among Brazil's five fully protected areas with the highest number of invasive species (Dechoum *et al.* 2021) and has the highest number of recorded occurrences of invasive species in the Cerrado Biome (Sampaio & Schmidt 2013). Horowitz

et al. (2007) reported the species' presence in the BNP more than a decade ago and considered it as a significant problem, noting its expansion into native ecosystems and its potential to alter their structure, function, and composition (D'Antonio & Vitousek 1992, D'Antonio *et al.* 2000, Brooks *et al.* 2004).

Leucaena leucocephala is a predominantly tropical species, native of the current territory of Mexico, but it occurs on all continents (CATIE 1991, Walton 2003). This study aimed to investigate its invasion in the native and disturbed areas of the BNP, since there are no studies that examine invasions of this species in areas covered by native plant formations, thus addressing a gap identified by Walton (2003) and Costa & Durigan (2010). While other studies have explored this issue, they have focused on different invasive species, such as the invasion of *Pinus oocarpa* (Pinaceae) in a Cerrado area of the Brasília Botanical Garden (Braga *et al.* 2014). Therefore, the objectives of this study are (i) to evaluate the stage of occurrence of *L. leucocephala* in the BNP and (ii) to verify the effects of environmental characteristics and the distance traveled by the species in relation to the number of classes of identified individuals.

Material and methods

Species characteristics and ecology - *Leucaena leucocephala* is a tropical legume, native to the current territory of Mexico. Individuals have bushy and arboreal sizes, between five and 18 meters high. Optimal growth requires temperatures between 25 and 30 °C. It blooms throughout the year, but development and flowering occur in rainiest months (Costa & Durigan 2010), in the range of 600 to 1,700 mm per year (Franco & Souto 1986, Drumond & Ribask 2010). Its inflorescences are made up of globose heads 1.5 to 3 cm in diameter. Each head is composed of 100 to 180 small white flowers (Lima 2005, Gonçalves & Lorenzi 2007, Pitchandikulam Forest Virtual Herbarium 2020), with a mild sweet aroma, evoking melons (Zárate 1994). Pod-type fruits are long, thin, flattened and acuminate, 12 to 18 cm long and 1.5 to 2 cm wide. They contain from 15 to 30 bright brown, flat and elliptical seeds, 6 to 8 mm long and 3 to 4 mm wide (Lima 2005). Seeds are dry, hard and dispersed by gravity (Costa & Durigan 2010, Pitchandikulam Forest Virtual Herbarium 2020). Human action explains the species' widespread range, since it is domesticated and commonly cultivated to be used as animal fodder (De Angelis *et al.* 2021) and as an ornamental (Costa & Durigan 2010).

¹ Brazilian Law N° 9,985, July 18th 2000, created two classes of protected areas: fully protected areas (*proteção integral*) and sustainable use areas (*uso sustentável*). Fully protected areas are closed to any productive activities; sustainable use areas allow a varied range of managed productive activities.

The species grows in all Brazilian regions, from the Northeastern semiarid interior to the temperate areas in the South, and can form dense groves (Lima 2005). It has been recorded as ruderal as it booms in severely degraded areas (Costa & Durigan 2010), and as an invasive plant, competing with or eliminating other plants (Zenni & Ziller 2011). Currently, the genus *Leucaena* is found in most tropical and subtropical countries (CATIE 1991, Walton 2003). Since 2007 the BNP's staff dealt with its invasion by cutting specimens in the primary dissemination hub, located along a swath on the park's border, close to a concrete producing plant (Horowitz *et al.* 2007).

Study area - The study was conducted inside Brasília National Park-BNP (figure 1), a federal protected area managed by the Chico Mendes Institute for Biodiversity Conservation (ICMBio). The study area is adjacent to a private property in which there is a concrete manufacturing plant (responsible for planting a *L. leucocephala* hedgerow, discussed ahead) and to a public facility -the Nursery II of the Department of Parks and Gardens (DPG), in charge of Brasília's urban landscaping. This area covers part of the BNP's "intensive use zone". According to the park's management plan (FUNATURA & IBAMA 1998), this zone lies near the park's entrance and includes swimming pools, the visitor center and other public facilities, commonly used by numerous visitors. The topography of this zone oscillates from flat to gently rolling. Oxisols and hydromorphic soils predominate. Native vegetation is cerrado *stricto sensu* and gallery forest formations (Horowitz *et al.* 2007).

The Cerrado is a vast biome that originally covered about two million sq. kilometers (21% of Brazil's territory). It has different habitat types, one of which is the cerrado *stricto sensu*, characterized by a continuous grass layer overlaid by discontinuous shrub and small tree cover. This vegetation type is one of the Brazilian Cerrado's main physiognomies (Eiten 1972, Ribeiro & Walter 1998). The study site is formed by an area with preserved cerrado *stricto sensu* adjacent to an altered swath, close to the "entry point" of the invasive species. It was chosen for sampling because it has a population of *L. leucocephala*, recorded in Horowitz *et al.* (2007), a report written by members of the park management staff. The primary point of dispersion is the property occupied by the concrete production plant. In 2007, park managers estimated the exotic *L. leucocephala* population at 180 plants, both juveniles and adults, colonizing spontaneously and densely distributed. They classified *L. leucocephala* as

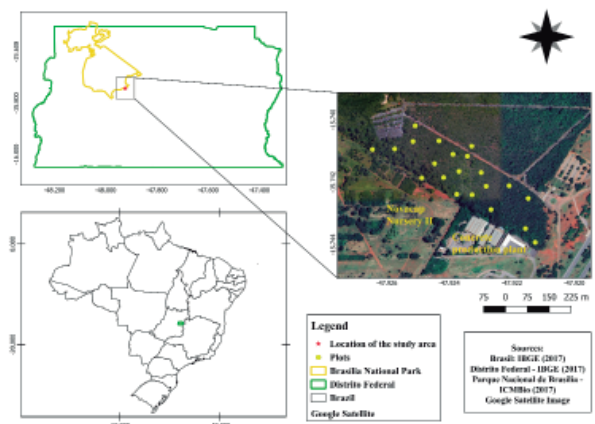


Figure 1. Study area, located inside the Brasília National Park, in its "Intensive Use Zone". Yellow dots represent the plots, individually numbered. The Novacap Nursery II appears on the lower left of the image and the concrete production plant is on the lower center-right. Produced by the authors. Sources: Brasil - IBGE, (2017); Distrito Federal - IBGE, (2017); Parque Nacional de Brasília - ICMBio, (2017); Google Satellite Image.

an invasive exotic species in a medium/advanced stage of dispersion/colonization (Horowitz *et al.* 2007).

There is no record of when the concrete producing company planted individuals of *L. leucocephala*. The company intended to form a hedge along the park's border. However, we used a historical series of orbital images available on Google Earth, using the *menu bar*, the *view tool* and *historical images* (<https://earth.google.com/>) to estimate the age of these trees and to verify changes in vegetation cover in the years of interest. The images showed that planting occurred in 2004. BNP managers notified the company and requested the replanting of the hedge, using one or more native species (Horowitz *et al.* 2013). Our field research, carried out in 2015 and 2016, found that in 2010 the company cut down the original trees. However, they have regrown. By 2015-2016, regrown trees had already reached the adult stage. Therefore, the area continued to be a point of dispersion of the exotic species.

Data collection - Twenty-one square plots, each with 100 m², were selected where individuals exist close to the point of introduction and at other more distant points. The plots were marked out in forest and cerrado *stricto sensu* areas. Geographical locations of each plot were taken at their central points, using GPS (figure 1). The first round of data collection took place between November 2015 and January 2016. The second round occurred between November 2016 and January 2017. The taxonomic identity

of the species as *L. leucocephala* (Lam.) de Wit., *leucocephala* subspecies was confirmed by a specialist from the *Universidade de Brasília* (UnB) based on botanical materials submitted to him - two branches containing leaves, flowers and fruits taken from two individuals in two different plots. Collected material was incorporated into the *Universidade de Brasília's* publicly accessible herbarium collection under the code number UB1284266 (<https://specieslink.net/search/>).

Qualitative characterization of each area was made using the checklist method, in the descriptive checklist modality (Medeiros 2010, p. 44): We classified the types of environments as: (i) preserved - with abundant native vegetation, native herbaceous stratum covering soils and sparse presence of exotic gramineous species; and (ii) altered - with sparse native vegetation, uncovered and exposed soils and dense stands of exotic gramineous species. We also classified the status of canopy cover (fully exposed to sunlight, shaded, fully shaded). Data collected in each plot recorded numbers of plants; classes of individual plant development (seedling, juvenile or adult; see table 1); numbers of fruits on adult individuals; and straight-line distances from the point of introduction (hedge). To record the abundance of the species in each plot, we used the hiking method (Filgueiras *et al.* 1994); each located individual received a plaque with an identifying number. Distances between the point of introduction and the central points of each of the more distant plots were measured with Google Earth's *ruler* tool applied on orbital imagery (<https://earth.google.com/>). Distances to the nearest plots were measured in the field. Individuals found in each plot were organized into classes, according to their height and to the presence or absence of reproductive structures. Individuals with fruits were considered adults. Heights of individuals were measured with a laser ruler or a measuring tape (Bosch Professional GLM 20), depending on plant height. In order to verify if the studied species comply with the rule of invasive woody plants with seeds (above >100 m in < 50 years) (Richardson *et al.* 2000), we measured the distances reached by plants from the point of introduction.

To count the number of fruits in adult classes 1 and 2, we examined the plants themselves and counted all fruits present. For individuals in adult classes 3, 4 and 5, the method of visual observation was used (Zhang & Wang 1995) and an average number of fruits in each cluster was computed, considering that each cluster is formed by eight fruits (simple average computed from the number of fruits counted in 40

bunches). We divided the crown of each tree into four sections and counted the clusters of fruits present in only one section. The number of clusters in the selected section was multiplied by four and the result was multiplied by eight, yielding each tree's estimated number of fruits. A cluster analysis was employed (using principal component analysis) to identify a relationship of similarity between the plots, regardless of the type of environment.

All the data were tested with Shapiro-Wilk's test before following through with further analysis in order to confirm that there was a tendency for normal distribution of the residuals in each data set. To assess the effect of distance from the point of introduction on the number of classes of individuals and how this effect depends on the type of environment, we performed a covariance analysis (ANCOVA) with the *glm* function and Tukey test, using the number of classes of individuals as a dependent variable and the distance as the independent variable. Statistical significance was considered for values of $p \leq 0.05$. All data analyses were performed using RStudio® (R Core Team).

Results

Evaluation of the invasive potential of *Leucaena leucocephala* - Based on the analysis of historical images, we assumed that the *L. leucocephala* hedge was planted in 2004. Therefore, 13 years separated planting and our field work, finished in 2017. The maximum recorded distance of a young individual of *L. leucocephala* from the hedge was 385.84 m, amounting to an average dispersion of 29.68 m.year⁻¹. In preserved environments, considering an individual fruit-producing adult, the maximum distance was 177.5 m, amounting to an average dispersion of 13.65 m.year⁻¹. In altered environments, an adult individual with fruits was found at a distance of 188.54 m, an average dispersion of 14.5 m.year⁻¹. Fieldwork conducted in 2015 allowed us to count a total of 648 individuals of *L. leucocephala*, 461 in preserved environments and 187 in altered environments. In 2016, we counted 827 individuals, 611 in preserved environments and 216 in altered environments.

In 2015, average plant density was 58.9 individuals.plot⁻¹. Examining the values per environment, a plot located in a preserved environment had the lowest number of individuals (2), while another plot also located in a preserved environment had the highest

Table 1. Classes of *Leucaena leucocephala* Lam. de Wit (Fabaceae) individuals identified in plots, with corresponding heights.

Classes of individuals	Symbol	Height
Seedling	S	≤ 0.5 m
Juvenile 1	J1	$0.51 \geq x \leq 1$ m
Juvenile 2	J2	$1.01 \geq x \leq 1.5$ m
Adult 1	A1	$1.51 \geq x \leq 2$ m
Adult 2	A2	$2.01 \geq x \leq 3$ m
Adult 3	A3	$3.01 \geq x \leq 4$ m
Adult 4	A4	$4.01 \geq x \leq 5$ m
Adult 5	A5	>5.01 m

number of plants (317). In this case, the state of the environment was not determinant. Eleven adult trees were counted in all plots, producing 6,928 fruits. 5,976 fruits (86.25%) came from trees growing in altered environments and 952 (13.75%) from preserved environments. Considering values per environment, a plot in a preserved environment had the lowest number of fruits (360) and a plot in altered environment had the highest number of fruits (1,624). In this case, the state of the environment influenced findings.

In 2016, average plant density grew to 71 individuals.plot⁻¹. Tallied values per environment showed that two plots had the lowest number of individuals (2) and one plot had the highest (308), all of them in preserved environments. 20 adult trees were recorded in all plots, producing 12,848 fruits. 10,833 (84.31%) came from trees in altered environments and 2,015 (15.69%) from preserved environments. In absolute values, one plot in a preserved environment had the lowest number of fruits (30) and another plot in an altered environment had the highest (6,244). In this case, greater production of fruits occurred in altered environments. Also, the number of fruits grew between the two censuses. In both of censuses the number of adult and mature trees suggests that the studied population is self-sufficient, no longer depending on additions from the point of origin. Therefore, the current population is probably larger than the number of individuals planted on the hedge.

Fruit production, considering the variable luminosity, behaved similarly in both censuses. More fruits were produced in plots located in shaded environments. In 2016, two plots displayed greater fruit production, one in an altered and shaded environment (2,560) and the other in an altered environment with full exposure to sunlight (5,974). Figure 2 shows the numbers of fruits, per environment, 2015 (2a) and 2016 (2b), and the numbers produced in 2015 and 2016, taking luminosity into account (2c, 2d).

Evaluation of the similarity between plots independently of the environment - Figure 3 shows the groupings of the plots in relation to the type of environment. Figures 3a and 3b show the groups in 2015 and 2016, respectively. Principal components 1 and 2 validate 84% of the model. Principal component 1 presents the highest values for distance and the lowest values for light and classes of individuals. Principal component 2 presents the highest values for classes of individuals and the lowest values for light and distance. The two groups of plots can be viewed by their mutual proximity. The groups formed by plots in different environments are located according to the determining variables. One of them is the group formed by plots 1, 15, 3 and 9, located in shaded areas. Plots 1, 15 and 9 are located in an altered environment and plot 3 lies inside a preserved environment. The other group is formed by plots 20, 4, 5, 7 and 2. These plots are fully exposed to sunlight. Plots 20, 4, 5 and 7 are in a preserved environment and plot 2 is found in an altered one.

Effect of distance on the number of classes of individuals in each plot - Analysis of covariance did not show a statistically significant effect of the interaction between the distance from the point of introduction and the variable condition of the environment on the number of plants in each class of individuals in each plot in the periods under study. Results show that the effect of distance on the number of classes does not depend on the type of environment. The inference is that distance has the same effect for both types of environments. Figure 4 shows the distribution of classes of individuals by environment in relation to distance. Figure 4a shows the distribution in 2015. Figure 4b shows the same distribution in 2016.

In 2015 (figure 4a), plots characterized by altered environments displayed the highest number of classes of

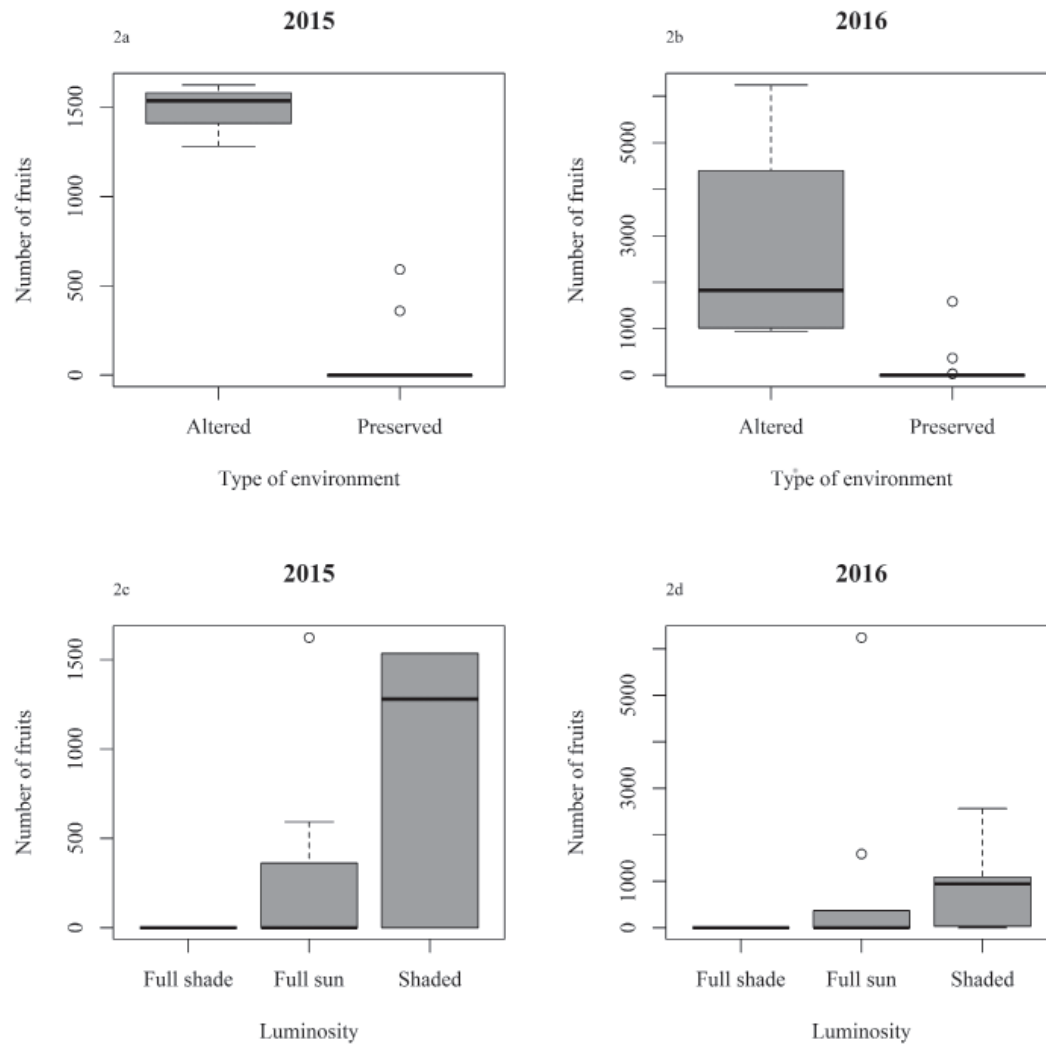


Figure 2. Fruit production of *L. leucocephala*, according to the condition of the environment, 2015 (2a) and 2016 (2b), and according to classes of luminosity, 2015 (2c) and 2016 (2d).

individuals at distances of less than 100 m. Only one plot had four classes of individuals, at a distance of almost 200 meters. Most plots located in preserved environments did not present *L. leucocephala* individuals. Data in figure 4b (2016) show positive growth for plots located in altered environments. One plot had one less class of individuals, but in two others the numbers of classes grew to five; one plot went from four to five classes at a distance of 200 m.

Results show that, in 2016, the number of individuals in each class grew more in preserved environments. Figure 4b shows an increase in the number of individuals per class in distances between 100 and 200 m. In absolute values, the number of classes grew in both environments (preserved and altered) from 2015 to 2016. For the preserved

environment, the increase was 32.5%; for the altered environment it was 15.5%.

Discussion

Results corroborate the propositions that there is a set of environmental factors responsible for the success of exotic plants in different environments and that the invasive potential of exotic species depends on these environmental factors (Pyšek *et al.* 1995, Thompson *et al.* 1995, Richardson & Pyšek 2006, Jauni & Hyvönen 2012). In our study area, increased soil exposure to sunlight may have been the initial trigger of the *L. leucocephala* invasion. More luminosity affected the environment, which led to the formation of a relatively dense population of *L. leucocephala*, a

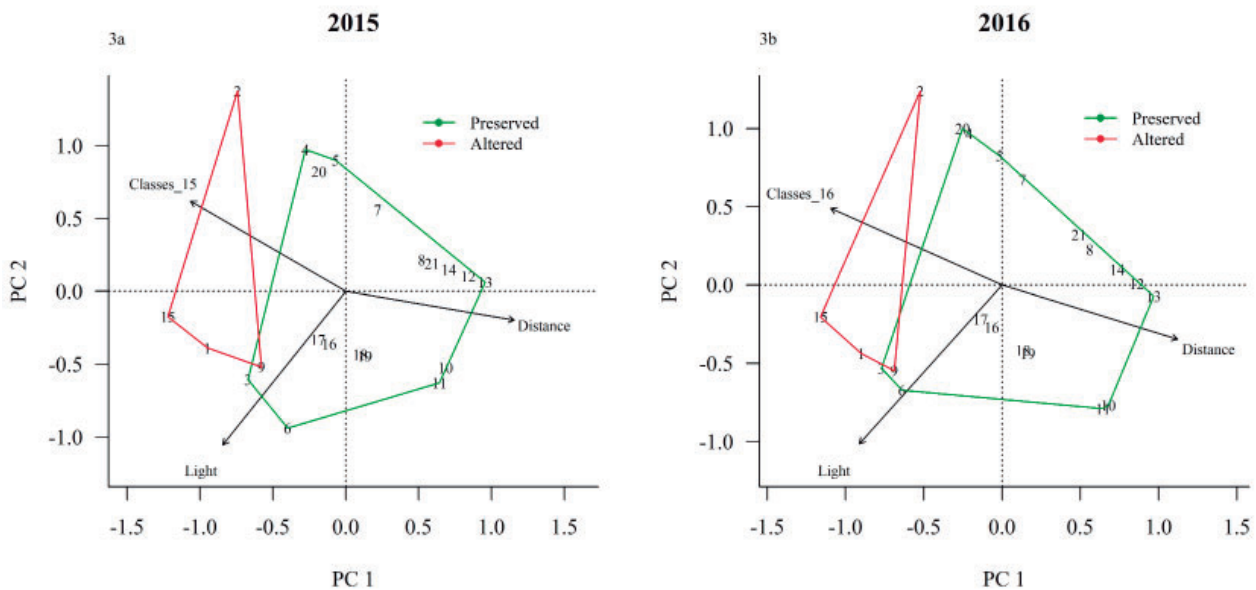


Figure 3. Similarity between demarcated plots, per environments, 2015 (3a) and 2016 (3b).

pioneer heliophyte plant (Rejmánek 1996). Also, we found that the population is associated with both types of environments, preserved or altered. However, our results differ from those of other studies that consider *L. leucocephala* as ruderal, and not invasive (Walton 2003, Costa & Durigan 2010). Results also showed that the plot composition in the study area displayed similarities between groups located in altered and preserved environments. The similarity occurs in the number of classes of individuals and in the availability of luminosity.

Regarding the dispersion distances of *L. leucocephala* individuals, the studied population is showing clear signs of invasiveness and seems to be in an initial stage of invasion. Growing distances from the locations where young individuals were found and the increase in average density, from 58.9 to 71 individuals.plot⁻¹, indicate that invasion was happening between 2015 and 2016. According to the unified framework for biological invasions (Blackburn *et al.* 2011, p. 337), the studied population is characterized as a self-sustainable population in the wild. Considering that the hedge was planted in 2004, the current population can be considered invasive also according to the criteria of Richardson *et al.* (2000).

The results also shown that the species proliferates without human interventions, both in altered and preserved environments, which reinforces its invasive potential (Richardson *et al.* 2000). However, we did not address another invasiveness criterion:

Whether this invasion is reducing the abundance of native species and displacing them (Richardson *et al.* 2000, IPBES 2019). Considering biophysical factors, luminosity also proved to be relevant to the establishment of *L. leucocephala* in both altered and preserved plots, as previously reported by Colon & Lugo (2006). The invasive plant flourishes better in open areas where luminosity is intense. The absence of individuals in fully shaded plots can be explained by the low intensity of sunlight.

Despite our characterization of the population as invasive, individuals found in the study area display physiological characteristics that differ from those of other studied populations. Growth was slow in the period (Blossey & Nötzold 1995), as many individuals in the early classes remained at the same stage during one year elapsed between our censuses. Slow growth may result from soils with high aluminum content (Drumond & Ribask 2010), typical of Cerrado soils. The reproductive period was also shown to be longer than that reported by Costa & Durigan (2010), as few young individuals migrated to the adult class between 2015 and 2016.

Just over a decade after the hedge planting, the population of *L. leucocephala* is clearly established in the BNP. Average density of the species in the community and growing numbers of adult individuals suggest that the population may continue to expand in the long run, in contrast to previous conclusions that *L. leucocephala* does not behave as an invader

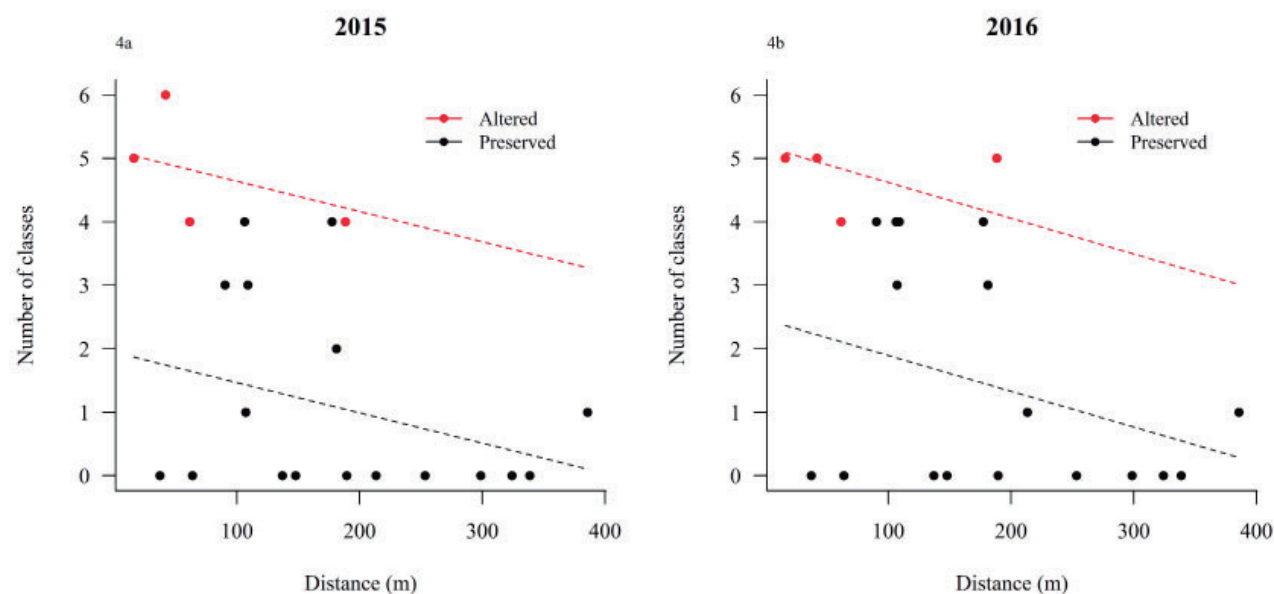


Figure 4. Distribution of the number of classes of *L. leucocephala* individuals in each plot in relation to the distance from the point of introduction, by state of the environment (altered or preserved), 2015 (4a) and 2016 (4b).

(Siqueira 2006), despite its presence in many lists of invasive species (Global Invasive Species Database-GISD 2019, Sampaio & Schimdt 2013, Zenni & Ziller 2011).

Conclusion

This research demonstrates that a population of *L. leucocephala*, planted on the border of the BNP, invaded the protected area, established itself and behaves as an invader, even in areas where the native vegetation is preserved. This shows the influence of biophysical factors on the success of the invasion. Altered environments and stronger luminosity determined more strongly the abundance of the species than the distance from the initial point of invasion. Luminosity is quite difficult to control in open field formations. However, our findings do show that the invasive plant fares better in open areas in which luminosity is strong and does not thrive as much in shaded areas.

Concerning priorities for future research, we suggest continual focus on population dynamics, as presented here. This may indicate preventive measures (i) to avoid the introduction of exotic species, especially in the buffer zones of protected areas, and (ii) to find effective ways to eradicate or control invading populations. The BNP management staff may find our results valuable in devising preventive and containment strategies for *L.*

leucocephala populations both within and beyond the park's boundaries.

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Conflicts of interest

The authors declare that they have no conflicts of interest.

Author's contributions

The three authors identified in the submission process participated fully in the research design, in its execution and in the drafting of the submitted manuscript. **Marília Teresinha de Sousa Machado:** material preparation, sample design, data collection and analysis;

wrote the first draft of the manuscript; participated in the search and use of relevant analytical and conceptual literature for the drafting of the text (including results and discussion); conceived maps and graphs.

José Augusto Drummond: analyzed and commented on previous versions of the manuscript; participated in the search and use of relevant analytical and conceptual literature for the drafting of the text (including results and discussion); as a native English speaker, he was responsible for finishing the submitted text in the English language.

Cristiane Gomes Barreto: analyzed and commented on previous versions of the manuscript; participated in the search and use of relevant analytical and conceptual literature for the drafting of the text (including results and discussion).

Declaração de disponibilidade de dados

O conjunto de dados deste artigo está disponível no SciELO Dataverse de Hoehnea, no link: <https://doi.org/10.1590/2236-8906e412022>.

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Supplementary material

Plot	Distance	Fruits_15	Fruits_16	New	Regrown	Class_15	Class_16	Environment	Light
1	61.53	1536	1088	17	41	4	4	Altered	Shaded
2	41.87	1624	6244	31	44	6	5	Altered	Full sun
3	109.01	0	33	75	5	3	4	Preserved	Shaded
4	106.32	592	1584	12	16	4	4	Preserved	Full sun
5	177.5	360	368	22	0	4	4	Preserved	Full sun
6	107.23	0	0	7	0	1	3	Preserved	Shaded
7	181.28	0	0	5	0	2	3	Preserved	Full sun
8	189.6	0	0	0	0	0	0	Preserved	Full sun
9	188.54	1536	941	14	8	4	5	Altered	Shaded
10	385.84	0	0	2	0	1	1	Preserved	Full shade
11	324.18	0	0	0	0	0	0	Preserved	Full shade
12	298.73	0	0	0	0	0	0	Preserved	Full sun
13	338.77	0	0	0	0	0	0	Preserved	Full sun
14	253.49	0	0	0	0	0	0	Preserved	Full sun
15	16.12	1280	2560	29	3	5	5	Altered	Shaded
16	63.88	0	0	0	0	0	0	Preserved	Full shade
17	37.4	0	0	0	0	0	0	Preserved	Full shade
18	137.1	0	0	0	0	0	0	Preserved	Full shade
19	148	0	0	0	0	0	0	Preserved	Full shade
20	90.46	0	30	312	5	3	4	Preserved	Full sun
21	213.52	0	0	0	0	0	1	Preserved	Full sun

[illegible]

Supplementary material

Plot	J2_16	A1_16	A2_16	A3_16	A4_16	Total_15	Total_16
1	47	0	0	1	0	58	73
2	50	2	4	1	0	75	66
3	48	2	0	0	0	79	100
4	21	0	1	0	0	24	33
5	5	0	0	1	0	23	147
6	4	0	0	0	0	7	8
7	4	0	0	0	0	9	11
8	0	0	0	0	0	0	0
9	5	2	0	1	0	22	38
10	2	0	0	0	0	2	2
11	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0
15	14	0	1	0	1	32	39
16	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0
20	139	3	0	0	0	317	308
21	0	0	0	0	0	0	2